RESPONSE OF HOP CULTIVARS TO TWO-SPOTTED SPIDER MITE INFESTATION

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This thesis contains no material which has been accepted for the award of any other degree in any University or Institute and to the best of my knowledge and belief the thesis contains no material previously published or written by another person except where due reference is made in the text of the thesis.

Apichart Lawanprasert

ABSTRACT

The two-spotted spider mite (TSSM), *Tetranychus urticae* Koch, is one of the most serious pests in regions where hops,*Humulus lupulus* L., are grown. Resistant cultivars would be ideal to reduce plant damage caused by this pest. Studies on the biological interaction between cultivated hop cultivars and TSSM were conducted over three growing seasons to gain a greater understanding of plant mechanisms involved in the response to mite attack under both natural and controlled environmental conditions.

In field observations, the results revealed a generalised pattern of growth and decline in naturally occurring mite populations infesting commercial hops during the growing season. The mites peaked after hops had formed the visible bases of inflorescences. Eggs were the predominant stage for most of the season and stage-specific percentages changed as the season progressed. The spatial and vertical distributions of the mites for each stage also varied with time. Natural enemies did not appear at levels sufficient to give control.

Studies on the susceptibility of different hop genotypes to artificial and natural infestations by the mites indicated that all the genotypes tested expressed an intermediate to highly susceptible reaction, with M26 (Huller Bitterer) being the most susceptible. Despite no outstanding evidence of antibiosis, there were significant differences in susceptibility among hop genotypes in terms of tolerance, non-preference and plant avoidance in which plant growth exceeds the mite dispersive capacity. Significant differences in mite densities between the hop cultivars of European and American parentage were also detected in that the European cultivar was more susceptible than the American.

Morphological variation in external and internal characteristics of hop leaves were found among the genotypes studied. Significant differences were found in ventral gland size, trichome density, trichome size, length of trichomes, stomatal density, stomatal size and moisture content. The morphological characteristics of the hop leaves collected from the same genotype may vary significantly according to leaf age and growing conditions. Under controlled conditions, none of these morphological characteristics were found to influence TSSM population reproductive parameters.

In addition to genotypic effects, the findings demonstrated that environmental factors did influence life history traits of TSSM. These factors included temperature, relative humidity, light intensity and plant variables.

Physiological and chemical responses of hop genotypes to mite feeding damage were examined in field and glasshouse experiments. Feeding damage by mites increased hop leaf resistance to CO_2 uptake through stomatal closure and decreased photosynthetic rates. The stomatal response to infestation differed between cultivars. Analysis of chemicals extracted from hop leaves indicated that phenolics, alkaloids and volatile compounds in infested leaves were qualitatively and quantitatively similar to those detected in undamaged control leaves.

Hop-canopy microenvironments do play an important role in seasonal population development of two-spotted spider mites. This role was amplified by hop susceptibility to the mites. For the hop genotypes studied, the populations of mites, and their predators, tended to increase more rapidly on sparsely leaved canopies than on densely leaved canopies. The overall results strongly suggest that TSSM performance was mainly regulated by the microenvironments that exist within the canopies of different cultivars with (1) sparsely leaved canopies favouring population increase and (2) reduced temperature and light and increased humidity within dense canopies limiting population increase.

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CHAPTER 1 INTRODUCTION

In pest management systems, development of resistant cultivars represents a fundamental means of reducing the damaging effects of pest infestation on crop plants (Adkisson and Dyck, 1980). The resistant cultivars can be applied as an ecologically compatible alternative to the use of chemical pesticides and enhance biological control. Considering the obvious economic and environmental advantages, several studies on plant resistance to pests have well been expanded to realize these benefits (Gallun, 1972; Gallun et al., 1975). Evidently sufficient genetic variation is present in breeding populations of some crop plants to effectively select for resistance to the pests. However, there is only fragmentary information available regarding the mechanisms in the plant that condition pest biology. Until the morphological and biochemical factors of plant mechanisms are better understood, screening and selection for resistance must be based on actual plant responses to the attacking pests. The ultimate objective will be to genetically alter those plant characteristics responsible, thereby maximizing the production of the crop plants to meet growing demands imposed by future needs.

In addition to the benefits, genetically changing the biochemical or morphological characteristics of crop plants for developing host plant resistance to their pests has some risks. These include chemical toxicants, nutritional effects, effects of crop yields, effects on beneficial invertebrates and microorganisms, increased susceptibility to other pests, effects on other crops, and loss of resistance by evolution in the pest (Pimentel, 1986). It is likely that the plants use many different characteristics as defences against pest attack, and some of these characteristics contribute to these risks. For example, some plants can contain compounds that are toxic not only to the pests but also to livestock and humans.

With regard to the historical view of plant resistance, the first extensive work on plant resistance to the pests was published by Painter in 1951 (Ortman and Peters, 1980). He included a comprehensive review of the literature to that time and the principles of plant resistance to pests. The subsequent review papers were reported by Painter (1958), Beck (1965), Maxwell et al. (1972), Gallun et al. (1975), and Farrell(1977). Several other reseachers have reported on various aspects of plant resistance to pests (Jermy, 1976; Russell, 1978; Rosenthal and Janzen, 1979; Maxwell and Jennings, 1980; Hedin 1983). Recently, empirical studies of interactions between plants and herbivores have increased exponentially, but progress toward a unifying and organizing theory of plant defence has not kept pace (Herms and Mattson, 1992).

According to Russell (1978) and Gallun and Khush (1980), plant resistance is the heritable ability of the host plant to reduce infestation and/or damage by their pests. The interaction of a suite of genetically based chemical and structural traits causes plant resistance to the pests. Phenotypic variation in herbivore resistance, however, results primarily from variation in plant nutrient and secondary metabolite concentrations (Herms and Mattson, 1992). Numerous plants in nature have evolved to limit the feeding of the pests on them (Pimentel, 1968; Pimentel et al., 1975; Hedin, 1977). Through careful selections and breeding, genes resistant to particular pests can be incorporated into a commercial plant type and provide the plant with effective pest control (Pimentel, 1986).

Breeding crop plants for genetic resistance to the pests may be classified into two main types: vertical and horizontal resistance (van der Plank, 1963). Vertical resistance occurs when a crop is very resistant to only certain genetic variants of a specific pest, whereas horizontal resistance is generally polygenic and effective against a greater number of pests. Selection of resistance can be accelerated if specific resistance

mechanisms are identified (Pillemer and Tingey, 1976). Successful identification of sources of resistance is directly related to the diversity of germplasm available and the probability of resistance occurring in the host populations (Ortman and Peters, 1980).

The role of plant resistance to the pests in a breeding or pest management program varies with each crop and each pest. The pest which obtains its nutrition from the plant may encounter an array of physical and chemical defences designed to protect the survival of plant host tissues (Tallamy, 1986). Furthermore, the plant resistance to the pest may shift with age from an obvious mechanical barrier to a chemical characteristic (Johnson, 1975).

In describing pest-plant interactions, one often overlooks the influence of environmental conditions which may favour the plant or the pest unequally and unpredictably, or may alleviate or aggravate damage, and therefore affect the expression of resistance (Horber, 1980). Environmental conditions can influence plant genetic expression of plants which may induce plant resistance. These prospects make an appreciation of environmental influence in breeding for pest resistance essential, because knowledge of the influence of environment on genetic and induced plant resistance may facilitate (1) manipulation of the cropping environment for maximum levels and expression of resistance within the range of environmental variation considered optimum for other aspects of crop production, and (2) use of induced resistance as an adjunct to genetic resistance in management of plant pests (Tingey and Singh, 1980).

At present the two-spotted spider mite, *Tetranychus urticae* Koch, is one of the most serious pests on numerous cultivated plants, among which are hops, *Humulus lupulus* L. If left uncontrolled, this key pest can cause complete crop loss annually (Sites and Cone, 1985). Various

attempts have been made in the past to assess hops of different genetic background for resistance against the mites (Regev and Cone, 1975; Peters and Berry, 1980a; Lesezynsky et al., 1986). Very little is known about structural and physiological changes of hops which occur during mite attack. Additional information on this subject is needed, particularly as it related to a better understanding of population dynamics and factors regulating field populations of these spider mites.

In Australia, the majority of hops grown is in Tasmania, with a total of 810 hectares of 'Pride of Ringwood', located in the South (Bushy Park and Huon Valley, 328 ha.), Scottsdale (320 ha.) and Gunn's Plains (162 ha.). The production of hops accounted for 6.5% of gross value for all crops in Tasmania (Anonymous, 1985). The pioneers of hop growing in Tasmania brought not only their cultivars but their cultural methods from the hop-growing county of Kent, in England. The first hop yards were established at Glenorchy, but soon afterwards others were planted farther up the Derwent Valley and by the 1830s there was a flourishing hop growing industry (Davies, 1973). Pride of Ringwood, released in 1958, was a seedling of one of open-pollinated seedlings of the variety Pride of Kent, crossed with a Tasmanian male hop plant; subsequently, this variety came to dominate the Australian hop industry, reaching over 90% of the acreage (Neve, 1991).

The overall objective of the research reported herein was to gain a greater understanding of resistance mechanisms in hop cultivars in a system including the two-spotted spider mites as their pests. This overall objective was divided into seven subobjectives:

1. determine the seasonal abundance and the distribution of the two-spotted spider mites infesting commercial hops in Tasmania;

2. evaluate some hop genotypes for their resistance to the two-spotted spider mites;

3. adapt a standard life table to bioassay activity of the two-spotted spider mites on different hop genotypes;

4. characterize the effects of environmental factors on the biology of the two-spotted spider mites;

5. examine the morphological features of different hop genotypes and evaluate the relationship of these features to mite life histories;

6. assess the effects of hop leaf canopy on the two-spotted spider mites and their predators;

7. determine the morphological, physiological and chemical responses of hop cultivars to infestations of the two-spotted spider mites.

CHAPTER 2 LITERATURE REVIEW

2.1. BIOLOGY AND PRODUCTION OF HOPS

2.1.1. Phylogenesis of cultivated hops

The genus *Humulus* (Urticales: Cannabinaceae) comprises three species, viz. *H. lupulus* L., *H. japonicus* Sieb. & Zucc. and *H. yunnanensis*. All cultivated hops are varieties of *H. lupulus* which normally have a diploid chromosome number of 20 in both male and female plants. In contrast, *H. japonicus* has 16 chromosomes in the female and 17 in the male. Since there are very few herbarium specimens and no plants in cultivation, the cytology of *H. yunnanensis* is still obscure. The occurrence of these species in China suggests very strongly that this area may be the centre of origin of the genus. Expansion eastwards into America and westwards into Europe would have caused distinct populations within these two areas and this is in agreement with observations of the differences in Y chromosomes between European and American hops and the similarity in morphological characters between wild hops from America and Japan (Neve, 1991).

The historical development of cultivated hops began with the gradual domestication of the wild climbing hop followed by conscious cultivation (Rybacek, 1991). These activities subsequently led to the greater homogeneity of the hop, and once this happened, commercial varieties were obtained by selection based upon the suitability of different types for brewing, i.e. aroma hops and bitter hops (Neve, 1991). In addition, the types of commercial varieties may be distinguished on the basis of the following criteria (Rybacek, 1991):

Method of selection : there are original local varieties, cultivated local varieties, collective selections from a local variety, selected clones, and hybrid clones.

The length of the period of vegetative growth : there are early, half-early, half-late, and very late varieties.

Genetic origin : these groups include genetically related varieties which may have different territorial origins such as Czech and Slovac hops, German hops, English hops, American hops and French-Belgian hops.

These varieties have been named according to the name of the region where they are cultivated or, in some cases, from the name of the the person who first introduced them (Verzele and de Keukeleire, 1991). In the past, developing hop varieties aimed specifically at improving pest resistant cultivars and the new varieties to be discovered were very different in aroma from their parents. The origins of most of the old parent varieties are obscure but several of them are almost certainly clonal selections that differ from one another in only one or two characters. Some hop varieties, for which improvements in aroma have been made, are grouped according to the original regions as follows:

English hops such as Keyworth's Midseason, Keyworth's Early, Bramhing-Cross, WGV, Density, Defender, Janus, Progress, Alliance, Fuggle N and Fuggle 37;

German hops such as Hallertau Anfang, Hallertau Start, Hallertau Fortschritt, Hallertau Bitterer and Perle;

American hops such as Cluster, Gold, Cascade, Williamette, Columbia and Mt. Hood;

Czech and Slovac hops such as Saaz, Zatec, Zlantan and Aromat;

Russian hops such as Serebrianka, 38/19 and Zitomia 8;

Japanese hops such as Kirin and Golden Star.

As is the case with aroma hops, the following varieties of bitter hop have been improved:

English hops such as Brewer's Gold, Bullion, Northern Brewer, Wye Northdown, Wye Target and Yeoman;

German hops such as Orion;

American hops such as Comet, Galena, Eroica, Nugget, Olympic and Chinook;

Japanese hops such as Toyomidori;

Australian hops such as Pride of Ringwood and

New Zealand hops such as Smoothcone, Green Bullet and Roborgh Super alpha (Neve, 1991).

2.1.2. Occurrence and main components of hop plants

The cultivated hop is a dioecious perennial climbing plant with unisexual male and female flowers growing on separate plants (Burgess, 1964). These plants needs a fertile soil and specific climatic conditions, especially in terms of the length of the days and the summer temperature. Hop growing areas are restricted to the temperate zone of the northern and the southern hemisphere. The amount of rain and ground water is also significant for the successful cultivation of hops. Hence, the hop is one of the most difficult plants to raise (Verzele and de Keukeleire, 1991).

According to Rybacek (1991), hop plants can be divided into four parts on the basis of the organ systems, namely: two underground systems and two above-ground systems. These organ systems are different in their morphology and main functions. The two underground organ systems of hop plants are the underground stem organs, i.e. the so-called rootstock, and the root system. The underground stem organs are important not only because they are situated between the

root system and above-ground parts but also, primarily, for the key function of their dormant buds providing the basis for the perennial life of the hop plant. The root system used to obtain water and nutrients from the soil comprises all roots, regardless of the underground part of the stem from which they develop. Two separate organ systems, namely vegetative and generative organs emerge successively in the above-ground part of the hop plant. The vegetative organ system, consisting of vines and leaves, has as its main function the production of organic substances by photosynthesis and connected procedures. The generative organs, i.e. flowers and cones, arise from terminal buds of the vegetative system and inhibit any further growth of the vine and its branches in the fertile parts of the plant. From both the biological and the industrial viewpiont, vegetative growth and reproductive development are vitally important processes for the formation of above-ground and underground parts of hop plants which have the annual cycle as shown in Fig. 2.1. In addition, each individual system of a hop plant contains the main groups of substances, i.e. crude fibre, ether-extractable substances, nitrogenous substances, nitrogen-free substances and mineral substances or ash.

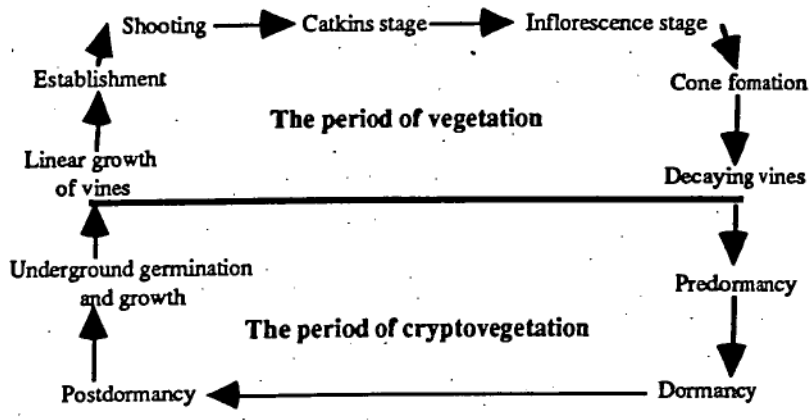


Fig. 2. 1. Diagram of the annual cycle of hop plants.

Commercially the hop cone produced by female plants without fertilization is the most important part of the hop plant (Burgess,1964). From the brewing point of view, lupulinic resins are the most valuable substances in this organ, as they provide the bitter taste (Rybacek, 1991). These resins belong only to the hop and have not been found in any other plant species (Neve, 1991). They are produced in the golden-yellow lupulin glands which occur on the undersides of the leaves and the entire surface of the cones (Burgess, 1964). The bitter acids, essential oils and tannins are the commercially important constituents of the lupulin glands. Other components of the lupulin glands are saccharides, nitrogen compounds, lipids, waxes, sulphur dioxide and heavy metals (Rybacek, 1991).

The hop bitter acids, which are the main components of lupulinic resins, consist of a mixture of the alpha and beta acids. At present, five homologues of alpha acids, as well as of beta acids, have been identified, namely: humulone, cohumulone, adhumulone, prehumulone and posthumulone for alpha acids; lupulone, colupulone, adlupulone, prelupulone and postlupulone for beta acids. As mixtures they show themselves as soft resins which are soluble in hydrocarbon solvents. Through air oxidation the hop bitter acids are transformed into hard resins which are no longer soft and soluble in hydrocarbons (Rybacek, 1991; Verzele and de Keukeleire, 1991). The hop resins impart to beer its bitterness which is affected largely through alpha acids. The final bitterness is not due directly to humulones but mostly to isohumulones derived from the alpha acids during boiling with wort (Anonymous, 1974; Verzele, 1986).

In Rybacek (1991), it was reported that the percentage of cohumulone in the total alpha acids was used to classify the well-known hop varieties into four groups, viz. cones with 20 % cohumulone (all

Czech and Slovac varieties and German varieties 'Tetnang', 'Spalt' and 'Hallertauer'), those with 30 % cohumulone (English varieties in the groups of 'Fuggles', 'Goldings' and 'Northern brewer' and American varieties 'Oregon Fuggles', 'Oregon Seedless' and 'Canadian Pride'), those with 40 % cohumulone (varieties 'Brewers Gold', 'Early Promise', 'Oregon Cluster' and 'Washington Seedless') and those with more than 40 % cohumulone (varieties 'Bullion Hop', 'Yakima Seedless' and 'California Seedless'. Additionally, it appears that most of the hop varieties grown on the European continent contain approximately equal amounts of two homologous beta acids, namely lupulone and colupulone. In most cases lupulone is present in slightly greater proportion. British, American and Australian hops contain, in general, higher colupulone. Actually, there is no main individual beta acid as is the case for the alpha acids (Verzele and de Keukeleire, 1991).

The essential oil of hops comprises a mixture of hydrocarbons and oxygenated complexes of terpene series which contain such important oils as humulene, myrcene, farnesene, caryophyllene and selinene. The synergistic mixtures of these compounds endow beer with its aroma and flavour (Rybacek, 1991; Neve, 1991). The ratios of humulene to caryophyllene and humulene to selinene appear to be a specific trait of individual varieties and are useful for their identification (Green, 1986).

Lupulinic tannin is a mixture of water soluble polyphenolic compounds which react with proteins in the wort or beer to form insoluble precipitates, which are removed by filtration. The main substances of tannin are the group of anthocyanins and leucoanthocyanins, flavonols and catechins. Not all of the polyphenol substances in beer come from hops but are derived mainly from malt (Rybacek, 1991; Neve, 1991).

2.1.3. Idiotype of hop varieties

Growth habits of the above-ground parts of hop plants can be separated into three basic types, namely; conical (steeple), cylindrical and reverse cylindrical (umbrella) with intermediate phases (Fig. 2.2). The conical type is the best type of growth habit with regard to balanced cone production. However, the short length of side branches of this type produces a very low yield of cones. Having top branches occasionally over-growing and shadowing the lower ones, the umbrella form, by contrast, produces not only a lower yield but also lower quality cones. The cylindrical shape, which has approximately the same length of fertile branches in the central and top region of the whole plant is the best habit with regard to overall yield and quality of cones. Therefore, the growth type of the above-ground parts of the hop plant highly affects both the yield of plant and the quality of cones. The yield of hop plants depends on the number of cones produced. The quality of cones is assessed by three different evaluations, namely: organoleptic indicators, morphological analysis and chemical quality. The organoleptic indicators comprise the structure and the scent of cones. The percentage of strigs (a part of the axis of a cone) in the total mass of cones, and the regularity of strigs are used for analysis of the morphology. The content of humulone, lupulone and tannin are the main indicators of chemical quality (Rybacek, 1991).

In addition, pests and diseases have also been suggested to have significant effects on the yield and the quality of hops (Neve,1991). The severity of pest problems is influenced by plant resistance which depends on several factors including physical environmental variables such as temperature, relative humidity, and light intensity (Tingey and Singh, 1980). These factors are affected by differences in the habit of above-ground plant parts (Rybacek, 1991).

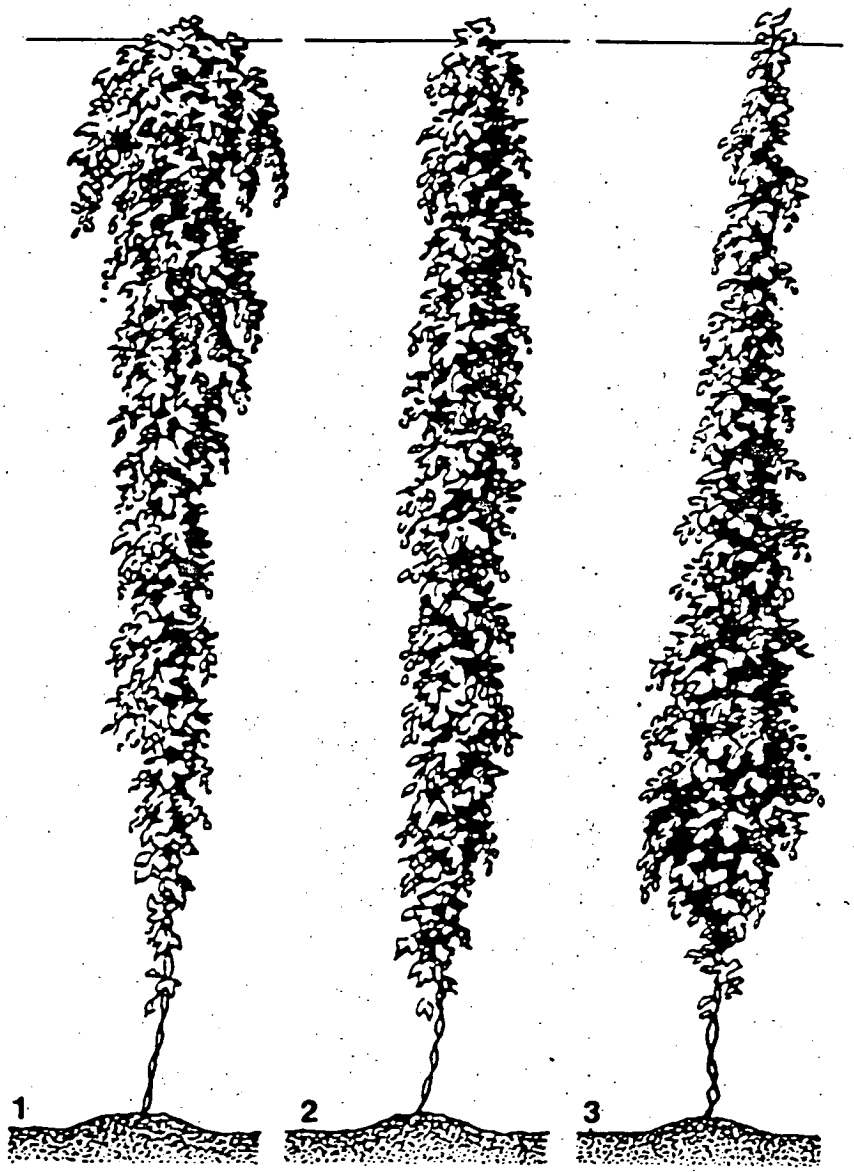


Fig. 2.2. Growth habits of the above-ground parts of hop plants : 1 - umbrella (hat-type), 2 - cylindrical, 3 - conical (from Rybacek, 1991).

2.1.4. Utilization of hop cones

At present, hops or hop-derived products are normally boiled with wort for precipitating wort proteins, sterilizing the wort, removing volatile off-odours by steam distillation and transforming the alpha acids into beer-soluble and bitter iso-alpha acids. The amount of hops added in the wort depends on the wort density, the hop variety and its alpha acid content. This addition is not necessarily made at the beginning of the wort boiling process. Bitter hop is usually added at the start, while a smaller amount of aroma hop is added before the end of wort boiling. After fermentation, some hops or hop essential oil may be added to accentuate the hop aroma. Additionally, bittering of beer can be achieved by using pre-isomerized hop extracts, in which the alpha acids have been already isomerized into iso-alpha acids. Hence, wort boiling of the alpha acids is unnecessary and these preparations can be added at a later stage in the brewing process (Verzele and de Keukeleire, 1991).

There are several modifications of hop cones used in the brewery. Such modifications include ground hops, granulated hops and hop extracts (Rybacek, 1991). Rabak (1950) reported that hop powder from hops dispersed more readily in the boiling wort and this accelerated the isomerization reaction. Hop pellets or granulated hops not only break up readily in the boiling wort but also can be handled easily (Schwartz and Grant, 1974). Another formulation of hop cones is the 'hop extract' which contains practically all the substances important in brewing. It can, therefore, be used to replace a large proportion of the hop cones normally used (Rybacek, 1991).

2.1.5. Crop protection in hop yards

In addition to some hop diseases caused by abiotic factors such as poor nutrition and unfavourable meteorological conditions (Rybacek,

1991), hops are vulnerable to attack by several pests and diseases which, if uncontrolled, are capable of completely destroying the crop (Neve, 1991). The two most important pests damaging the hops are the damson-hop aphid (*Phorodon humuli* Schrank) and the two-spotted spider mite (*Tetranychus urticae* Koch) (Cranham, 1985). Furthermore, the cultivated hop is very prone to attack by certain fungal and virus diseases (Burgess, 1964). Adequate control of these pests and diseases is of primary importance in hop yards, to prevent any decrease in marketable value and to avoid undesirable visible residues (Neve, 1991).

According to Rybacek (1991), integrated protection involving all methods economically, ecologically and toxicologically appropriate to maintain pests and diseases below the threshold of damage, becomes gradually more significant as it includes natural limiting factors. In general, methods of pest protection in hop yards can be divided into two groups, namely: direct and indirect methods. The direct methods of protection involve both the biological and chemical controls for the suppression of pests. The indirect methods, which are mainly preventive, involve cultural practices, resistant varieties and legislation, and these will be dealt with first.

2.1.5.1. Cultural practices

Cultural control includes such measures as time of planting, plant spacing, choice of location, irrigation, green manuring, crop rotation, sanitation, and roguing. Many of these methods have been used to prevent the occurrence of pests and diseases in various crops (Sill, 1982). Sanitation or hygiene is always used to protect the hops from several kinds of diseases (Neve,1991). Keyworth (1942) showed that the potential sources of infection of verticillium wilt,*Verticillium albo-atrum*, were all diseased vines or leaves and the soil from around diseased plants. The spread of this disease, which cannot be chemically controlled, can be

checked by careful hygiene (Neve, 1991). Coley-Smith (1963) suggested that identifying and grubbing the rootstocks contaminated by downy mildew, *Pseudoperonospora humuli*, helped to reduce the amount of primary infection in gardens. The stripping of the base of the vine is also helpful in the control of this disease (Glasscock, 1956). In the case of powdery mildew,*Sphaerotheca humuli*, the same techniques as for downy mildew can be applied to the infected area (Neve,1991).

Pitcher and McNamara (1976) reported that a two-year fallow could eliminate Arabis Mosaic Virus from infected areas although it did not destroy the dagger nematode population that was its vector. In addition, correct ploughing of soil and the provision of optimum nutrition to the crop protect hops from damage (Rybacek,1991).

2.1.5.2. Resistant varieties

Recently, the greatest use of host plant resistance has been for the control of plant pathogens, and varying degrees of resistance to disease have been incorporated into most major crop varieties (Pimentel, 1986). For hops, resistance to pests and diseases was an important attribute of hop varieties before pesticides were extensively used (Campbell, 1983). Research on development of varieties resistant to disease was one of the principal reasons for the founding of the Hop Research Institutes in several countries such as Germany, the USA, and other countries (Zattler, 1951; Smith, 1937; Neve, 1991). Successful control of downy mildew of hops was an outstanding example of using resistant varieties (Rybacek, 1991). Fuggle was found to be one of the most resistant varieties to downy mildew (Magie, 1942). This variety, however, was affected seriously by verticillium wilt; and new varieties such as Huller Bitterer and Perle with resistance to both diseases were released (Maier and Narziss, 1979). In England powdery mildew is proving very difficult to control by chemical methods, giving rise to much interest in the

development of resistant varieties. Although Australia and New Zealand have escaped most of the diseases that are detected in the northern hemisphere, they have suffered considerable problems with black root rot caused by *Phytophthora citricola*. No effective control measures are available against this disease except through breeding programmes which have produced resistant cultivars (Neve, 1991).

2.1.5.3. Legal Control

The plant quarantine and plant material introduction divisions of world governments are one area of plant protection which has always received a considerable amount of cooperation from regulatory bodies (Sill, 1982; Dent, 1991). Salmon and Ware (1931) reported that the introduction of hop downy mildew into Australia was prevented due to strict quarantine measures. At present, this disease has spread through almost all of the hop growing areas of the northern hemispere and also into South America (Neve, 1991). The control of virus diseases is another example. In this case, an official certificate indicates that materials used when planting up a new hop garden have been tested and shown to be virus-free (Keyworth, 1945; Jary, 1955).

2.1.5.4. Biological Control

The manipulation of any living organism for pest control purposes can be defined as biological control (Beirne, 1967). There have been a number of efforts to use biological control to protect hops from important pests, i.e. damson-hop aphid, two-spotted spider mites and Verticillium wilt (Neve,1991). Recently, a large number of natural enemy species of Anthocoridae, Coccinellidae, Chrysopidae, Syrphidae and Cecidomyidae have been recorded from hops (Zeleny et al., 1981; Cranham, 1982).

Parker (1913) reported that the appearance of ladybird larvae delayed the damage of hops heavily infested with aphids in North America. Mohl (1924) observed that under conditions of high

temperature and strong sunlight, ladybirds, lacewings, hoverflies and birds were more effective against the aphids in Czech and Slovac Federal Republics. Blattny and Osvald (1950) indicated that natural enemies had important effects on aphid populations. Later, increasing problems of aphids resistant to many insecticides have led to increased attention on the potential of natural enemies to control them (Neve,1991). Most studies involving anthocorid bugs (Anthocoridae) and ladybirds (Coccinellidae) have succeeded in reducing the numbers of aphids effectively (Campbell, 1978; Zeleny et al., 1981; Ruzicka et al., 1986).

The important predators of two-spotted spider mite on hops include the coccinellids *Stethorus punctillum* Weise and *Scymnus* spp., the staphylinid *Oligota flavicornis* Boisduval, and probably the bugs *Anthocoris* and *Orius* spp (Cranham, 1985). Blattny and Osvald (1950) reported that *S. punctillium* was the most significant predator destroying large numbers of the mite at all stages. In addition, several species of predatory mites, e.g. *Phytoseiulus persimilis* and *Typhlodromus pyri* , have been introduced to control the spider mites. *P. persimilis* has occurred at levels high enough to give control; however, *T. pyri* is less promising, as the webbing which the two-spotted spider mites create reduces its efficiency (Solomon and Cranham, 1980; Neve, 1991).

Studies on three possible approaches to biological control of verticillium wilt were initiated by Wilderspin et al. in 1983 (Neve, 1991). Firstly, the resistance of hops was elicited by treating the roots with heat-killed conidia or with culture filtrates. Secondly, the antagonism of other organisms was increased by organic soil amendments supplemented with chitin, Laminaria or yeast waste. Finally, an investigation of the 'wilt-suppressive' effect that was observed in some gardens.

2.1.5.5. Chemical control

Pesticides, once believed to be a panacea for the control of pests, have resulted in the resurgence of pest populations, the development of resistance to pesticides and residues in environment and commodities. Therefore, the ideal pesticide would be the chemical which is effective against the target species but has little or no side-effects on human beings, livestock, crop plants, or beneficial and other non-target organisms. Selective chemicals have been of paramount importance in weed control, where harm to crops must be avoided, but most other groups of pesticides have had a broader spectrum of activity (Matthews, 1984).

Since the widespread use of non-selective insecticides over the past 100 years has seriously depleted natural predator populations, any effort to produce hops today without the use of insecticides probably results in even greater losses than those of the prespray era (Neve,1991). Generally in commercial hops in Europe, the frequent use of broad-spectrum pesticides to maintain aphids and mites at low levels also minimizes biological control (Cranham, 1985). Although Cone (1975) reported the occurrence of *Typhlodromus occidentalis* Nesbitt, in which organophosphate insecticide resistant strains occur on tree fruits, it is usually absent from commercial hop yards. The probability for permanent establishment of predatory mites in hop yards seems low considering the annual nature of regrowth, the total weed control commonly practised, and the lethal effects of aphicides and certain fungicides (Cranham, 1985). Various alternative products have been introduced as miticides but all appear to be subject to the risk of resistance developing, while some have been found to be phytotoxic (Neve,1991).

2.2. LIFE HISTORY AND ECOLOGY OF THE TWO-SPOTTED SPIDER MITE

2.2.1. Economic status

The two-spotted spider mite (TSSM),*Tetranychus urticae* Koch (Acari: Tetranychidae) often reported inaccurately as *T. bimaculatus* ,*T. telarius* (Unwin, 1971; Bellotti, 1985) and *Epitetranychus althaeae* (var. Hanst) (Neve, 1991) is a serious pest of more than 150 economically important plants throughout the world (Jeppson et al., 1975). This spider mite damages plants by feeding mainly on tissues on the undersides of the leaves (Russell, 1978; Tomczyk and Kropzyncka, 1985). Chlorophyll from plant tissue is removed, resulting in a decrease in photosynthesis and transpiration. Under slight attack, foliage becomes covered with pale silver specks, which eventually turn necrotic. Under severe attack, foliage becomes covered with silk webbing produced by the mites. Furthermore, the leaves turn bronze and then drop from the plant. Fruit, produced from the plants or trees damaged by these spider mites, may be reduced in both size and quality (Pedigo, 1989).

The general upsurge of mite problems have been explained by two main hypotheses, namely: predator inhibition and reproductive stimulation (Huffaker et al., 1969). The spider mite was not recognized as a serious pest until the general use of synthetic organic pesticides, such as DDT. These pesticides upgraded the pest status of this species by suppressing naturally occurring predators, and eliminating the need for oil additives mixed with lead arsenate insecticides, which formerly acted to keep mite populations under control (Unwin, 1971; Pedigo, 1989). Secondly, by inducing improved nutrition or growth factors in the foliage (Huffaker and Spitzer, 1950; Fleschner, 1952; Klostermeyer and Rasmussen, 1953; Rodriguez et al., 1957; Rodriguez et al., 1960; Saini and Cutkomp, 1966) such pesticides can indirectly increase the mite fecundity (Huffaker et al., 1969; Unwin, 1971).

2.2.2. Food plants

Undoubtedly TSSM is the most polyphagous species of the Tetranychids (van de Vrie , 1985a) feeding on a wide variety of crops, including fruits, vegetable crops, forage crops and ornamentals (Kantaratanakul and Rodriguez, 1979). It is also commonly found on many weeds (van de Vrie et al., 1972) and hedgerow plants (Cranham, 1985). According to Belloti and Kawano (1980), there are more than 400 host plants for this pest. Unwin (1971) described TSSM as the most widespread, common, and destructive mite of world agriculture.

In the United States, the most common spider mite infesting strawberries is TSSM (Wysoki, 1985). Outbreaks have been reported in California (Oatman et al., 1977a;b;1981;1982), in Florida (Poe, 1976), in the midwestern states (Dabrowski and Rodriguez, 1971; Rodriguez et al., 1971) and in the Pacific northwest (Shanks and Barritt, 1975). Oatman and McMurtry (1966) found that yield reductions in strawberry plantings commonly occur when mite populations were allowed to increase. Smith and Mozingo (1983) reported that TSSM has regularly caused severe damage to the peanut, *Arachis hypogea* L. in the Virginia-Carolina area. Growers often apply acaricides to this pest otherwise they encounter possible yield and economic loss. In the Central Valley of California, TSSM is considered to be a major pest of almond trees, *Prunus amygdalus* Batsch (Andrews and Barnes, 1981). Leaves, branches, and entire trees can become webbed over from high densities of the mites; hence, it is difficult to achieve thorough spraying with an acaricide (Hoy, 1985).

In Southern England, overwintering female spider mites begin to invade the strawberries protected by glass cloches or low polythene tunnels from late February onwards. The crop may become heavily infested before fruiting unless control measures are applied during April (Gould and Vernon, 1978).

In South Africa, Smith Meyer (1981) studied the tetranychids found on strawberries. The results showed that TSSM was one of the most important pests of this crop.

In Asia, the most important species of mites identified as feeding on cassava is TSSM. Information about other *Tetranychus* species on cassava reported from Asia is scarce (Bellotti and Byrne, 1979).

In Australia, hops do not suffer from serious fungal diseases or insect pests which break out in the major hop growing regions of the Northern Hemisphere. Therefore TSSM is the only pest for which regular control measures are essential (Legget, 1987). Other crops commonly damaged by TSSM include pome fruit, stonefruit, cotton and bananas (Unwin, 1971).

2.2.3. Stages of development

TSSM develops through an egg stage, three immature stages and the adult stage (Plate 1). Each of the immature stages has an active and a resting phase of equal duration (Anon, 1976). The active immature stages of typical tetranychids are called larva, protonymph and deutonymph and each stage is followed by intervening periods of quiescence called the protochrysalis or nymphochrysalis, deutochrysalis and teleiochrysalis, respectively (Crooker, 1985). During these inactive periods, the mite anchors itself and moults to the succeeding stage (Boudreaux, 1963).

The egg of TSSM is spherical and approximately 0.13 mm. in diameter. The newly deposited egg is clear but turns yellow and subsequently becomes yellow-orange as embryonic development progresses (Rybacek,1991). There are two types of eggs, namely three and six chromosome eggs. Males develop from unfertilized eggs and are haploid, whereas females develop from fertilized eggs and are diploid (van de Vrie et al., 1972). The newly hatched larva with 6 legs and bright

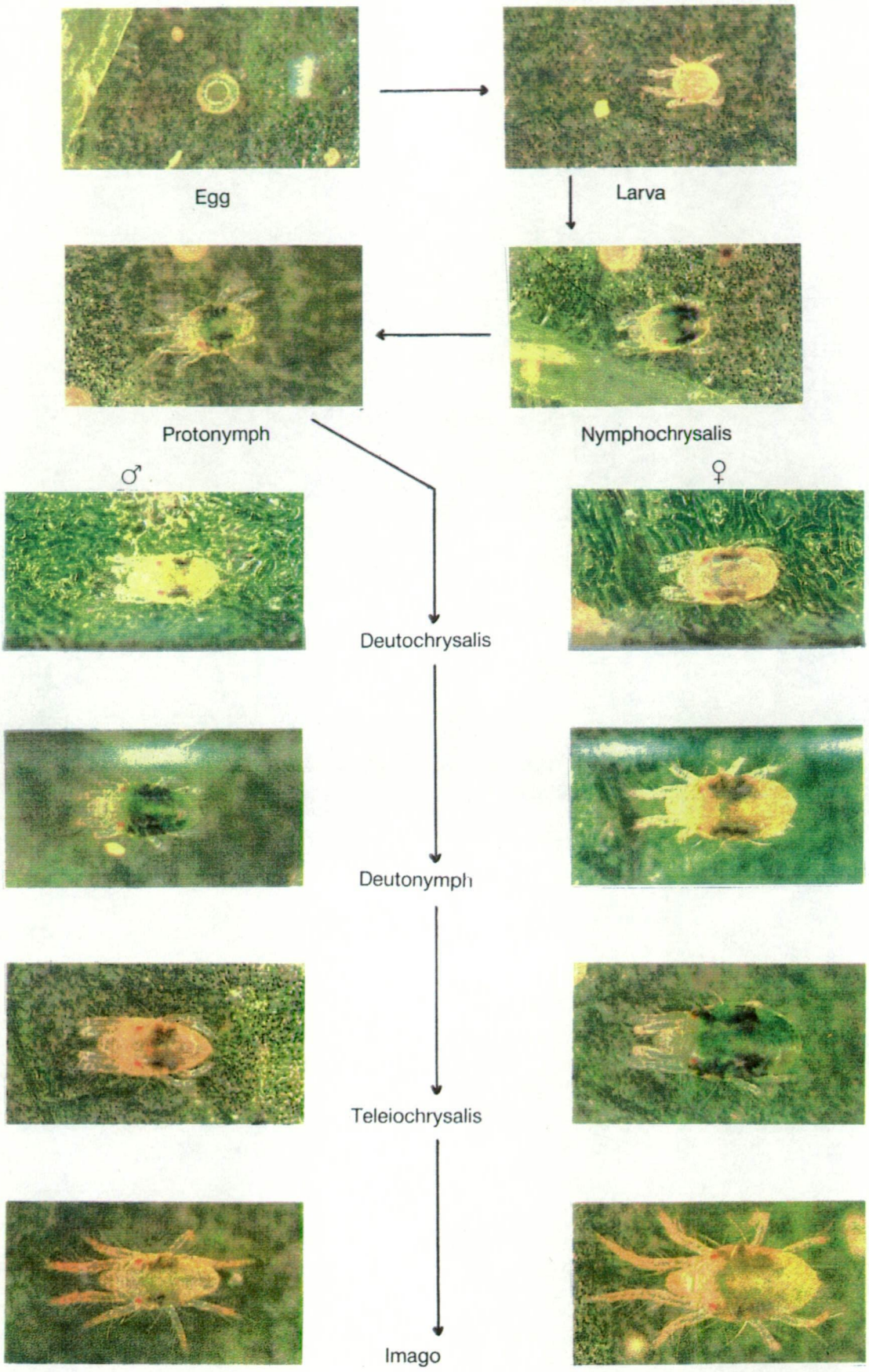


Plate 1. The developmental stages of TSSM (from Zoebelein and Kniehase, 1985).

carmine red 'eye' spots is nearly spherical in shape, colourless and measures 0.15 x 0.11 mm. Feeding begins immediately and the colour changes to grey-green. After a short feeding period, the larva enters the protochrysalis stage, after which it moults to the protonymph stage which has four pairs of legs. This, in turn, moults to the deutochrysalis and, after casting the old exuvium, the deutonymph and the teleiochrysalis stage occur to complete juvenile development and the mite enters the adult stage. The female adult is approximately 0.48 mm. long and 0.28 mm. wide. The male is smaller and slimmer, 0.35 mm. long and 0.18 mm. wide. Both males and females have the same general morphology. Their oval bodies are inconspicuously articulated. They have long setae on a convex dorsum set in six transverse rows. The mouthparts act as a piercing and sucking apparatus. The final section of the chelicerae is modified into a long piercing seta. The red 'eyes' are placed on the sides of the cephalothorax which is separated from the rest of body only by an indistinct seam. The adult TSSM has four pairs of single articulated legs. The distal segment possesses in comblike structure called the empodium, the shape of which is useful for the identification of the species (Rybacek, 1991).

Herbert (1981) studied the developmental time for each life stage of female and male TSSM. The results showed that the developmental period of the egg stage was greater, by a factor of approximately 2, than the individual immature stages. For the male, the developmental period for each immature stage was roughly equal and almost one-half of the time of the stages were inactive period. For the female, developmental periods for larvae and protonymphs were similar but duration of the active and resting phases of these stages showed a slight difference. The duration of the female deutonymph stage was similar or slightly longer than larval or protonymphal stages. A comparison between sexes showed that the

developmental periods for the active and resting phases were similar for larvae and protonymphs. The active deutonymphal period was significantly longer in the female than in the male but the resting phases were similar. Hence, female immatures take longer than males to become adults. In addition, female adults live longer than males.

The duration of the embryonic and juvenile development of the tetranychids depends on many factors such as temperature and humidity (Crooker, 1985). Herbert (1981) reported that the development time, in hours, for each life stage of female and male TSSM differed significantly for the three rearing temperatures (Table 2.1). Nickel (1960) observed that TSSM developed faster, with higher egg production, at low humidities (25-30%) than at high humidities (85-90%).

Table 2.1. Development time in hours of TSSM reared at 15°, 18°, and 21°C (from Herbert, 1981).

Stage	Female			Male		
	15°	18°	21°	15°	18°	21°
Egg	255	172	113	262	175	116
Larva	140	86	64	134	90	66
Protonymph	124	88	58	116	80	55
Deutonymph	159	111	70	131	89	59

2.2.4. Behaviour and reproduction

2.2.4.1. Social behaviour

The behaviour involved with courtship and mating is the only form of social behaviour reported for the tetranychids. Nevertheless, the web-spinning behaviour characteristic of the tetranychids might also be considered under either co-operative or altruistic behaviour (Crozier, 1985).

Courtship behaviour of TSSM begins with spinning of silk strands by the female deutonymph into a pad on a leaf surface for settlement prior to the final molt. This silk webbing, as well as a sex attractant of the female, influences wandering males to discover the quiescent female (Cone, 1985). Later, three consecutive reactions of the males to the females occur. These are hovering, guarding and mating behaviour respectively (Cone et al., 1971).

In terms of spinning behaviour, the web around the colonies of TSSM is produced from spinnerets of both males and females and is intended to protect them against harmful external factors (Rybacek, 1991). The pattern of webbing is considered to be of a highly complicated and irregular type (Saito, 1985).

2.2.4.2. Dispersal

Another significant behaviour of the tetranychids is dispersal which can be considered as the intra-plant and inter-plant movement of individual mites away from the colony in which they developed. There are three means of dispersal, namely: crawling, aerial dispersal and phoretic dispersal (Kennedy and Smitley, 1985).

The tetranychids which have a wide host range, like TSSM (van de Vrie et al. 1972), have well-developed dispersal mechanisms which enable their populations to distribute over large areas and colonize widely separated plants (Kennedy and Smitley, 1985). Margolies and Kennedy (1985) reported that the population movements of TSSM in maize fields resulted from crawling between plants. It is apparent that the direction of crawling involved the movement of dispersing mites towards illumination, as opposed to diapausing mites which move away from light (Hussey and Parr, 1963). Dispersal by crawling to other plants or plant parts has also been indicated to happen in response to not only population density but also the presence of predators (Bernstein, 1984).

Under light infestations, populations of the summer form disperse throughout the unoccupied plant chiefly by crawling (McEnroe and Dronka, 1971). Under heavy infestations, a change in the behaviour of individual mites results in dispersal from the plant. The migrating mites show a positive phototactic response which is absent from sedentary and non-dispersing mites. The response results in mites moving up the plant and aggregating around the periphery of the host where, seemingly, they are more exposed to winds and visiting animals which might cause their aerial or phoretic dispersal (Kennedy and Smitley, 1985).

2.2.4.3. Diapause

The diapause in TSSM occurs in response to 3 factors, namely: photoperiod, temperature and nutrition (van de Vrie et al., 1972); for this reason, the female mite leaves the host plant in search of hibernation sites. Before migrating from the plant, they feed only very little and, though mating takes place after the final molt, no eggs are laid. Once the body colour has changed and the hindgut has been emptied the mite becomes positively geotactic and negatively phototactic. The negative photoresponse of the diapausing females is a response not only to red and green light but also to the ultraviolet region of the spectrum (Veerman, 1985).

Termination of diapause depends mainly on temperature and the presence of suitable nutrition. Photoperiod appears to exert little influence (van de Vrie et al., 1972). Veerman (1977) reported that diapause development has already ceased at the beginning of the winter, the mites continuing in diapause until spring under the influence of prevailing low temperature.

2.2.4.4. Reproduction

In addition to their ability to disperse widely, TSSM possess a high intrinsic rate of increase and reproduce by arrhenotoky, i.e. a type of

haplo-diploidy in which the haploid males result from unfertilized eggs. The colonizing success of TSSM is appropriately that of an r-strategist (Rodriquez and Rodriquez, 1987; Sabelis, 1985a). TSSM is a fast developing organism because the life cycle can be completed in a 10-day period (Helle and Overmeer, 1973). Wrensch and Young (1975) found that the rate of physiological development was the most important factor determining the intrinsic rate of increase. Their results also showed that fecundity was the most influential character affecting fitness in this haplo-diploid phytophagous mite, on which the fertilization status of the female had no effect.

2.2.5. Natural enemies

Several orders of arthropods have been reported to feed on the tetranychids. These belong to Thysanoptera, Coleoptera, Hemiptera, Diptera, Neuroptera, Acarina, Araneida (Huffaker et al., 1969) and Dermaptera (Chazeau,1985). Some pathogens, including the viruses and fungi, also have potential as control agents of spider mite populations (van der Geest, 1985b).

Control of TSSM was found to be successful in strawberries when several species of phytoseiid mites were used, e.g. *Phytoseiulus persimilis* Athias-Henriot *Typhlodromus occidentalis* Nesbitt and *Amblyseius californicus* (McGregor) (Oatman and McMurtry, 1966; Oatman et al., 1967,1968, 1977a, b). Other predators of tetranychid mites which were found in strawberry fields in California were predaceous thrips, *Scolothrips sexmaculatus* (Pergande), the cecidomyiid *Arthrocnodax occidentalis* Felt (Oatman and Voth, 1972), *Stethorus picipes* Casey, *Orius tristicolor* (White), *Oligota oviformis* (Casey), *Geocoris punctipes* Stal and a species of hemerobiid (Wyman et al., 1979; Oatman et al., 1981).

Horsburgh and Asquith (1968) found more than 30 predators of TSSM in apple orchards in Pennsylvania, with the ladybird beetle, *Stethorus punctum*, the most efficient. Both the adult and larvae of this beetle prey on mites (van de Vrie, 1985). In cassava, the predator *Stethorus* sp. is closely related to populations of TSSM. Surveys of predator populations in the field under heavy infestions of TSSM have shown that 98% of the predators were *Stethorus* spp. and 2% *Oligota minuta* (Bellotti, 1985). Both Readshaw (1975) and Schicha (1975) also reported that *Stethorus* spp. were the main predators of high mite populations in Australian orchards.

Chant (1961) noted that *P. persimilis* was a specialized predator of tetranychids. Some success has been achieved with *P. persimilis* for the control of TSSM on foliage of tropical plants, particularly on *Codiaeum, Dieffenbachia, Dracaena, Ficus* and *Hedera* spp. used for interior landscaping (Scopes, 1981). In Japan, TSSM was suppressed by *P. persimilis* on soybeans but not on blackberries (Mori and Imbayashi, 1975).

Some disadvantages of *P. persimilis*, namely its limited capacity to disperse, lack of alternative prey, natural enemies and susceptibility to high temperatures, have restricted the use of this predator to control the tetranychids on outdoor crops (Wysoki, 1985). In terms of their ability for numerical increase and predation in greenhouses, Sabelis (1981) ranked predators in the following decreasing order: *P. persimilis, Amblyseius bibens* Blommers, *T. occidentalis* and *Amblyseius pontentillae* (German). With regard to their ability to survive on alternative food, *A. potentillae* ranked highest, followed by *A. bibens, T. occidentalis* and *P. persimilis*. Generally, *P. persimilis* feeds only on living mites and does not take any alternative food (Wysoki, 1985).

2.2.6. Relationships with environmental factors

Spider mite outbreaks associated with prolonged hot weather and drought have been explained by several hypotheses, namely that: (1) lifespan, development, reproduction and survival of the mite are increased under hot and dry environmental conditions; (2) nutritional intake of mites is more efficient during drought; (3) natural enemies and their effectiveness are decreased by hot, dry weather; and (4) mites become more numerous due to the higher nutritional quality of stressed host plants (Oloumi-Sadeghi et al., 1988).

Temperature influences the behaviour and activity of the tetranychid to a great extent (van der Geest, 1985a). Mori (1961) reported that the temperature preferences of TSSM varied from 13°C to 35°C.

TSSM exhibits a negative hygrotaxis; and, when given the choice between moist and dry areas it avoids areas of high moisture (van der Geest, 1985a). Mori and Chant (1966) found that TSSM became sluggish and nearly immobilized under humid conditions.

The photoperiodic response to white light by TSSM is influenced by its physiological condition (van der Geest, 1985a). However, the degree of photoresponse to light also depends on the angle of incidence and the intensity of the light (Suski and Naegele, 1963).

Daily periodicity influences the physiological processes of organisms. Consequently, TSSM displays periods of activity and inactivity which are often related to daily environmental fluctuations (van der Geest, 1985a).

The effects of weather and nutrition on TSSM are interrelated. Weather may directly affect increases or decreases in the food supply and may have indirect effects through its influence on the natural enemies of TSSM (van de Vrie et al., 1972).

2.3. PLANT RESPONSES TO HERBIVORY

2.3.1. Mechanisms of plant defences against herbivores

Various kinds of morphological and chemical characteristics are involved in the defence mechanisms evolved by plants in response to herbivory. These characteristics alter herbivore utilization of host plants (Beck and Schoonhoven, 1980). Morphological defensive traits, such as tissue toughness, trichomes, surface waxes, colour and shape interfere physically with herbivore locomotory mechanisms and more specifically with host selection, feeding, ingestion, digestion, mating and oviposition. In contrast, chemical defensive traits, including inorganics (e.g. selenium), primary and intermediary metabolites (e.g. citric acid, cysteine and certain aromatic amino acids) and secondary substances (e.g., alkaloids), affect chemically mediated behavioral and metabolic processes. Morphological and chemical defences are interrelated with a continuum of defence (Norris and Kogan, 1980). For instance, glandular trichomes not only impede the movement of small herbivores but also contain toxic constituents which spill into the surrounding tissue when the gland is ruptured, making it unpalatable or toxic (Stipanovic, 1983).

2.3.1.1. Morphological defences

Morphological defences can be classified as remote or contact. The majority of these plant factors operate on contact with the herbivore (Norris and Kogan, 1980). In a number of examples, tougher plant tissues confer greater resistance against herbivores, particularly to the feeding of neonate forms and tissue penetration by stem borers (Beck and Schoonhoven, 1980). Tanton (1962) reported that the feeding rates and larval growth of the mustard beetles were retarded when they fed on relatively tough turnip, kale, and Brussels sprout leaves. Bjorkman and Anderson (1990) showed that Ithomiid larvae fed to a lesser extent on

tough leaves of a South American blackberry (*Rubus bogotensis*) than on more tender ones. In rice, thicker hypodermal layers have been regarded as a resistant factor to the rice stem borer, *Chilo suppressalis* (Patanakamjorn and Pathak, 1967). Tissue toughness may result from high fibre or silica (Beck and Schoonhoven, 1980). While hardness of the rind and fiber content of stalks are responsible for the resistance of sugar cane to *Diatrea saccharalis* larvae (Agarwal, 1969; Martin et al., 1975), Mensah and Madden (1991) pointed out that hardness of the terminal shoot played a important role in the resistance of *Boronia megastigma* to oviposition of the psyllid, *Ctenarytaina thysanura* Ferris and Klyver. Silication of rice plants reduces attack by the rice stem borer larvae (Sasamoto, 1958). Leaf trichomes or hairs can act as physical barriers that deter small herbivores such as phytophagous insects (Levin, 1973) and mites (Stipanovic, 1983). There are several examples of resistance mechanisms related to the presence of trichomes. Kamel and Elkassaby (1965) found that a cotton variety that had long, highly branched and abundant trichomes was more resistant to spider mites and leafhoppers than other cotton varieties. Length and/or density of trichomes in other major crops were also reported to be correlated with resistance to various insect pests (Singh et al,. 1971; Broersma et al, 1972; Turnipseed, 1977; Khan et al., 1986: Sosa, 1988). Another example of contact defences was reported by Woodhead and Padgham (1988) who found that the surface wax influenced settling and probing of the brown planthopper, *Nilaparvata lugens*, on rice.

With respect to flying insects, Kennedy et al. (1961) reported that alate aphids appeared to be attracted to plants at a physiologically appropriate stage of growth; being attracted to leaves reflecting light of approximately 500 nm, regardless of the species of plant. Boller and

Prokopy (1976) also found that leaf reflectance as well as tree shape and size remotely affected host selection behaviour of *Rhagoletis* sp.

2.3.1.2. Chemical defences

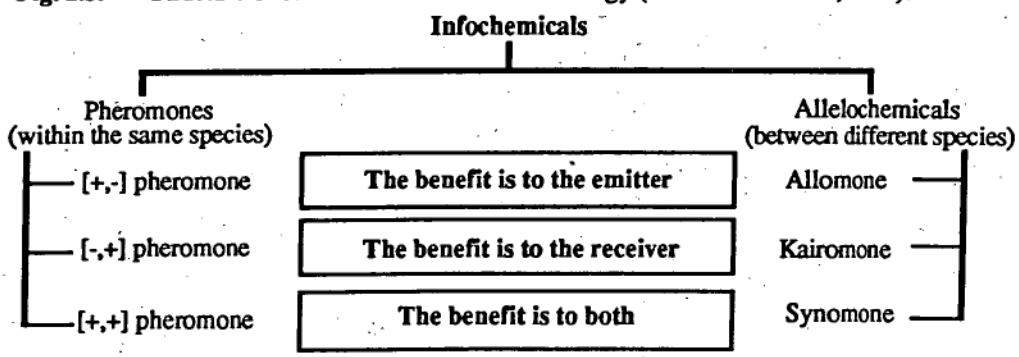
Phytochemicals produced as metabolic by-products with defensive functions are generally known as "secondary plant chemicals" (Fraenkel, 1959; 1969). Even though primary roles for these secondary metabolites have been involved in some physiological processes (Seigler and Price, 1976; Seigler, 1977), defence is generally assumed to be their "raison d'etre" (Fraenkel, 1959; Rhoades, 1985). Later, the term "allelochemics" was proposed to describe "a non-nutritional chemical that is produced by an individual of one species and that affects the growth, health, behaviour, or population biology of another species" (Whittaker, 1970). According to Whittaker and Feeny (1971), allelochemics can be divided into 2 effective classes: "allomones", which are allelochemics tending to give an adaptive advantage to the producing organism and "kairomones", which impart an adaptive advantage to the receiving organism. The effects of allelochemics on herbivores may be behavioral or metabolic (Beck and Schoonhoven, 1980). Visser and Nielsen (1977) showed that volatiles of several solanaceous plants attracted the Colorado potato beetle by influencing their olfactory orientation. Sinigrin, a glycoside found in most cruciferous plants, is toxic to the larvae of black swallowtail butterflies, *Papilio polyxenes*, which do not normally attack crucifers. The southern armyworm, a generalist feeder, is also inhibited by high concentrations of sinigrin. By contrast, this compound stimulates feeding by the cabbageworm, a crucifer specialist (Blau et al., 1978).

In addition, chemical defence mechanisms can be classified not only on the chemical properties of the compounds involved, but also on the way these compounds function in relation to herbivore attacks (Haukioja, 1980). Levin (1976) distinguished between constitutive

compounds, ie. those chemicals present before herbivore attack, and induced compounds which are chemicals synthesised as a result of attack. An example of constitutive defences is the cucurbitacins, which are responsible for bitterness in the cucurbits, thus offering protection from mites and cucumber beetles (DaCosta and Jones, 1971). Dicke and Dijkman (1992) indicated that volatile "infochemicals", whose production is induced in detached Lima bean leaves, affected the behaviour of TSSM and its predator, *P. persimilis*.

According to Dicke and Sabelis (1988), an infochemical was defined as "a chemical that, in the natural context, conveys information in an interaction between two individuals, evoking in the receiver a behavioural or physiological response that is adaptive to either one of the interactants or to both". A summary of current infochemical terminology is shown in Fig. 2.3.

Fig. 2.3. Structure of current infochemical terminology (Dicke and Sabelis, 1988).



In recent years, various hypotheses have been proposed to explain quantitative and qualitative patterns of chemical defence mechanisms

(Herms and Mattson, 1992). Firstly, Rhoades (1979) summarized the basic tenets of the optimal defence theory by stating that there is a limited amount of resources that a plant can devote to defence, and that there are alternative demands for these limited resources, e.g. growth. Selection is predicted to favour an optimal defence allocation which maximizes plant fitness. Defences are costly, and thus will only evolve when and where their benefits overcome their costs (Rhoades, 1979; Tuomi, 1992). These costs of defences can be considered to show inverse relationships between defence and growth because the allocation of resources by plants to antiherbivore mechanisms decreases growth by diverting resources from the foliage production area and other vegetative structures (Herms and Mattson, 1992). For example, Bjorkman and Anderson (1990) presented evidence for a resource allocation between antiherbivore mechanisms (i.e. glandular trichomes) and other plant traits (i.e. prickle numbers and size) by using data from the South American blackberry.

Secondly, Feeny (1976) hypothesized that the type of chemical defence was influenced by plant apparency. The quantitative defences (e.g. tannins and resins) are characteristic of the ecologically conspicuous "apparent" plants, whereas qualitative defences (e.g. alkaloids, cyanogenic compounds etc), are characteristic of "unapparent" plants (Feeny, 1976; Rhoades and Cates, 1976). Apparent plants are easily discovered by herbivores and therefore show a large investment in quantitative defences effective broadly. Unapparent plants were predicted to rely on escaping attack by specialist herbivores and hence needed only to invest in qualitative defences effective against nonadapted generalist herbivores. Thus, the defence differences between apparent and unapparent plants were proposed to reflect differential effectiveness of quantitative and qualitative defences against specialist and generalist herbivores and

differential selection pressure by generalists and specialists due to plant apparency (Feeny, 1976; Rhoades and Cates, 1976; Coley et al., 1985).

Thirdly, the resource availability hypothesis, which extends the optimal defence hypothesis, assumes that both the amounts and types of plant defences are determined by the resource availablity in the environment. Natural selection favours plants with faster growth rates and lower defence levels in environments with high resource availability, whereas the plants with slow growth rates and high levels of defence are favored under conditions of low resource availability (Coley et al., 1985). However, Bryant et al. (1983) suggested that phenotypic variation in secondary metabolism, which has important implications for palatability and resistance to herbivores, is regulated by carbon-nutrient balance. According to this hypothesis chemical defences are largely carbon-based under nutrient-limited environments because plants store proportionately more carbon in their leaves. On the other hand, plants growing under high-nutrient or low-carbon environments store proportionately more nitrogen and other nutrients and less carbon; hence carbon-based defences decline, and nitrogen-based defences become more important (Bryant et al, 1983; Karban and Myers, 1989). Not all data are in agreement with the carbon-nutrient balance hypothesis. For instance, Clark and Menary (1980) found that fertilization increased concentrations of carbon-based secondary metabolites in peppermints.

In a recent review, Herms and Mattson (1992) proposed that the plant growth-differentiation balance concept formed a framework that unified both the evolutionary responses regulated by the optimal defence theory and the specific phenotypic responses outlined by the carbon-nutrient balance model. As a unifying concept, this hypothesis does not so much create new predictions (Tuomi, 1992); its explanatory power depends chiefly on specific assumptions in relation to the physiological

and biochemical mechanisms that regulate differentiation processes in each specific case.

2.3.2. Role of plant defences in the population dynamics of herbivores

There are various case studies indicating that generally it is important to include plant defences when considering fluctuation in herbivore numbers (Haukioja, 1980). The term "genetic feedback" was proposed as the foundation of the mechanism for herbivore population regulation, stemming from the genetic change of host plants to herbivore feeding pressure and vice versa (Pimentel, 1968). According to van Emden and Way (1973), the impact of host plants on colonizing insect populations leads to changes in the herbivore population. White (1974) suggested that most herbivores usually remain at low levels of abundance relative to the apparent abundance of their host plants. Werner (1979) found that food quality of host plants influenced the biology of the herbivore, such as survival and development of spear-black moth larvae on deciduous plants. Kidd (1985) also showed that the food quality of host plants determined the population dynamics of the herbivore. In addition, Karban and English-Loeb (1988) pointed out that plants varied in their resistance to tetranychid spider mites, and this could have profound effects on spider-mite population dynamics.

Plants employ several types of defensive strategies for reducing the chance of their being driven to extinction by herbivores (Haukioja, 1980). Among these defensive strategies are ecological mechanisms, such as escape in time and space (Feeny, 1975), physical and chemical mechanisms, and even variance of defensive properties within and between individuals (Haukioja, 1980). These defensive strategies of plants have a coevolutionary relationship with the offensive strategies of herbivores. The coevolutionary relationship consists of adaptations of

plants and counteradaptation of herbivores (Rhoades, 1985). Several studies have shown that herbivores evolve a number of strategies for circumventing the resistance mechanisms of their hosts, including physical sabotage of antiherbivore defence systems, and the enzymatic detoxification of secondary metabolites (Herms and Mattson, 1992). These strategies can explain why population levels of some species of herbivores are variable while those of others are relatively invariant. Thus, herbivore population dynamics are probably better known in terms of varying quality and quantity of both plants and herbivores than in terms of only quantitative changes in amount of vegetation and numbers of herbivores (Rhoades, 1985).

2.3.3. Plant compensation to herbivory

Due to the compensatory growth responses of plants, many effects of herbivores upon their host plants that are presently perceived as deleterious may be less deleterious than presumed (McNaughton, 1983). This phenomenon is implicit or explicit in several studies of the effects of herbivores on plant growth and yield (Kumar and Joshi, 1972; Vickery, 1972; Chew, 1974; Dyer, 1975; McNaughton, 1976; 1979). In nature, plant species fitness that can compensate for herbivore feeding has obvious selective advantages that result in the maintenance of the genotype. Reports of plant compensation in agricultural crops, however, are mostly concerned with yields rather than plant fitness (Trumble et al., 1993).

In general, the ability of plants to photosynthesize and transfer products to the fruits, tubers or other harvested parts is reduced by damage which is caused to leaves and other parts of plants. Some losses can be compensated without affecting yield since plants may naturally produce an excess of photosynthetic products (Matthews, 1984). For example, when turnips and sugar beet plants suffer defoliation, the

remaining leaves grow larger than comparable leaves on undamaged plants, and photosynthetic efficiency is enhanced (Taylor and Bardner, 1968; French and Humphries, 1977).

The ability to compensate for damage relies on the growth characteristics of the plants which are infested. Additionally, the effects of pests on an agricultural crop need to be assessed carefully for a particular farming area, because differences in agronomic practices and environmental factors will influence the severity of pest damage (Matthews, 1984).

A generalized response curve (Fig. 2.4) to show the relationship between severity of infestation and yield was described by Tammes (1961), Bardner and Fletcher (1974), Pedigo et al. (1986) and Funderburk et al. (1993). Tammes (1961) divided the curve into three stages: the first stage in which the injurious factors have slight influence on yield because of compensation, the second stage which reveals a yield loss correlated with an increase in the injurious factor, and the final stage in which a level of maximum possible injury and the self-limiting effect of the injurious factor occur. Subsequently, this curve was divided into six types of relationship, as shown in Fig. 2.5 (Matthews, 1984).

Fig. 2.4. Generalized response curve of plants (from Bardner and Fletcher, 1974).

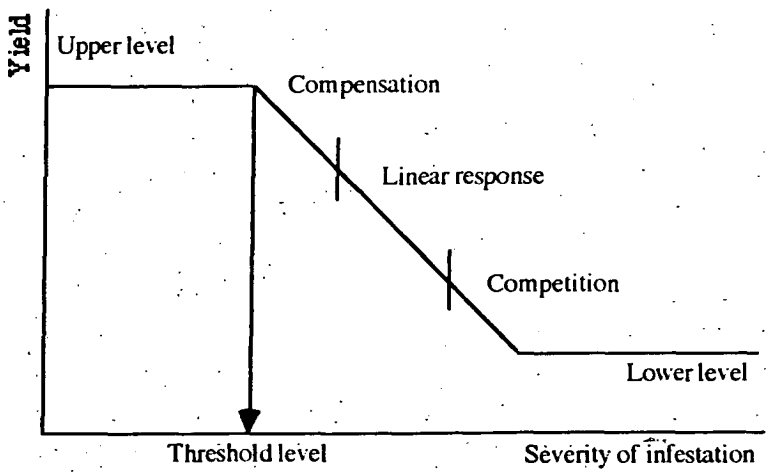
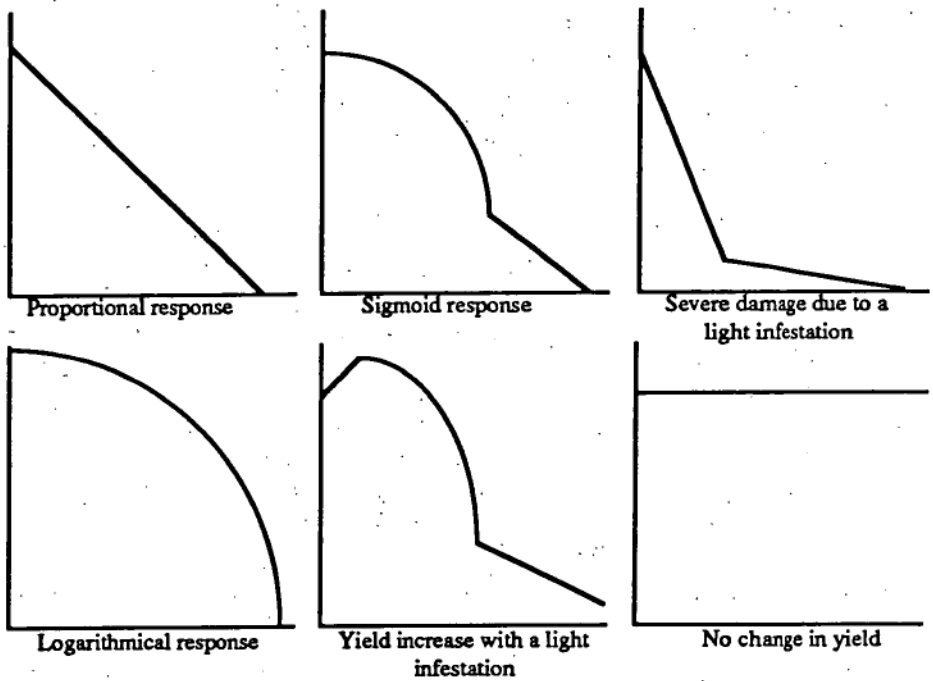


Fig. 2.5. Variations in yield response to infestation (from Matthews, 1984).



Compensatory mechanisms contribute to the alleviation of the potential deleterious effects of tissue damage, both to vegetative and reproductive organs. The mechanisms that cause compensatory responses in plants following herbivore damage are complex and interrelated, but can be divided into intrinsic and extrinsic mechanisms (McNaughton, 1983).

The intrinsic mechanisms, considered as endogenous factors, which influence compensatory responses in plants are mainly affected by allocation or reallocation of resources within the plant (Trumble et al., 1993). These may involve changes in physiology and development (McNaughton, 1983) and include regrowth patterns, photosynthetic activity, senescence, leaf morphology, and canopy architecture. A variable distribution of resources can cause major changes in the form of plant compensatory responses which are strongly affected by source-sink relationships (Trumble et al., 1993). A well-known response of grasses to

defoliation is tillering, resulting from the activation of meristems. These cells are promoted to divide by cytokinins (McNaughton, 1983).

In contrast the extrinsic mechanisms, known as exogenous factors, are not directly under the physiological control of the plant (Trumble et al., 1993). Extrinsic mechanisms that influence compensatory responses in plants include changes in general environment (McNaughton, 1983), nutrient and water availability, temperature, intensity and timing of defoliation and herbivore distribution (Trumble et al., 1993).

2.3.4. Induced responses in plants

Physiological and chemical traits of many plant species have been found to change in response to real or simulated herbivory (Schultz, 1988). Changes in both current growth and regrowth of plants following this injury have been called "induced responses" (Rhoades, 1983; Edwards and Wratten, 1985; Fowler and Lawton, 1985). These changes often have significant effects on the behaviour, growth, survivorship, feeding and oviposition of the herbivore (Schultz, 1988), and the mechanism underlying this phenomenon is frequently referred to as "induced resistance" (Karban et al., 1987). Herbivore-induced responses which not only reduce herbivore preference or performance but also increase plant fitness are known as "induced defences". Field studies on the impacts of induced responses on herbivores have given extremely variable results among plants within a population, and among populations. Much of this variation may result from differences in species, age, genotype, history, and environmental factors (Karban and Myers, 1989).

Numerous studies on the influence of plant responses on herbivory support the phenomenon of herbivore-induced resistance (Kogan and Paxton, 1983). Loper (1968) reported that feeding by the pea aphid on alfalfa induces an increase in coumestrol that may influence

additional feeding by other pea aphids. Under glasshouse conditions, Karban and Carey (1984) indicated that TSSM and strawberry spider mite, *T. turkestani* Ugarov and Nikolski, feeding on cotyledons of cotton seedlings induced resistance to the mites in the true leaves which appeared later. The practical potential of induced resistance in cotton was demonstrated by Karban (1986). Karban and English-Loeb (1988) described that previous or concurrent feeding by phytophagous herbivores influenced expression of plant resistance to spider mites. Brown et al. (1991) showed that an initial infestation of soybean cotyledons yielded a reduction in subsequent mite populations. However, no evidence for induced resistance of *Phaseolus vulagaris* to TSSM was detected (English-Loeb and Karban, 1991). Other related works in this field for commercial purposes were explained by Day (1993).

Even though the studies mentioned above have tended not to focus on classification of induced responses, they can nevertheless be classified as rapid or long-term responses (Haukioja and Hanhimaki, 1985). Rapid responses occur during the attack such that the attacking individuals experience the consequences of the changes they induce. Long-term responses can occur following the attack. Although they have little impact on the attacking herbivores, long-term responses can affect herbivores that attack the plant at later times (Karban and Myers, 1989).

2.3.4.1. Induction of plant resistance by non-herbivores

A variety of mechanisms appear to be involved in plant resistance. These include changes in (1) phenological synchronization between the plant and its complement of herbivores; (2) the physiological state of the plant; (3) nutrient concentration; (4) stimulation of compensatory mechanisms; (5) concentrations of allelochemics; and (6) de novo synthesis of phytoalexins. Other factors, apart from previous or

concurrent herbivore attack, that influence induction of plant resistance include temperature, light, relative humidity, soil fertility, pesticides, and plant growth regulators (Kogan and Paxton, 1983).

Temperature, which is a major factor affecting fundamental plant and pest physiological processes, can modify the level and expression of genetic resistance in at least three ways (Tingey and Singh, 1980): (1) by indirectly affecting plant suitability to herbivore performance; (2) by directly affecting plant physiological and growth responses to herbivore attack; and (3) by directly affecting the biology of the herbivore. Among the first to propose that temperature alters plant resistance were Dahms and Painter (1940) who reported that alfalfa resistance to pea aphids was modified by temperature.

Light and relative humidity can also modify fundamental physiological processes of herbivores and their host plants (Tingey and Singh, 1980). Loomis et al. (1957) found that light intensity influenced levels of chemical resistance factors in maize to the European corn borer, *Ostrinis nubilalis*. In the case of relative humidity, Rogers and Mills (1974) showed responses of sorghum varieties to maize weevil infestation under different relative humidities.

Quantitative and qualitative variation in soil fertility exerts striking effects on plant growth and development, which may result in changes in nutritional suitability of plant tissue for herbivores (Tingey and Singh, 1980). For example, McMurtry (1962) found that potassium deficiency led to reduced resistance of alfalfa clones to the spotted alfalfa aphid, *Therioaphis maculata*, whereas phosphorus deficiency resulted in increased resistance.

Pesticides and plant growth regulators influence the expression of plant resistance due to their stimulatory or inhibitory effects on herbivore populations. These can include (1) effects on populations of natural

enemies and competing species, (2) direct effects on the physiology of the herbivore, and (3) effects on the nutritional quality of the host plant (Tingey and Singh, 1980). Among the first to study the effect of pesticides and plant growth regulators on insect development, as mediated through change in host plant condition, were Maxwell and Harwood (1960) who showed that reproduction of the pea aphid *Acyrthosiphon pisum* on broad bean was consistently increased with foliar applications of 2,4-D at 4.1 and 41.0 ppm made 24 hours before infestation.

2.3.4.2. Primary physio-chemicals involved in induced defences

According to Craig et al. (1986), when herbivores feed on a plant resource three following consequences are possible: resource quality may increase, resource quality may remain unchanged (Mattson and Addy, 1975; McNaughton, 1976, 1979,1983; Owen and Wiegert, 1976; Montgomery, 1980; Owen, 1980), or resource quality may decline if there are induced defences (Green and Ryan, 1972; Haukioja and Niemela, 1979, Ryan, 1983). The last consequence to resource quality may result from a passive rearrangement of resources within the plant (Karban and Myers, 1989).

Carbon and nitrogen are the two primary resources which not only can be allocated to defensive structures but may also be limiting in a plant (Mooney et al. 1983). Whether carbon or nitrogen is the limiting resource may determine the defence type (carbon-based or nitrogen-based) synthesised by the plant (Bryant et al., 1983). Carbon and nitrogen are utilized in the construction of secondary compounds or protective structures, and carbon is also used as an energy source to construct these components (Mooney et al. 1983). Among defensive compounds derived from carbon are fibre and carbon-based allelochemics, including terpenes, resins, tannins, and other other phenolics (Karban and Myers, 1989). In

the case of nitrogen, this element is a component of various types of compounds believed to be important in plant chemical defence, principally cyanogenic glycosides, glucosinolates, alkaloids, certain proteins, non-protein amino acids and peptides (Mooney et al. 1983). Levin (1976) suggested that these compounds are the offshoots of metabolic pathways with important functions in primary metabolism (Fig 2.6).

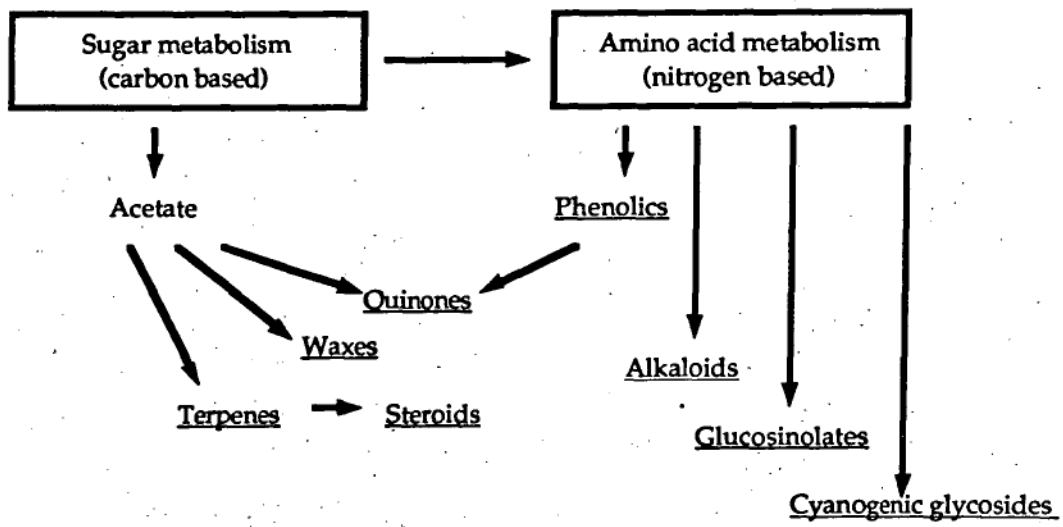


Fig. 2.6. Biosynthetic relationships between carbon and nitrogen based secondary plant products (from Levin, 1976).

2.4. MITE POPULATION ANALYSES

The above section (2.3) provides information which indicates that herbivore populations are influenced by their host plants. For this reason, analyses of herbivore populations are necessary for the study of the response of plants to herbivory. In the case of spider mites, these analyses may be expressed in various ways, including life tables, population growth rates and population dispersions. These three approaches have been used in the present study.

2.4.1. Life tables

There are basically two types of life tables, namely: time-specific (static, current, or vertical) and age-specific (cohort, generation, or horizontal) life tables. The former type is solely calculated on the basis of the age-grouping, at a specific time, of an imaginary cohort of individuals collected from a stationary population with overlapping generations, i.e. a multi-stage population. In contrast, the latter type is calculated on the basis of a real cohort; conveniently the members of a stationary or fluctuating population belonging to a single generation. A comparison of succesive estimates in time is necessary for age-specific life tables. Since several animals have discrete generations and their populations are fluctuating, the time-specific life table is not as applicable to the study of animal ecology as the age-specific life table (Dempster, 1976; Southwood, 1978).

To construct complete life tables, estimates of three dynamic features of a population must be available. Firstly, the total number of individuals which reach the beginning of each stage over the entire generation is necessary to construct a life table, especially the horizontal type. Numbers entering each stage either may be measured directly during the period that recruitment occurs or estimated from data on stage densities over time using one or more methods for analysis of stage-frequency data. Secondly, mortality from specific factors in each stage may be expressed in five ways, namely: real mortality, apparent mortality, indispensable mortality, marginal attack rates, and k-values. These terms vary in their ability to express unambiguously the mortality caused by a factor in ways that allow comparisons. Thirdly, lost fecundity can be a major factor leading to changes in numbers of individuals between generations. This factor in life tables is estimated by the difference between the potential and realized fecundity. Generally, potential

fecundity is estimated by reference either to dissection of gravid female adults, or to oviposition rates of adults held under controlled conditions intended to yield maximum reproduction. Realized fecundity is estimated by any methods used to assess increased numbers in each stage (Bellows et al, 1992). Fecundity is a measure of total egg production and fecundity is the number of viable eggs produced by a female (Southwood, 1978). In most cases, fertility losses have been used in life tables as a fraction of the potential fecundity (Bellows et al, 1992). Additionally, either fertility or numbers entering a stage can be considered as natality (Southwood, 1978).

Several types of graphs may be constructed from life table data, including mortality rate, life expectancy and survivorship curves (Brower et al., 1990). The survivorship curve is prepared by plotting the number of individuals living at a given age against time and is the simplest description of a life table (Southwood, 1978). This type of graph is most widely used among ecologists (Brower et al., 1990).

Life tables, as described by Deevey (1947) and Birch (1948), have been constructed for TSSM by several investigators including Laing (1969), Bengston (1969a), Shih et al. (1976), and Carey and Bradley (1982). Although natality and mortality differ to some extent between studies owing to different experimental conditions, under similar temperature regimes developmental rates as well as the patterns of age-specific survivorship and fecundity are usually similar. It is also clear that changes in fecundity tend to have a greater effect on the age profile of a TSSM population than do mortality changes because the role of fertility in shaping age distribution is simpler than mortality (Carey, 1982a).

2.4.2. Population growth

The growth rate of a population under given constant conditions of environment, where food and space are not limited, and where there are no mortality factors other than physiological ones is defined as the intrinsic rate of natural increase (r_m) of that population (Birch, 1948). This value can be determined from the life history components of the organism, including developmental time, fecundity, survivorship, and sex ratio (Sabelis, 1985a). Snell (1978) reported that developmental time and fecundity were the two life history components of paramount importance in determining the intrinsic rate of increase. Short duration of generations and high fertilities lead to large intrinsic rates of increase (Gutierrez and Helle, 1985). Cole (1954) showed that fecundity had a far smaller effect on r_m than did the age of first reproduction. With regard to increasing r_m, Lewontin, in 1965, also proved that small decreases in the developmental rate were equal to very large increases in fecundity (Wrensch, 1985).

Furthermore, r_m of the tetranychid depends on the breeding conditions which basically include the nature of the host plant, the surface available to each individual, temperature and humidity (Gutierrez and Helle, 1985). Rauwerdink et al. (1985), working with TSSM on cucumber, found r_m values ranging from 0.282 per day for susceptible lines to 0.218 per day for resistant lines under the same environmental conditions. In the case of the surface available, Wrensch and Young (1978) indicated that marked reductions in developmental rate, survivorship and sex ratio of TSSM populations occurred at high, rather than low density. The effect of temperature on the r_m value was studied by Carey and Bradley (1982) who showed that TSSM on cotton had r_m values at a relative humidity of 65% ranging from 0.219 per day at 23.8°C to 0.293 per day at 29.4°C. Herbert (1981), working with TSSM on apple, pointed out that developmental time was shown to decrease with

increasing temperature. For the r_m values at different humidities, Nickel (1960) reported that *T. desertorum* Banks had an r_m at 30°C ranging from 0.46 per day at 25-30% RH to 0.36 per day at 85-90% RH, reflecting the promotion of fecundity by lower humidities.

According to Lotka (1924) and Birch (1948), the following equation was derived to estimate r_m:

$$\sum \exp(-r_m x) l_x m_x = 1$$

where: x is the pivotal age for the age class in units of time; l_x is the age specific survivorship; and m_x is the age specific fecundity.

The age specific survivorship is the fraction of females surviving from age 0 until at least age x, which is:

$$l_x = y_x / y_o$$

where: y_x is the number of females alive during a given age interval; y_o is the initial population of females.

The age specific fecundity is the number of female offspring born per female of age x, which is:

$$m_x = N_x s$$

where: N_x is the mean number of offspring produced per female per age interval; and s is the proportion of the offspring that are females. In general, s is assumed to be 0.50 (Southwood, 1978).

Several workers have attemped to find other methods of determining the value of r_m (Wyatt and White, 1977). Laughlin (1965) proposed the capacity for increase (r_c) as an approximate r_m. It is defined:

$$r_c = \log_e R_o / T_c$$

where: R_o is net reproductive rate; and T_c is cohort generation time.

The net reproductive rate (Southwood, 1978; Murray, 1979; Brower et al., 1990) is considered as the number of times a population will multiply per generation, which is:

$$R_o = \sum l_x m_x$$

The cohort generation time is the mean age of the females in the cohort at the birth of female offspring or the pivotal age where $l_x m_x = 0.5 R_o$ (Bengston, 1969a). It is defined (Murray, 1979; Micinski et al., 1981) as:

$$T_c = \sum l_x m_x x / R_o$$

For the tetranychid mites, Wyatt and White (1977) suggested that the intrinsic rate of natural increase can be estimated from the simpler equation which is defined as:

$$r = 0.74 (\ln M_d)/d$$

where: d is the pre-reproductive development period; and M_d is the total reproduction per original female in the first part of the reproductive period of length which is equivalent to d.

Other parameters involved in the population growth are as follows:

(a) mean generation time (T) can be calculated as $T = \ln R_o / r_m$ (Southwood, 1978);

(b) finite rate of increase, $\lambda = \exp(r_m)$ (Southwood, 1978);

(c) doubling time, $DT = \ln 2 / r_m = 0.693 / r_m$ (Brower et al., 1990);

(d) natality, $b = 1 / \sum l_x \exp(-r_m x)$ (Murray, 1979);

(e) mortality, $d = b - r_m$ (Murray, 1979);

(f) gross reproductive rate, $GRR = \sum m_x$ (Firempong, 1988).

2.4.3. Population dispersion

The arrangement of individuals of a population within a habitat is referred to as dispersion, or the spatial distribution or pattern of a population. Fundamentally, there are three kinds of dispersion: uniform (or regular), random, and contagious (also called clumped, clustered, or patchy). Uniform and contagious patterns are sometimes known as underdispersed and overdispersed, respectively (Brower, et al., 1990).

Sampling is a procedure used to determine the distribution of a population (Southwood, 1978). Various techniques have been devised for the sampling of field populations of the tetranychids. These are direct counting, imprint counting, counting mites dislodged with the aid of a brushing machine, counting mites washed off their host plant leaves and counting mites dislodged by beating foliage. Among these techniques, direct counting is usually assumed to be the most accurate (Sabelis, 1985b).

Some aspects of statistics need to be considered before the data from the sampling can be analysed. These include the frequency distribution of data and transformation. For most statistical methods to be applied to a set of data the frequency distribution must be normal. This means that the variance is independent of the mean. In order to overcome the problem of the variance related to the mean the data are transformed; therefore, the actual numbers are replaced by a function. Taylor's power law (Southwood, 1978) can be used not only to choose the transformation but also to describe the pattern of the dispersion. The relationship between the mean and variance of series of samples in Taylor's power law is expressed by:

$$s^2 = ax^b$$

where: a and b are constant; s is the variance; and x is the mean (Taylor, 1961).

The value of b which appears to be an index of aggregation characteristic of the species as well as a component of the transformation. This value can be found from a linear regression model:

$$\log s^2 = \log a + b(\log x).$$

This relationship holds over a continuous series of dispersions from uniform through random to highly aggregated. It will usually be found appropriate to transform data from a uniform population by using

squares, data from a slightly contagious one by square roots and data from distinctly aggregated populations by using logarithms (Southwood, 1978).

An example of the application of Taylor's power law is the work of Jones (1990), who studied the sampling and dispersion of TSSM and the western orchard predatory mite (*T. occidentalis*) on tart cherry. The result showed that Taylor's power law was useful to quantify the relationship between mean and variance and to develop binomial sampling plans.

However, Taylor's power law has been criticized on both theoretical and statistical grounds (Pickett and Gilstrap, 1986). Iwao (1968) indicated that the index of aggregation has no theoretical grounds and Nachman (1981) observed that the independent variable is subject to error, violating assumptions of least squares regression.

According to Myers (1978), Green's coefficient, (C_x) is considered one of the more useful dispersion indices because the index varies independently from the the sample mean. This index determines departure from randomness and is calculated by:

$$C_x = [(s^2/m) - 1]/X - 1,$$

where: s^2 is sample variance; m is sample mean; and X is sample total. Values for the index C_x range from 0.0 (random), to 1.0 (maximun aggregation) (Green, 1966).

In addition, variance-to-mean ratio is another approach to the description and analysis of the spatial distribution of individuals. If the distribution is random, then the ratio is equal to 1.0; if uniform, the ratio is less than 1.0; and if aggregated, the ratio is greater than 1.0 (Brower, et al. 1990).

2.5. SCREENING OF PLANT VARIETIES FOR RESISTANCE TO SPIDER MITE DAMAGE

Inherent resistance to some herbivores is found in every green plant (Norris and Kogan, 1980). For animal pests, there are three main types of resistance that can be expressed by host plants (Russell, 1978). These are: (a) non-preference, which is displayed by plants that lack the characteristics to serve as hosts; (b) antibiosis, which includes adverse effects used by plants on the development or reproduction of pests; (c) tolerance, which enables a host plant to withstand infestation and to support pest populations that would severely damage susceptible plants (Painter, 1951). Besides these types of resistance, Russell (1978) proposed a fourth type defined as pest avoidance. This type is expressed as a tendency of the host plant to escape infestation. For example, some apple cultivars do not become infested by various species of insect pests since their buds do not break until after the main hatching or emergence period of the pest (Briggs and Alston, 1969).

Based on the mode of inheritance, some types of resistance to pests are governed by a single gene of major effect on the trait (monogenically), others by a few genes of major effect (oligogenically)) and still others by many genes each of which has a minor effect (polygenically) (van de Plank, 1963). Some of the resistance genes are recessive, others are dominant and their effects may be additive (Russell, 1978), complementary, or epistatic (Gallun and Khush, 1980).

Screening for resistance to pests can be carried out in the field or in the glasshouse. Experimental errors of field tests can be very high when the tests are conducted under natural, uncontrolled environmental conditions. These errors may subsequently result in spurious differences in pest resistance between genotypes or vaguely real differences in resistance. Nevertheless, field tests have several advantages since they are conducted under the real conditions of the infestation and greater numbers of host genotypes can usually be screened in the field than in

the glasshouse with the same amount of labour. In contrast, experimental procedures in the glasshouse can be standardized and controlled; because of this, reproducible results can often be achieved quickly and easily (Russell, 1978). Although artificial tests are often preferred, field tests still remain part of each study on resistance to confirm the results of artificial tests (De Ponti, 1977b).

For artificial tests of resistance to pests that attack the aerial parts of plants, large numbers of the pest are often reared on appropriate host plants in insectaries (Russell, 1978). Singh and Charles (1977) reported that lima beans (*Phaseolus lunatus*) were suitable food plants for rearing TSSM. Transferring a predetermined number of individuals either to each tested plant or to susceptible 'spreader' plants which have been planted uniformly among the tested plants is a simple but effective method of inoculating plants with pests, in field or glasshouse tests (Russell, 1978). Dahms (1972) suggested that resistance may be measured by (a) visual observation, (b) the effect of pests on plants, (c) the effect of plants on pests, or (d) indirect methods.

In the literature on resistance to TSSM, reviewed by van de Vrie et al. (1972) and De Ponti (1977a), reference is commonly made to the use of artificial tests. These tests have been investigated almost exclusively by measuring reproduction of the mites or by rating the extent of damage of infested plants. In most cases, the suitability of plants for the mites is detemined by measuring the reproduction during 24, 48 or 72 hours after inoculation. Occasionally all developmental stages of the progeny of the inoculum are watched, however mostly the observations are restricted to the eggs. These observations can be made by using leaf cage or leaf disc techniques (De Ponti, 1977b). To economize on labour, the latter technique is to be preferred (De Ponti and Inggamer, 1976). Helle and Overmeer (1985) also suggested that the leaf disc technique is a

convenient and efficient method for studying tetranychid biology. The biology of the mites on excised plant parts, like detached leaves and leaf discs, may differ from the normal pattern on an intact plant (Storms, 1969). Nevertheless, leaf discs have been popularly used to determine differences in reproduction of the two spotted spider mite (Rodriquez, 1953; Bengston, 1970; Dabrowski et al., 1971; Macdonald et al., 1971; Dabrowski, 1972; Aina et al., 1972; Tulisalo, 1972; Soans et al., 1973a, 1973b; Schalk et al., 1975; Al-Abbasi et al., 1987; Wilde et al., 1991; East et al., 1992).

Resistance to TSSM has been found in several plants as listed in Table 2.2.

Table 2.2. Up-to-date review of the literature on resistance to TSSM.

Host plant	References
Apple	Bengston (1970); Keppel (1989).
Cassava	Saradamma and Das (1974); Bellotti and Guerrero (1977); Bellotti and Byrne (1979).
Castorbean	Chandrasekharan et al. (1964)
Chrysanthemum	Markkula et al. (1969).
Corn	Kamali et al. (1989).
Cotton	Kamel and Elkasseby (1965); Schuster et al. (1973); Childress et al. (1976); Schuster and Maxwell (1976); Bailey et al. (1978); Trichilo and Leigh (1985); Botha et al. (1989); Pavlova and Egamberdiev (1990).
Cucumber	Dacosta and Jones (1971); Kooistra (1971); Tulisalo (1972); Soans et al. (1973a); Knipping et al. (1975); De Ponti (1977b); Gould (1978); De Ponti (1980).
Eggplant	Soans et al. (1973b); Schalk et al. (1975).
Geranium	Snetsinger et al. (1966); Potter et al. (1981); Walters et al. (1991).
Grape	Duschin (1967).
Hop	Mayberry (1968); Regev and Cone (1975); Peters and Berry (1980a); Gunson and Hutchins (1982); Leszcynski et al. (1988).
Impatien	Al-Abbasi and Weigle (1982); Al-Abbasi et.al. (1987).
Ivy	Osborne and Chase (1985).
Muskmelon	East et al. (1992).
Pepper	Zatyko and Martinovich (1986).
Potato	Gentile et al. (1969); Macdonald et. (1972).
Raspberry	Labanowska and Pala (1986); Wilde et al. (1991).
Soybean	Rodriguez and Freeman (1959); Carlson (1969); Parameswarappa et al. (1974); Bailey and Furr (1975); Rodriguez et al. (1983); Mohammad and Rodriguez (1985); Hildebrand et al. (1986); Wheatley and Boethel (1987); Wheatley and Boethel (1992).
Strawberry	Leska et al. (1964); Chaplin et al. (1968; 1970); Dabrowski et al. (1971); Shanks and Barritt (1975); Schuster et al. (1980); Shanks and Barrit (1984); Masis and Aguilar (1990).
Sugarbeet	Bush and Brewbaker (1956).
Tobacco	Patterson et al. (1974).
Tomato	Gilbert et al. (1966); Stoner and Stringfellow (1967); Stoner (1970).
Watermelon	East and Edelson (1990).

CHAPTER 3 SEASONAL ABUNDANCE AND DISTRIBUTION OF TSSM INFESTING COMMERCIAL HOPS IN TASMANIA

3.1. INTRODUCTION

Since early times, hops have been regarded as an important Tasmanian industry (Wade, 1988). Sixty per cent of annual hop production in Australia comes from Tasmania (Anonymous, 1988). Sutton (1982) reported that an estimated six percent loss in yield in the 1959/60 and 1978/79 growing season was due to the infestation of TSSM. Later, Cao (1989) showed that the damage caused by TSSM feeding on untreated hop plants, considering that losses up to 30 percent in 1987/88 and 10 percent in 1988/89 occurred in yield and associated deterioration in quality was also detected.

TSSM was already a pest in Tasmania before the turn of the Century since it was described as being a problem in the north-west and north-east regions of the state by Thompson in 1895 (Terauds, 1989). Control of TSSM has become increasingly difficult because mites have developed resistance to most commercially available pesticides (Herne et al., 1979). The detrimental effects of pesticides on the populations of natural enemies in commercial hop yards also appeared to be partially responsible for the increased populations of TSSM. This disruption in ecosystems along with the confirmation of pesticide resistance in TSSM has undoubtedly accelerated the search for alternative control methods.

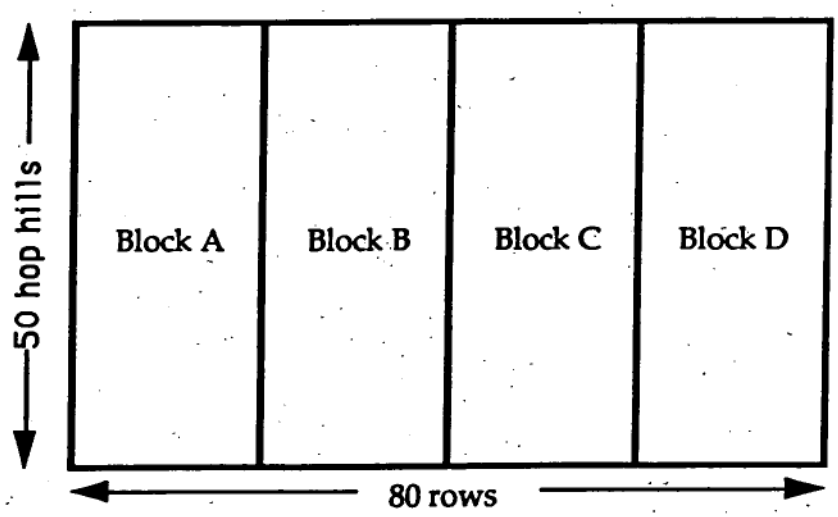
The first task of the research on TSSM was to learn about the field characteristics of this species and to understand the conditions that lead to high populations. A thorough knowledge of pest population dynamics and distribution patterns is necessary for improving control strategies in a pest management system. Several factors may have seasonal effects on

spider mite populations, including climatic factors, host plant quality, and agricultural practices. Consequently, the purpose of this study was to investigate the impact of host plant and seasonal factors on the dynamics and distribution patterns of TSSM populations on field hops.

3.2. MATERIALS AND METHODS

3.2.1. The study area: Field investigations were conducted in a 2.2 ha commercial hop yard at Bushy Park, Tasmania during the growing seasons of 1990/91, 1991/92, and 1992/93. An experimental plot was established in the middle of this hop yard which is surrounded by improved pasture for sheep grazing. The plot, which consisted of 80 rows of about 50 hop plants at a plant spacing of 1.8 x 1.8 m., was divided into approximately equal parts designated block A, B, C, and D (Fig. 3.1). Hop vines were trained on strings supported from an overhead trellis. There were three strings to each hill and the trellis was approximately 5 m. in height. The variety "Pride of Ringwood" was grown on the entire area under sprinkler irrigation. Maximum and minimum temperatures and precipitation recorded for the area during the investigation were obtained from the Australian Bureau of Meterology, Hobart, Tasmania.

Fig. 3.1. The layout of the experimental plot at Bushy Park.



3.2.2. Growing season 1990/91: The investigation commenced on November 21, 1990 and ended on March 7, 1991. The miticides, Apollo SC (clofentezine) and Omite 300W (propargite), were applied in blocks A and B in mid-January but blocks C and D were not sprayed throughout the study period. Therefore, blocks B and C became boundary areas for the treated and untreated areas. Hence, this naturally infested area could be divided into four levels of mite incidence, viz. very low mite attack (Block A), low mite attack (Block B), high mite attack (Block C), and very high mite attack (Block D).

Different sampling techniques were used for three different growth periods of the plants. Firstly, before the plants grew more than 2 m. above the ground, one mainstem leaf was collected from the middle region of each plant (Plate 2). Secondly, after the plants grew more than 2 m. above the ground, two mainstem leaves were collected at a height of 1.8 m. from each plant (Plate 3). Since 1.8-m leaves could be reached by hand from the ground, they were chosen as the sampling unit. A similar technique was used by Wright et al. (1990) for *Phorodon humuli* (Schrank) on hops. Sampling was undertaken weekly and the plants were selected randomly. A total of 10 plants was sampled from each block on each occasion. Finally, in the harvesting period, the influence of plant heights was investigated. Four leaves from each of 4 hop plants in Block D were sampled from the mainstems at: 0-2, 2-3, and 3-5 m. above the ground.

Samples from each plant were placed into a plastic bag and stored under cool conditions before examination. Leaves were inspected using a binocular microscope at 10-fold magnification. Microscopic observations provided more information on the distribution, habits and interactions of the leaf fauna than leaf brushing technique (Henderson and McBurnie, 1943; Readshaw, 1975).

Plate 2. Hop plants in the experimental plot during the early part of the growing season.

Plate 3. Hop plants in the experimental plot during the later part of the growing season.

Numbers of TSSM in various stages were counted and recorded separately from predators and other arthropods. Variation in the mite populations was monitored weekly for 16 weeks and was then compared with degree-days and mite-days calculated by the following formulae:

$$\text{Degree-days (DD.)} = \frac{\text{Maximum temperature} + \text{Minimum temperature}}{2} - \text{Threshold temperature} \quad \text{(Arnold, 1960)}$$

$$\text{Mite-days (MD.)} = \text{Average number of mites per leaf between 2 successive sampling dates} \times \text{Interval in days between samples} \quad \text{(Jones, 1990)}$$

where the threshold temperature of TSSM was taken as 10°C (Herbert, 1981).

Measurements of plant height were taken to monitor the growth of hop plants on every sampling date. In addition, the effect of mite attack on foliage under various levels of mite population as mentioned previously was assessed using leaf areas and dry weights of 20 leaves per block on the last five sampling occasions.

A planimeter (Paton Electronic Planimeter) was used to measure the surface area of leaf samples collected on February 7, 13, 21, 27 and March 7, 1991. For dry weights, all the hop leaves collected were placed in a 70°C drying oven following examination and area measurement (after Peters and Berry, 1980). Two days later, the dried leaves were removed and weighed on an Mettler PC4400 eletrical balance (Delta Range).

3.2.3. Growing season 1991/92: The investigation was conducted from November 14, 1991 to March 5, 1992. All of the blocks were treated by conventional chemical control. The miticides were applied in Blocks A, B, and C in mid-January and in Block D in early February. Leaves were collected randomly every 14 days, using the same procedure as in the 1990/91 season. In addition, leaf samples were collected at three heights:

0.9, 1.8, and 3.6 m, and the differences between the growth rates of leaves at the 3 positions were studied. The leaf surface areas obtained by using the planimeter as well as the dry weights were estimated over the whole season.

3.2.4. Growing season 1992/93: The investigations were conducted from November 4, 1992 to February 24, 1993. All of the blocks were sprayed with miticides by late December. Materials and methods were as employed in 1991/92 season, except that no leaves were sampled at the height of 3.6 m., and leaf surface areas were measured using a linear regression model that estimated area from measures of leaf length and width at the widest point. Furthermore, one mainstem leaf was also collected from the fourth node of each plant before the plants grew more than 2 m. above the ground.

In addition to the field investigation, the study on the effect of hop plants after spraying the miticides on TSSM populations was also carried out in Blocks A and D. On February 10 and 24, seven randomly selected hop plants in each block were infested with five teneral females per plant. These mites were confined to the dorsal surface of a mainstem leaf at the height of 1.8 m. using a clip-on cage of 2.0 cm in diameter. Two weeks after release, the cages (including the leaves) were removed from the plants and the number of mites of all stages were counted under a binocular microscope (20X).

3.2.5. Data analyses: Data were analysed using Staview SE + Graphics software on Macintosh computer. Taylor's power law was used to select the appropriate transformation of data by plotting log variance against log mean. Base 10 logarithms were used for the transformation of data for computation of the variance and mean. Linear regressions were performed using the curve fit procedure of the Cricketgraph computer

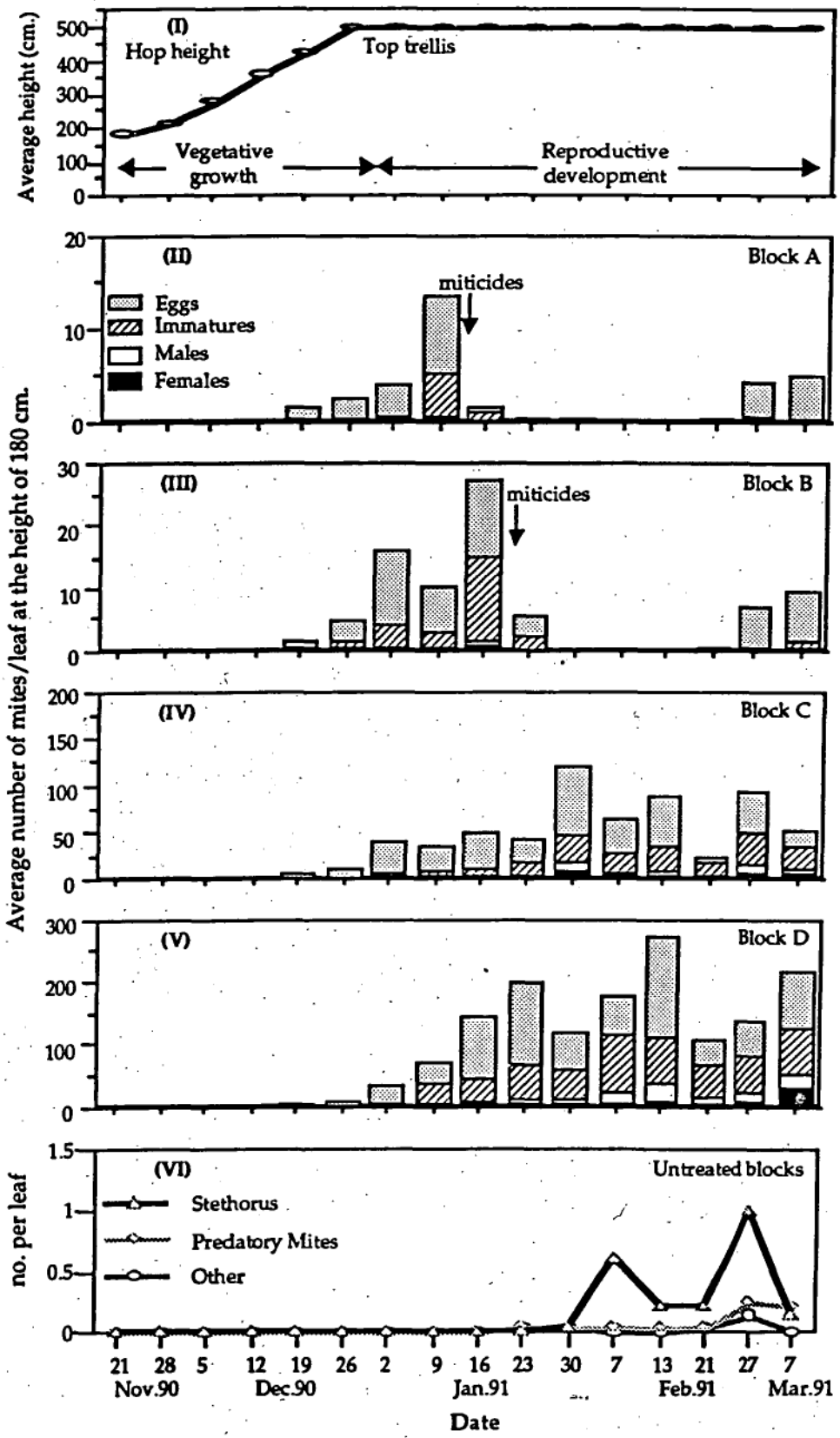
program. The two dispersion indices used to measure mite spatial distributions were the variance-to-mean ratio and Green's coefficient, C_x.

3.3. RESULTS

3.3.1. Seasonal abundance

3.3.1.1. Growing season 1990/91: As the majority of hop plants in the experimental plot had grown more than 2m. above the ground at the commencement of sampling, there were no leaves collected from the middle region of hop plants during this growing season. Fig. 3.2 illustrates the growth of hop plants relative to seasonal population trends of TSSM in various stages and other arthropods on 1.8-m mainstem leaves. The hops grew to the top of the trellis and started forming visible bases of inflorescences by the end of December (Fig. 3.2(I)). At this time, naturally occurring populations of TSSM in Blocks A and B were still at low levels, i.e. less than 10 mites of all stages per leaf (Fig. 3.2(II) and (III)). In early January, the TSSM populations reached as high as 13.5 and 26.8 mites/leaf for Blocks A and B, respectively. Miticides were then applied on one occasion for TSSM control in both blocks in mid-January. This spray appeared to eliminate TSSM from hops in the treated blocks. Consequently, no mites were found on the leaf samples for approximately 4 weeks, after which low level infestation was recorded in late summer and early autumn. This indicated that the mite population was suppressed after spraying, but began to increase again when the residual activity of the miticides disappeared. For Blocks C and D, TSSM populations showed a gradual build-up in early summer and then increased rapidly during the subsequent period (Fig. 3.2(IV) and (V)). However, Block D had consistently larger populations of mites than Block C during this period. The initial peaks in these blocks occurred when most of the hops were beyond the vegetative growth period.

Fig. 3.2. Average heights of hop plants in the experimental plot (I). Population trends of TSSM and other arthropods (II, III, IV, V, and VI) during the 1990/91 growing season.



During the period from late January to mid-February, TSSM on 1.8-m mainstem leaves reached the highest peaks of 118 and 268 mites of all stages per leaf in Blocks C and D, respectively. The counts of mites in different stages on leaves collected from these untreated blocks indicated that pre-adult stages, that is eggs and immatures, made up the largest proportion of mite populations throughout the growing season. Nevertheless, eggs were the predominant stage for most of the season. For instance, the stage distribution of mite populations in Block D on December 26, 1990 in total number of mites per leaf was 6.17% adults and 93.83% eggs while no immatures were found on the leaves sampled. However, as plant age increased the percentage of eggs relative to the other stages decreased. In this instance, the stage distribution of mite populations at the highest peak (February 13, 1991) was 13.65% adults, 27.19% immatures, and 59.16% eggs and on the final sampling date (March 7, 1991) the proportions of adults, immatures and eggs were 24.63, 34.26, and 41.11%, respectively. It indicated that the deterioration of host plants at suitability with time resulted in the reduction of female fecundities. In addition, the adult females observed in the early autumn started to change from the green summer form to the bright-orange overwintering form, also indicating a termination of egg laying.

Stethorus species, predatory mites and other arthropod populations were commonly found at low levels in the 1.8-m leaf samples of the untreated plot (Fig. 3.2(VI)). The average numbers of predators never exceeded 2 individuals per leaf throughout the study period. Obviously, predator densities were low in comparison to their prey and did not respond as well to prey density changes. *Stethorus* spp were the most common predators, followed by phytoseiid mites. Other arthropods found <u>in situ</u> included small spiders, native budworms

[*Helicoverpa punctigera* (Wall.)], looper caterpillars [*Euplexia nigerrima* (Guen.)], green aphids (*Myzus* spp.) and leaf hoppers (Fulgoridae).

Fig. 3.3 presents the proportion of all leaves containing a given total number of mites per leaf on each sampling occasion. To overcome the problem of the impact of miticides, only the data from Block D is shown. From this figure, it can be seen that all the leaves sampled in this block had 100 mites or less per leaf for the first seven sampling occasions, while at least 25% of all leaves were found to support over 100 mites from the eighth sampling occasion to the final (sixteen) occasion.

Fig. 3.3. Proportion of infested leaves at the height of 1.8m. in Block D during the 1990/91 season.

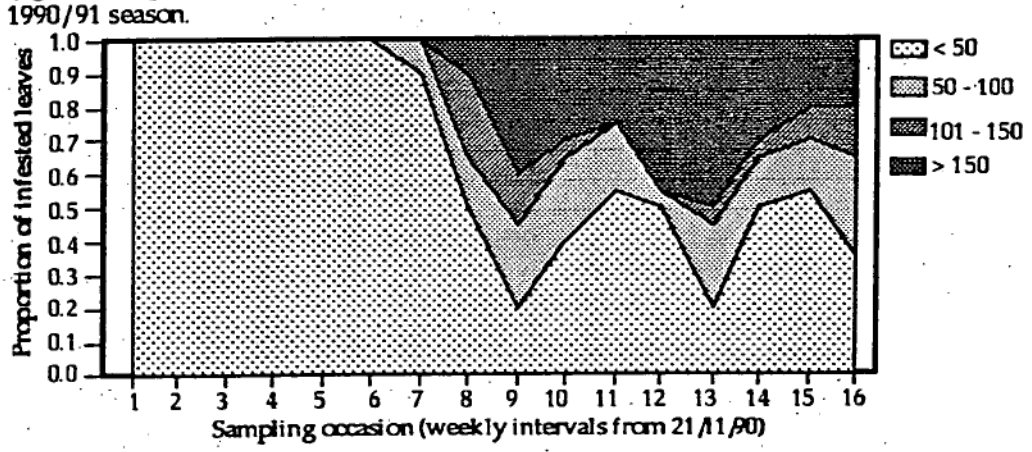
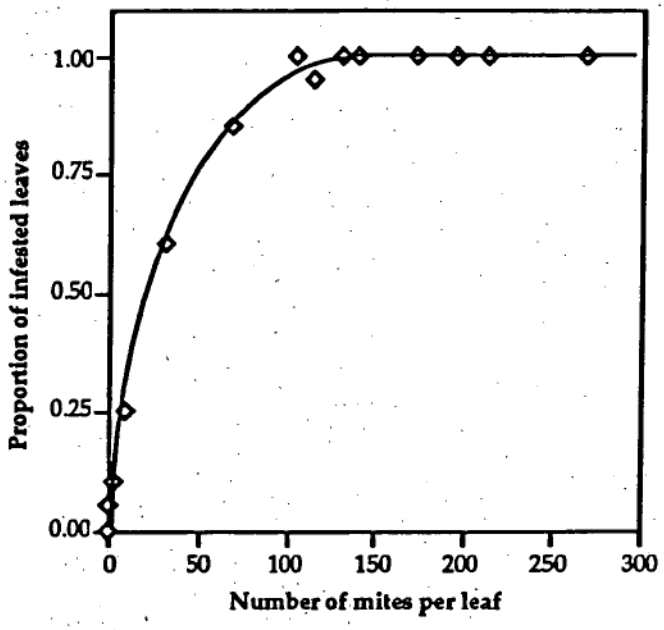


Fig. 3.4 shows a plot of the proportion of leaves infested against the mean number of mites per leaf. It was apparent that the proportion infested was closely related to the mean population level and that all the sample leaves could be infested with TSSM when the mean numbers of mites per leaf presented in Block D were more than 100.

Fig. 3.4. Relationship between proportion of infested leaves and mite density in block D during the 1990/91 season.



3.3.1.2. Growing season 1991/92: During the early season, a comparison of initial TSSM populations on the leaves collected in the middle region of plants between previously treated areas (Blocks A and B) and previously untreated areas (Blocks C and D) indicated that hops in untreated areas harboured more mites of all stages than did hops in treated areas. According to an unpaired t-test, significant differences ($p < 0.05$) in mite densities between these two areas were detected on the first two sampling dates (Table 3.1).

Table. 3.1. Mite densities in the middle region of hop plants in early 1991/92 growing season.

Area (n=20)	No. of mites/leaf		No. of mites/cm^2	
	14/11/91 (p=0.0474*)	28/11/91 (p=0.0335*)	14/11/91 (p=0.0459*)	28/11/91 (p=0.0343*)
Treated	0.00 ± 0.00	0.50 ± 0.50	0.000 ± 0.000	0.008 ± 0.008
Untreated	0.72 ± 0.36	73.98 ± 33.95	0.016 ± 0.008	1.428 ± 0.659

Changes in population density of TSSM and other arthropods on 1.8-m mainstem leaves in each block compared with the growth of hops throughout the season are illustrated in Fig. 3.5. During the vegetative growth period (Fig. 3.5(I)), much higher numbers of TSSM in each block were found on leaves in this growing season (Fig. 3.5(II), (III), (IV), and (V)) than those recorded at the corresponding time in the previous season. For example, on 26 December 1990 the mean numbers of total mites per leaf in Blocks A, B, C, and D were 2.4, 4.5, 10.1, and 8.1, respectively, whereas on the same date in 1991 total mites per leaf recorded were 3.1, 33.0, 511.5, and 445.5 for Blocks A, B, C, and D, respectively. From this figure, it can be seen that the mite populations in blocks C and D in this season were relatively high in comparison to the previous season, probably because of high numbers of overwintering mites in the untreated plot. The hops had reached the stage of reproductive development when the miticides were applied in blocks A, B, and C in mid-January, after which the mite populations were seriously depleted. However, the mite population in Block D continued to build up to a maximum of 1032 per leaf until miticides were reapplied approximately 2 weeks later. The average numbers of predators and other arthropods remained fairly low, ranging from 0.1 to 0.6 per leaf throughout the study period (Fig.3.5(VI)). Phytoseiid mites were the only mite predators found during the season.

When the average number of total mites per leaf at a height of 1.8 m. detected on December 12 and 26, 1991 and January 9, 1992, was regressed against those of adult females per leaf collected in the middle region of hop plants early in the season (November 28, 1991), highly significant linear regression lines were obtained (r^2 = 1.00, 0.471, and 0.907, respectively; Fig. 3.6). This indicated that infestations of TSSM on the upper part of hop plants found later in the season appeared to be related

Fig. 3.5. Average heights of hop plants in the experimental plot (I). Population trends of TSSM and other arthropods (II, III, IV, V, and VI) during the 1991/92 growing season.

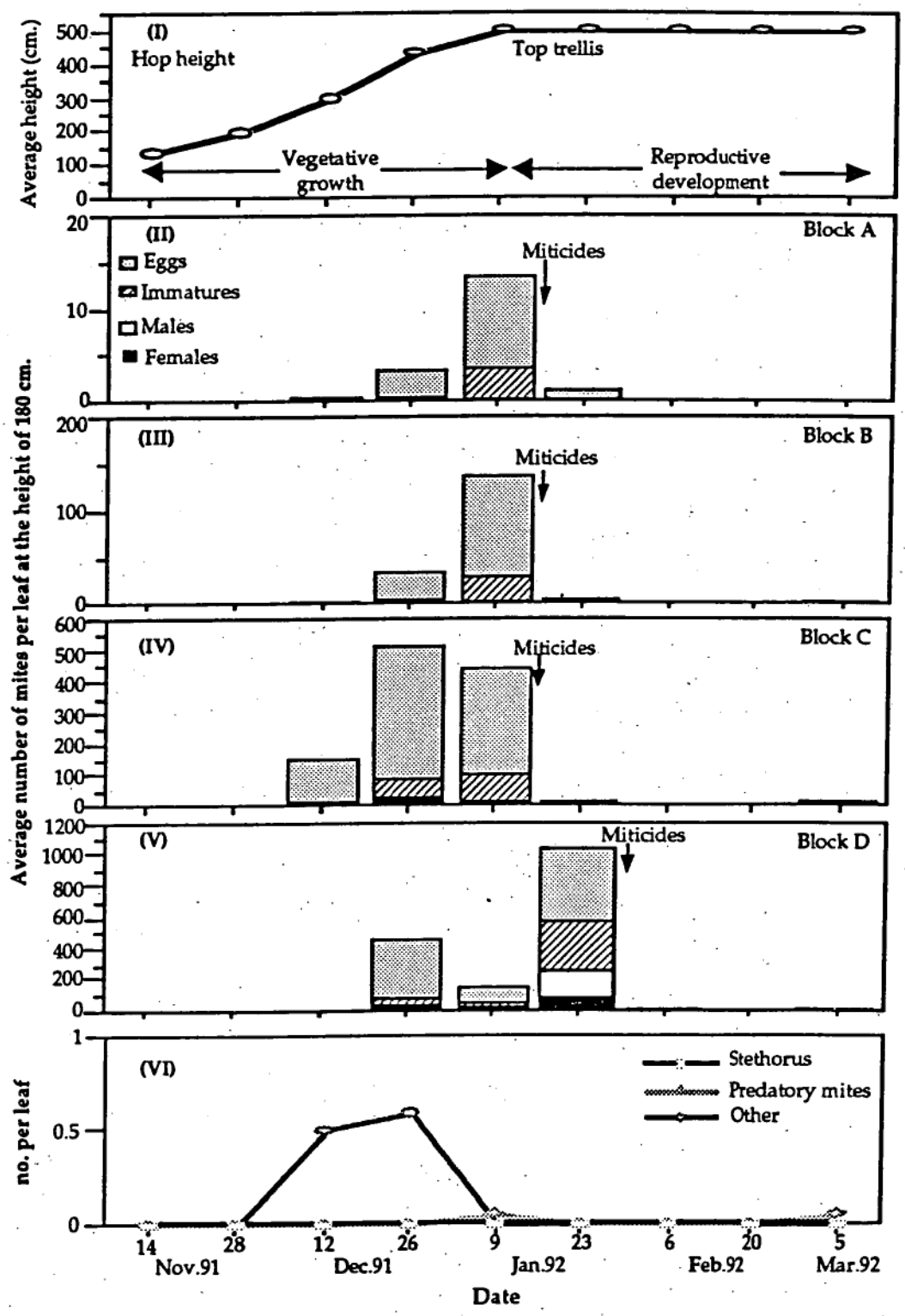
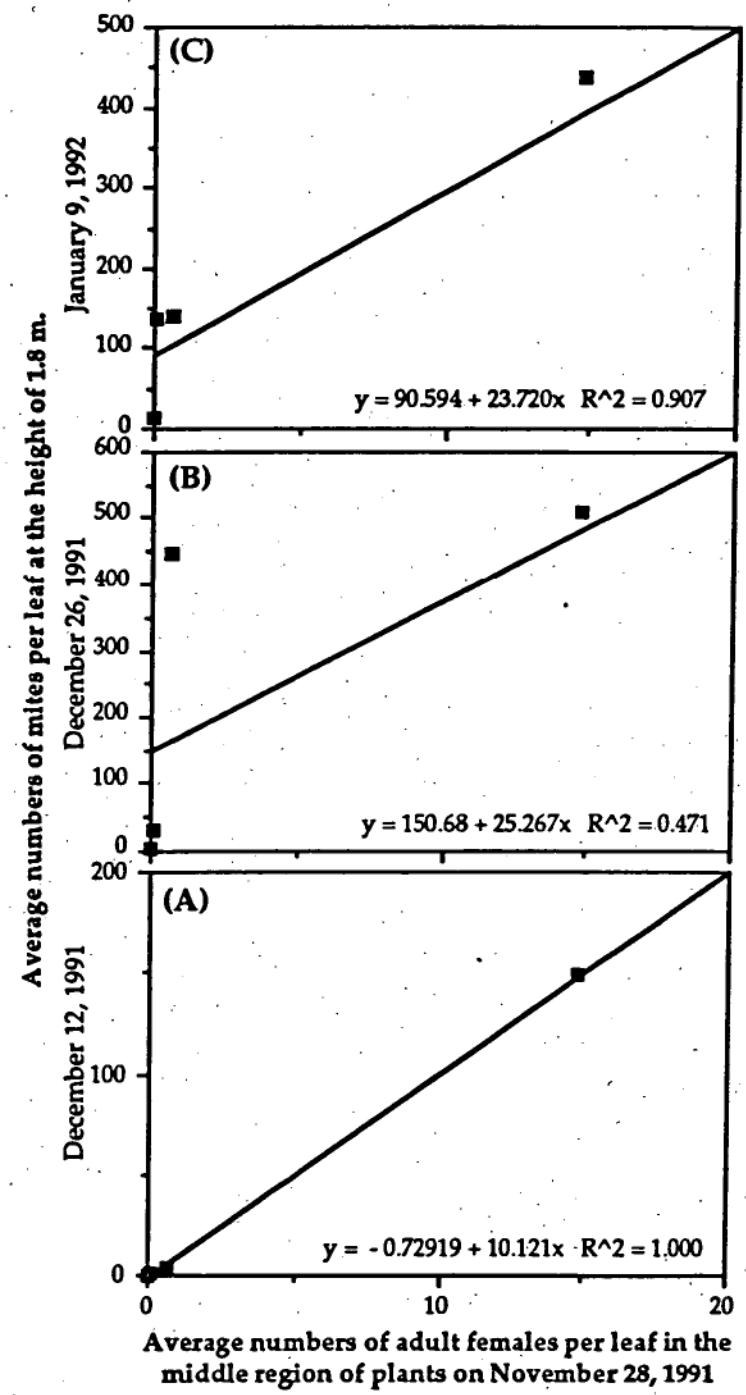


Fig. 3.6. Relationship between the average number of adult females per leaf in the middle region of the plant on 28 November and the average number of total mites per leaf at the height of 1.8 m. on (A) 12 December, (B) 26 December, and (C) 9 January for hops in different blocks during the 1991/92 season.



to the populations which initially infested the lower part. In addition, the results were confirmed by the highly significant positive relationship between the initial level of infestation in the middle region of hop plants and the percentage of 1.8-m. leaves infested on 12 December (r^2 = 0.955), 26 December (r^2 = 0.569), and 9 January (r^2 = 0.313) (Fig. 3.7).

3.3.1.3. Growing season 1992/93: The seasonal growth of hop plants and the abundance of TSSM and other arthropods on 1.8-m mainstem leaves is presented in Fig. 3.8. The pattern of mite population change in all blocks was similar (Fig. 3.8(II), (III), (IV), and (V)). Naturally-occurring populations of TSSM began to increase in early December. Eggs were the predominant stage during this period. The TSSM population density in each block was less than that recorded at the corresponding time in the 1991/92 season. This revealed that elimination of mites by miticides in the previous year resulted in low numbers of overwintering mites in the following year. After the hops grew to the top of the trellis (Fig. 3.8(I)), miticides were sprayed over the entire area. No TSSM were detected during the rest of the study period. The population densities of predators and other arthropods were recorded in extremely low numbers, ranging from 0.10 to 0.15 per leaf over the course of the season (Fig. 3.8(VI)).

In addition, a comparison of the number of mites in the cages after re-infestation between Blocks A and D is presented in Table 3.2. It was found that the mites released on February 10, 1993 were not able to survive in both blocks, whereas those infested on February 24, 1993 ranged from 11.43 to 5.57 individuals per cage in Block A and D, respectively. The results obtained in the field investigation during the time prior to miticide application indicate that the number of mites in Block A was much smaller than in Block D (Fig. 3.8). This revealed that after re-infestation the mite population on slightly damaged hop plants tended to increase faster than that on heavy damaged hop plants.

Fig. 3.7. Relationship between the percentage of infested leaves in the middle region of the plant on 28 November and the percentage of 1.8 m. mainstem leaves infested on (A) 12 December, (B) 26 December, and (C) 9 January for hops in different blocks during the 1991/92 season.

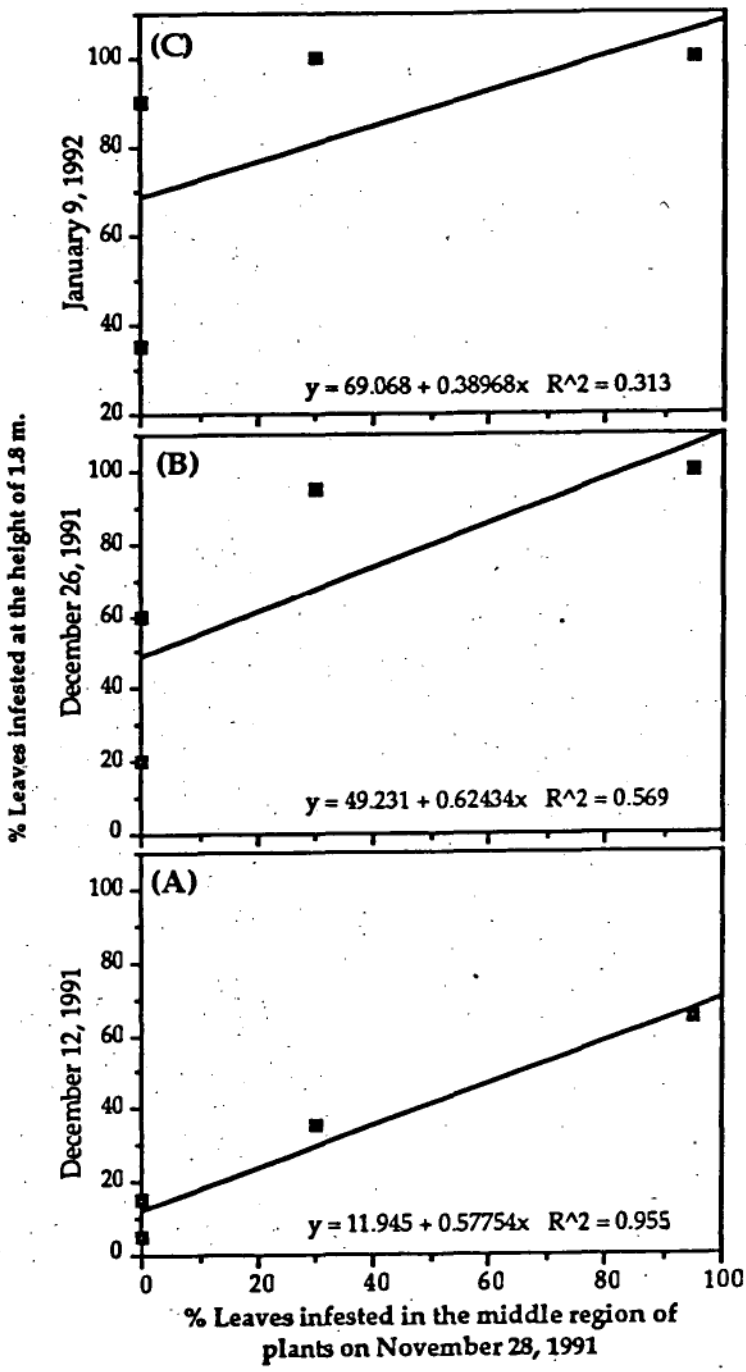


Fig. 3.8. Average heights of hop plants in the experimental plot (I). Population trends of TSSM and other arthropods (II, III, IV, V, and VI) during the 1992/93 growing season.

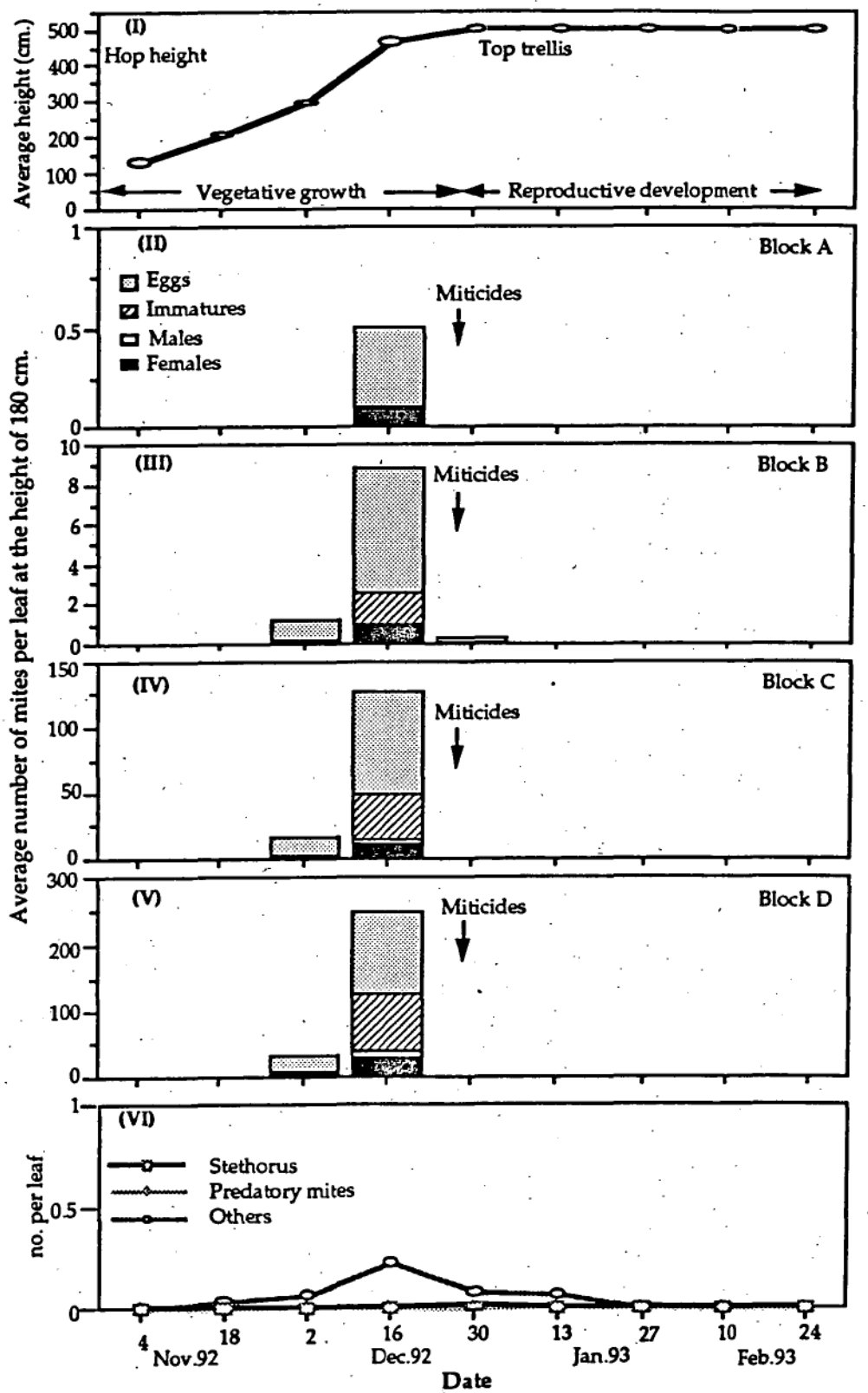


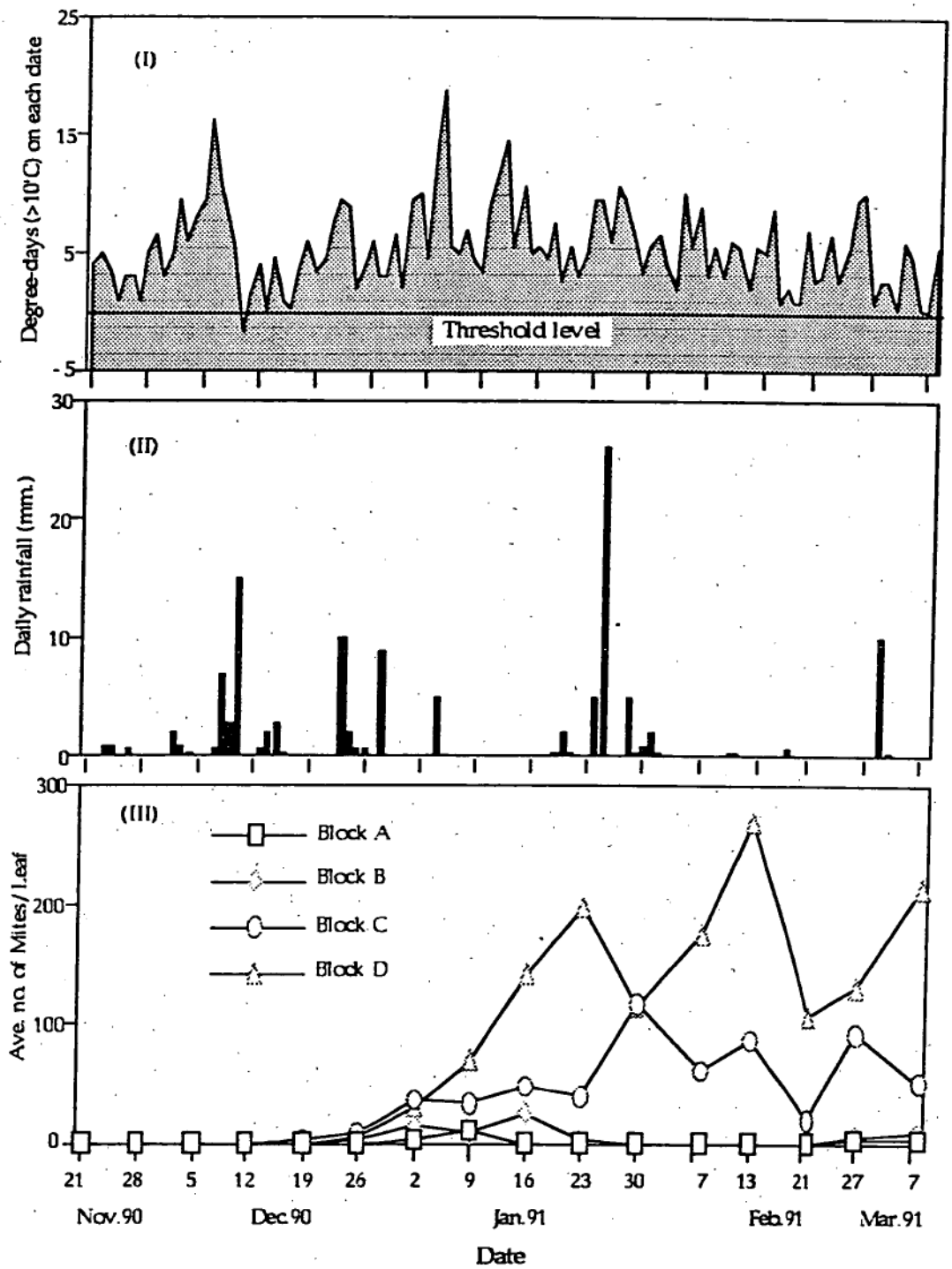
Table 3.2. Average number of mites in each cage after re-infestation on 10/2/93 and 24/2/93.

Block (n=7)	Average number of mites per cage (Mean ± SE)	
	Released on 10/2/93 (-)	Released on 24/2/93 (p=0.2467 ns)
A (slight damage)	-	11.429 ± 4.628
D (heavy damage)	-	5.571 ± 1.307

3.3.2. Climatic effects

3.3.2.1. Growing season 1990/91: The effects of heat sum and precipitation on TSSM infestation are shown in Fig. 3.9. On a degree-day basis, weekly fluctuations in mite populations for all blocks during the early part of the growing season (November 21, 1990 - January 16, 1991) gradually increased as the accumulation of heat units progressed (Fig. 3.9(I) and (III)). Abundant rainfall during this part of the season was probably responsible for the slow increases of TSSM populations (Fig. 3.9(II) and (III)). For the treated blocks, mite populations declined soon after spraying with miticides as mentioned previously, whereas the infestations of TSSM in the untreated blocks steadily increased during this time. A rapid population decline of TSSM on untreated hops, especially in Block D, occurred when the rains resumed in late January. The TSSM population in this block rebounded as the rains subsided. Thereafter, the infestations declined due to the relatively low temperatures in the latter part of the season. However, some increases in population levels were observed before harvest.

Fig. 3.9. TSSM population performance relative to temperatures and precipitation during the 1990/91 growing season.



3.3.2.2. Growing season 1991/92: Fig. 3.10 shows the daily changes in degree-days and rainfall relative to the growth and decline of TSSM populations at biweekly intervals. Because of the effect of miticide as mentioned above, only Block D was used for observations. A rapid population decline in Block D was observed on 9 January 1992 possibly due to continuous rains during early January (Fig. 3.10 (II) and (III)). Afterwards, the mite populaton in this block increased to a maximun level because of high degree-days and the absence of rain during mid-January (Fig. 3.10 (I), (II) and (III)).

3.3.2.3. Growing season 1992/93: The daily changes in degree-days and rainfall as well as the biweekly changes of the TSSM population in each block are shown in Fig. 3.11. Since miticides had been applied to all blocks before any observations were made, it was not possible to generalise on the effects of these two weather variables on the seasonal abundance of TSSM during this season.

3.3.3. Feeding damage

3.3.3.1. Growing season 1990/91: Mite-day accumulations obtained from active stages of TSSM per leaf in each block are presented in Table 3.3. From this table, it can be seen that the seasonal accumulation of mite-days was 59.85, 183.48, 1660.48 and 4541.56 in Blocks A, B, C, and D, respectively. In treated blocks (A and B), 6.42-13.83 and 86.19-93.56% of the total number mite-days were accumulated in the November-December and January-February periods, respectively, with the highest percentage (81.58-82.20%) occurring in January. In untreated blocks (C and D), 1.70-20.84 and 79.16-98.29% were accumulated in the November-December and January-February periods, respectively, with the highest percentage (55.19-57.60%) occurring in February.

Fig. 3.10. TSSM population performance in each block relative to temperature and precipitation during the 1991/92 growing season.

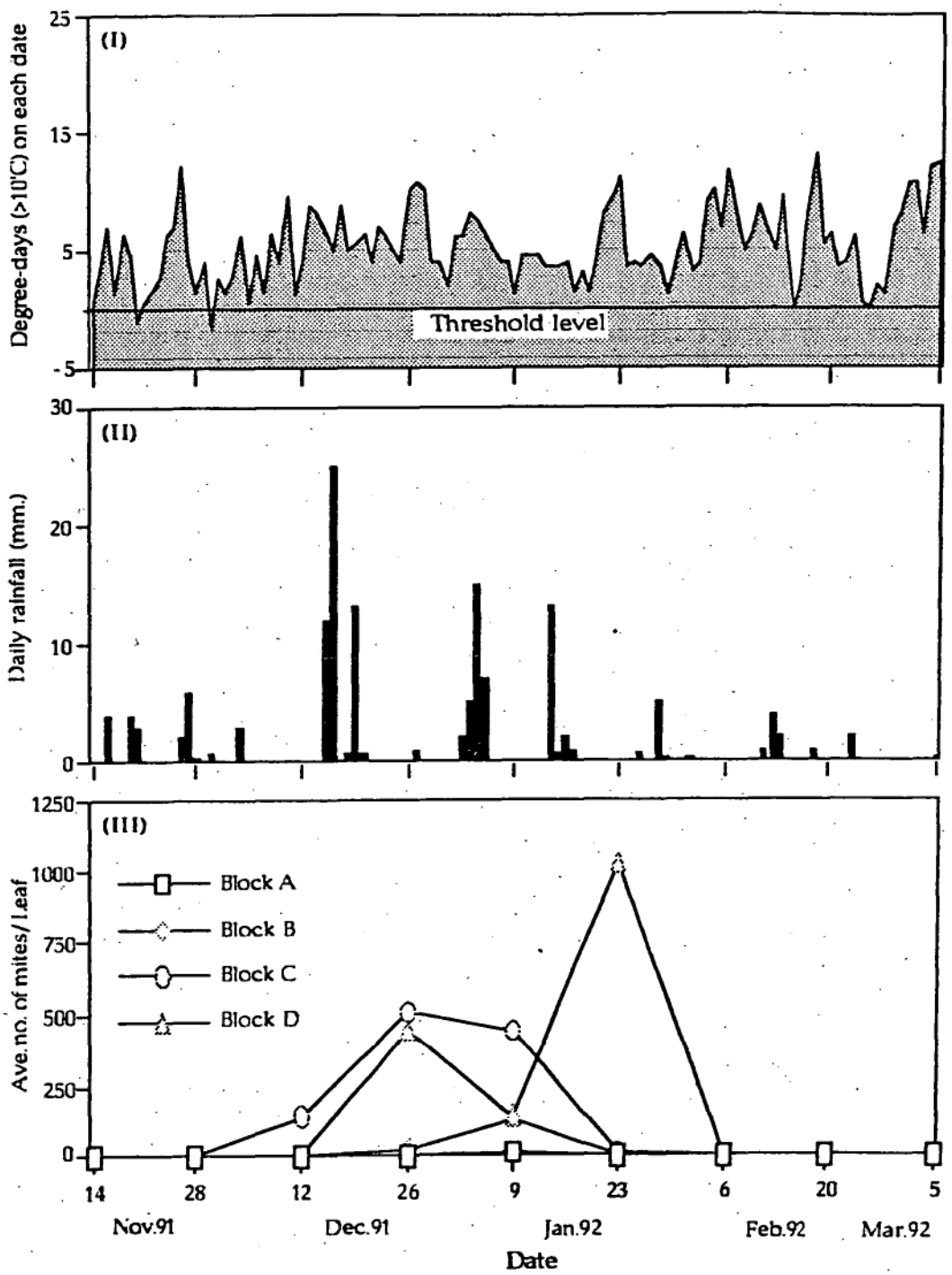


Fig. 3.11. TSSM population performance relative to temperatures and precipitation during the 1992/93 growing season.

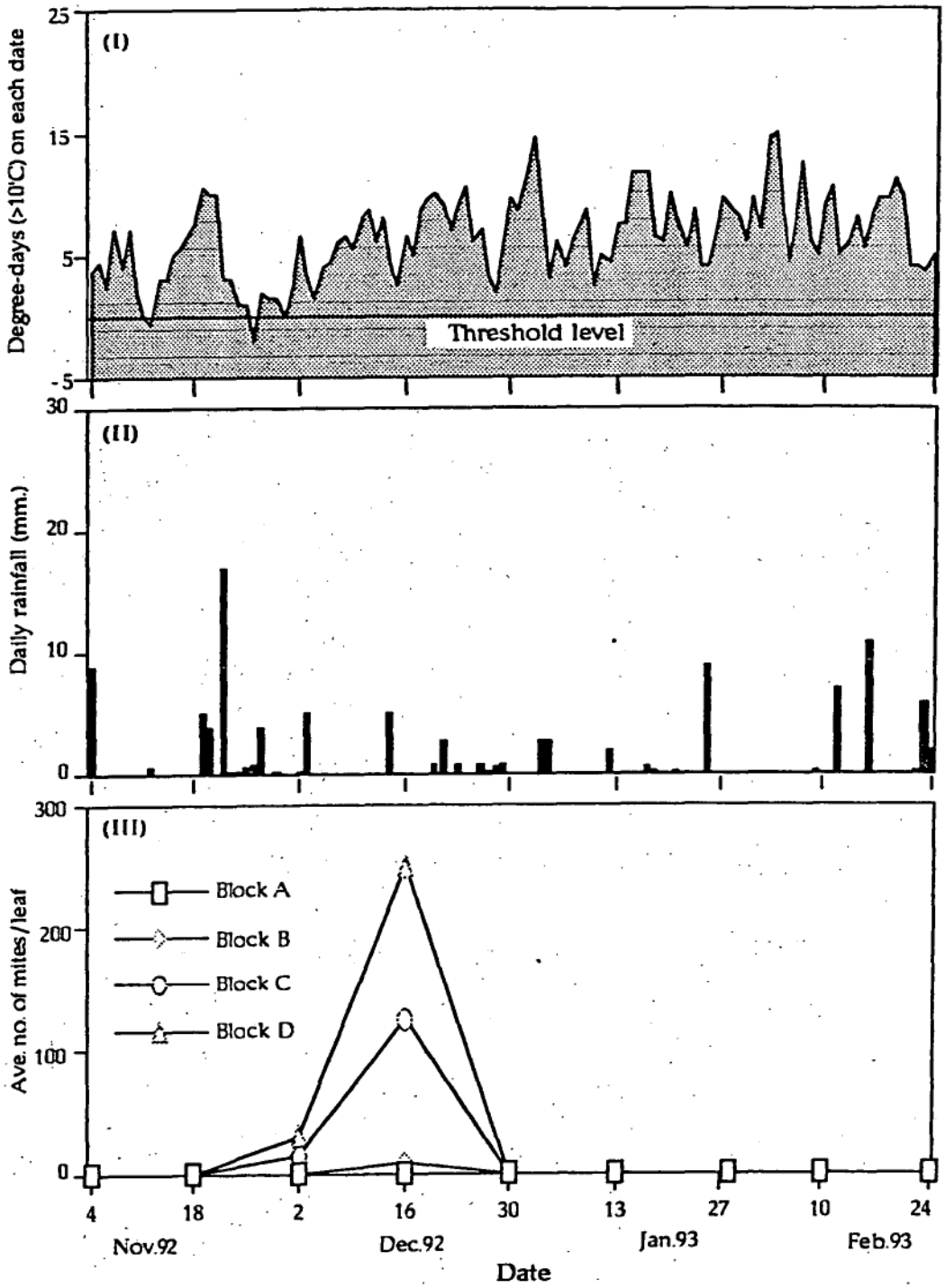
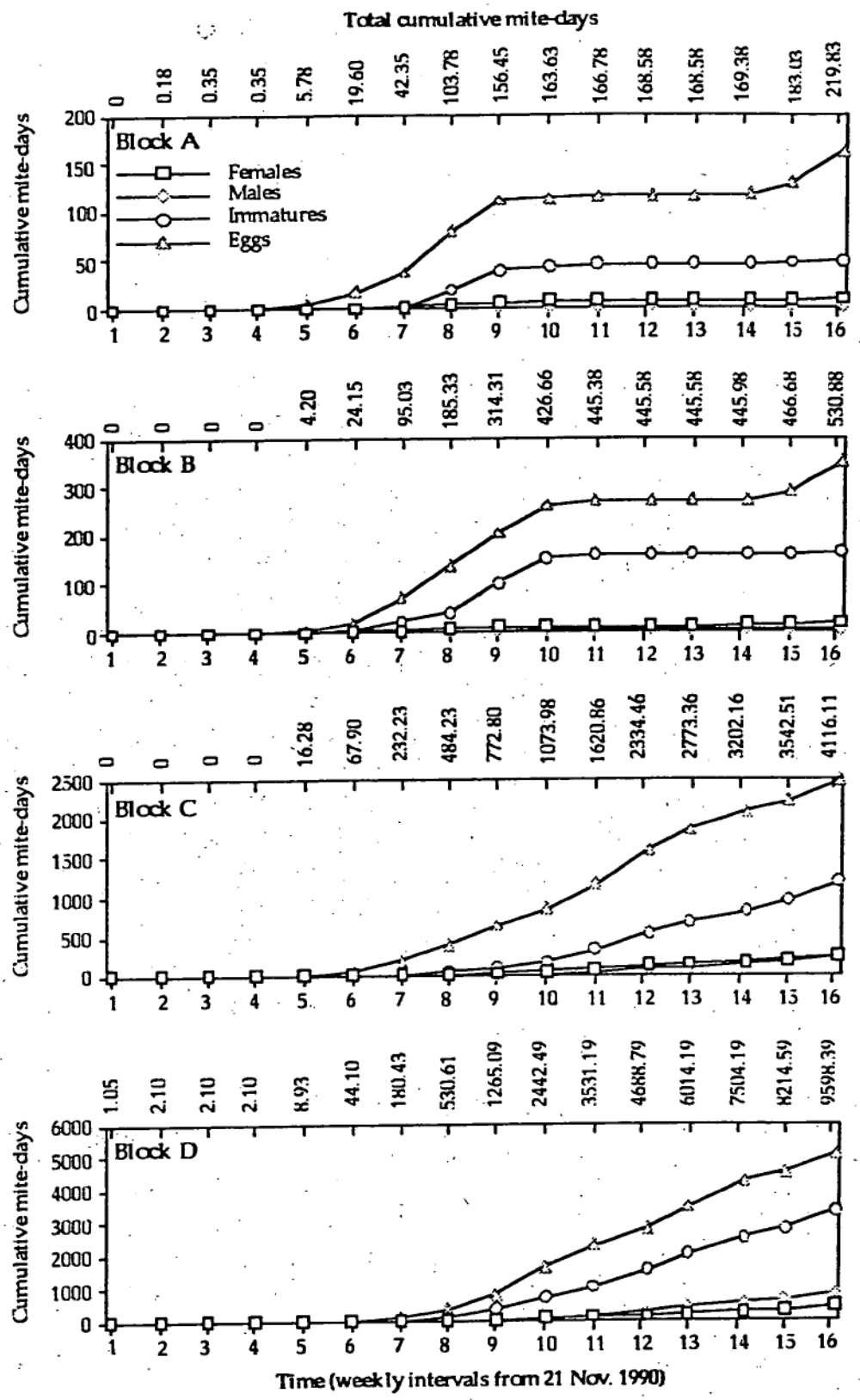


Table 3.3. Mite-day accumulations of TSSM at active stages during 1990/91 growing season.

Block	Cumulative mite-days of active stages per lea					No. miticide application
	November	December	January	February	Season	
Block A	0.36	3.50	49.21	6.80	59.85	1
Block B	0.00	25.38	149.46	8.45	183.48	1
Block C	0.00	28.36	715.78	916.35	1660.48	0
Block D	0.36	20.48	1904.58	2616.15	4541.56	0

The plots of cumulative mite-days at the various stages in time are presented in Fig. 3.12. Cumulative mite-days for the total population are also shown at the top of the graph. During the first six weeks of the study, the cumulative mite-days for the total mites in each block were less than 100. However, mite populations had increased to 219.83, 530.88, 4116.11, and 9598.39 mite days for Blocks A, B, C, and D, respectively, at the end of the study. From these values, the percentage of cumulative mite-days (percent) in treated blocks ranged from 65.44 to 72.77 for eggs, 22.38 to 30.68 for immatures, 0 to 2.3 for adult males and 3.45 to 4.85 for adult females. In the untreated blocks the percentage varied from 52.68 to 59.66 for eggs, 28.82 to 34.44 for immatures, 5.80 to 8.46 for males and 4.42 to 5.72 for females. Obviously, mite day accumulation levels for eggs were highest in all blocks, followed by immatures. Although mites at the adult stage were found at relatively low levels, the female adult was the dominant factor in population recovery from miticides of the mite population, and they continued to deposit eggs later. Adult male mites were at low to almost non-existent levels on treated hops, especially in Block A. Meanwhile, they were found to be relatively abundant several times in the untreated plot throughout the study period. Thus, the males were very sensitive to miticide and were not able to survive under chemical spraying.

Fig. 3.12. Seasonal accumulation of mite-days in each block during the 1990/91 growing season.



Relationships between mite-days per week obtained from the mean number of total mites per leaf and those obtained from the mean numbers of mites in various stages per leaf are shown in Fig. 3.13. There was a significant linear regression of the mite-days of total mites on that of females [$r^2 = 0.705$; Fig. 3.13(I)]. When the raw data was transformed by log (X+1), the coefficient of determination was increased to 0.874 [Fig. 3.14(I)]. Similar results were also obtained for the regression of the total mite-days on the mite-days of eggs with the coefficient of determination ranging from 0.945 to 0.988 for untransformed data [Fig. 3.13(IV)] and transformed data [Fig. 3.14(IV)], respectively. For males and immatures, the relationships between untransformed data, as shown in Fig. 3.13(II) and 3.13(III), were highly significant ($r^2 = 0.834$ and 0.954, respectively), as the coefficients of determination of transformed data were reduced {($r^2 = 0.671$) for males [Fig. 3.14(II)] and ($r^2 = 0.853$) for immatures [Fig. 3.14(III)]}. It was noted that females and eggs were the stages most commonly found in mite populations throughout the study period. This was confirmed by data points on the y-axis representing the relationships between transformed mite-days of total populations and those of females [Fig. 3.14(I)) and eggs (Fig. 3.14(II)] being fewer than the data points representing the relationships between the transformed mite-days of total populations and those of males [Fig. 3.14(III)] and immatures [Fig. 3.14(IV)]. However, eggs are not the destructive stage. For this reason, adult females could be the most appropiate group for estimating mite-days of total mite population.

Linear regression models describing the relationship between the numbers of all stages of mites and numbers of adult female mites for actual untransformed numbers of mites per leaf and mite-days per leaf had coefficients of determination (r^2) ranging from 0.498 to 0.813, respectively, as compared with the range of 0.606-0.924 for the

Fig. 3.13. Linear regressions of mite-days obtained from total numbers of mites (Y) on those obtained from numbers of mites in various stages (X) during the 1990/91 season.

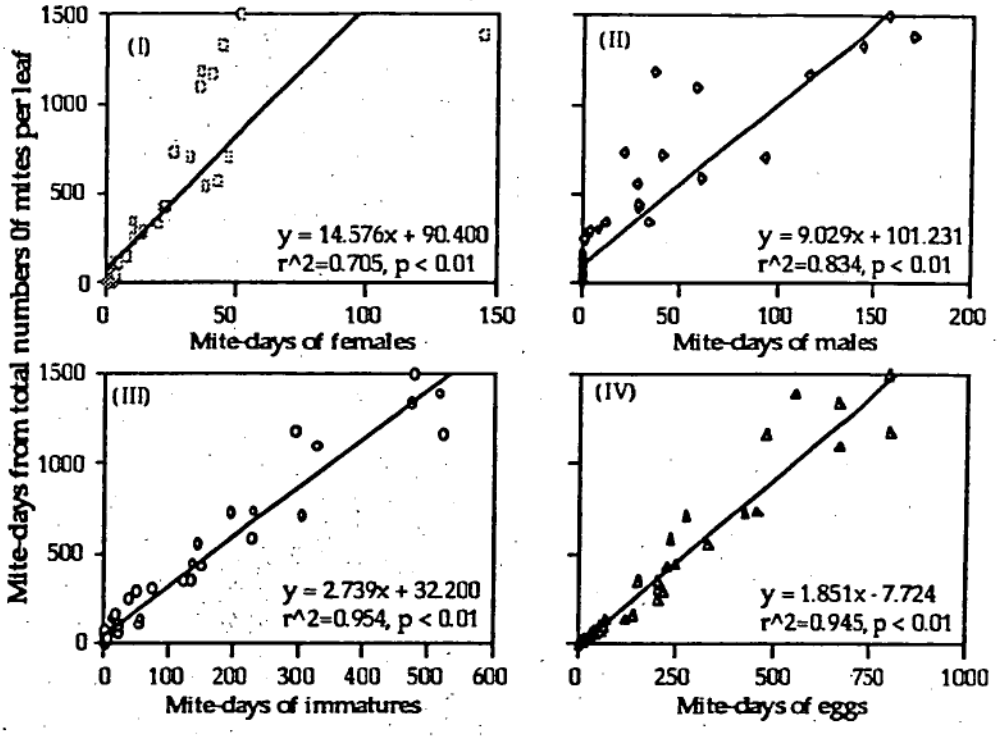
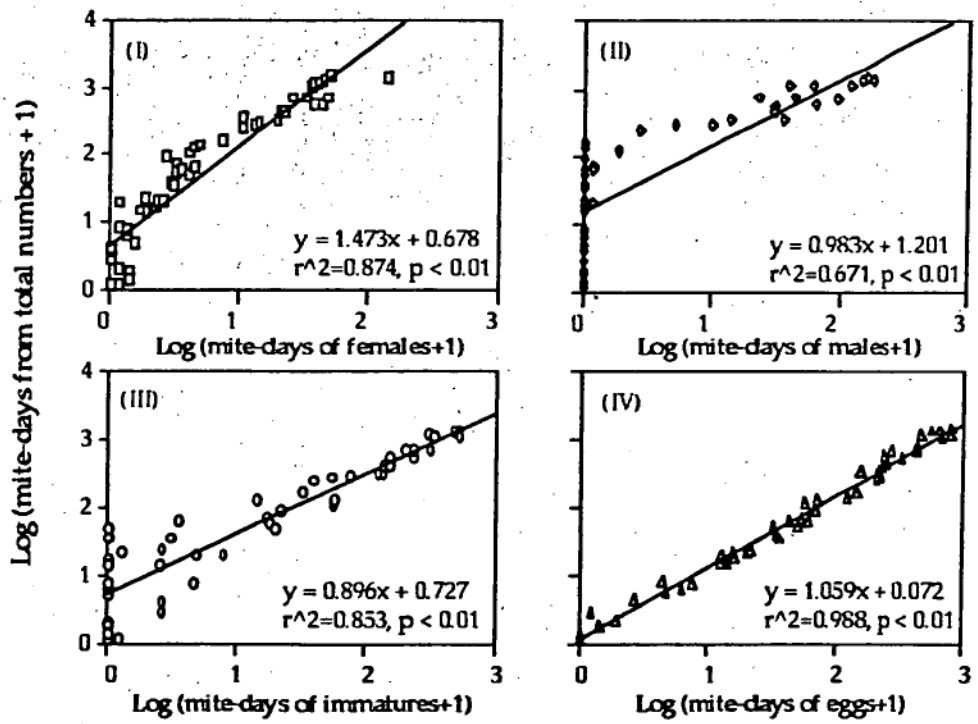


Fig. 3.14. Linear regressions of transformed mite-days obtained from total numbers of mites (Y) on those obtained from numbers of mites in various stages (X) during the 1990/91 season.



transformed data (Fig. 3.15 and 3.16). In addition, the relationships between numbers of adult females at time t and total mite numbers at time t+1 in terms of both actual untransformed numbers of mites per leaf per week and mite-days per week are presented in Fig. 3.17A and 3.18A, respectively. Each of the relationships were obtained from the data collected in Block D at weekly interval. The reason for using Block D was mentioned previously. Significant linear regressions were obtained between these variables (r^2 = 0.578 and 0.757 for actual numbers of mites and mite-days, respectively). When the data was transformed by log (X+1), the coefficients of determination for actual numbers of mites (Fig. 3.17B) and mite-days (Fig. 3.18B) were increased to 0.755 and 0.833, respectively. However, these coefficients decreased for the relationships between the adult females at time t and the total mites at time t+2, i.e. r^2 = 0.359, 0.675, 0.582, and 0.670 for actual numbers, mite-days, transformed actual numbers and transformed mite-days, respectively (Fig. 3.19 and 3.20). Hence, it would seem reasonable to use the numbers of adult female at time t as a predictor of total mite populations in future studies, particularly those at time t+1.

Highly significant differences in surface areas and dry weights of hop leaves among blocks with different levels of mite incidence were found ($p < 0.01$, Fig. 3.21). There were significant differences in mean surface areas and dry weights of foliage between the heavily attacked area (Block D) and treated areas, i.e. Blocks A and B ($p < 0.05$). The foliage from the moderate to highly attacked area (Block C), had a mean dry weight significantly lower than that from Block A only, whereas the surface area of the foliage was significantly smaller than that from Blocks A and B ($p < 0.05$). These results indicated foliage injury of hops with uncontrolled mite populations compared to hops on which nearly complete control of mites had been obtained.

Fig. 3.15. Linear regression of total numbers of mites per leaf at time t (Y) on numbers of females per leaf at time t (X).

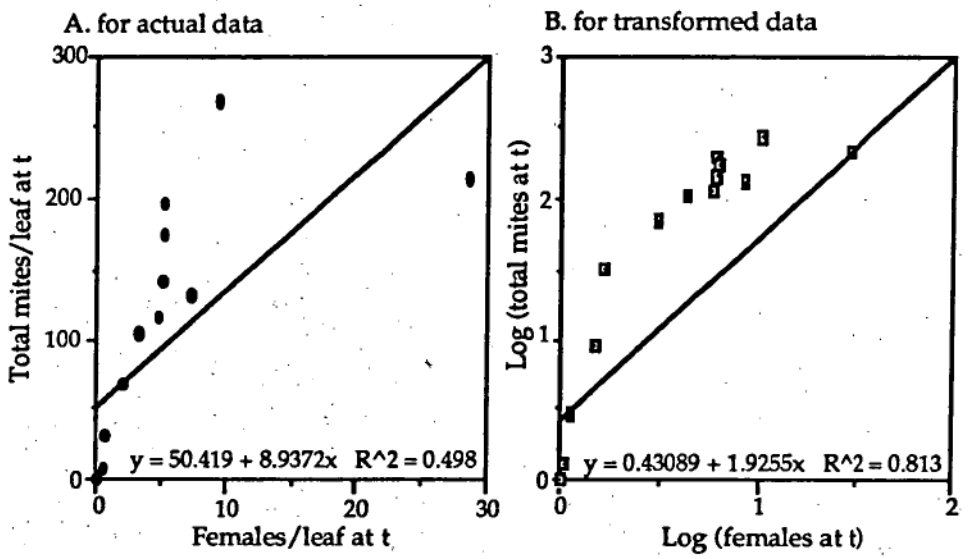


Fig. 3.16. Linear regression of mite-days obtained from total numbers of mites per leaf at time t (Y) on those obtained from numbers of females per leaf at time t (X).

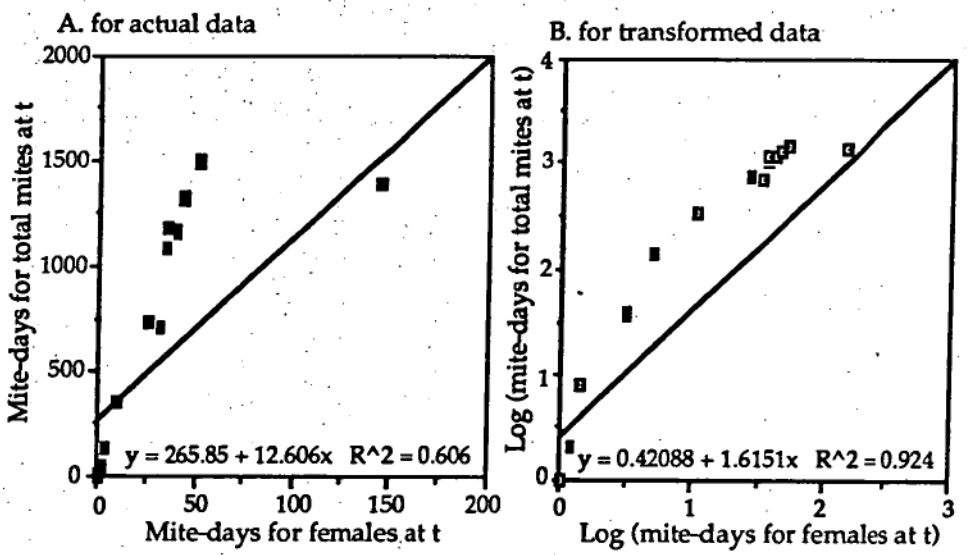


Fig. 3.17. Linear regression of total numbers of mites per leaf at time t+1 (Y) on numbers of females per leaf at time t (X).

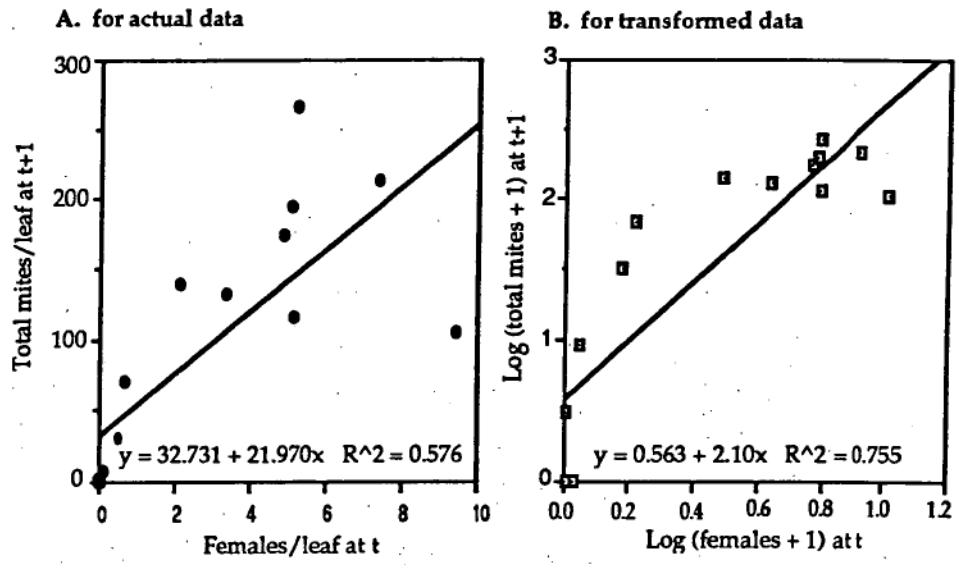


Fig. 3.18. Linear regression of mite-days obtained from total numbers of mites per leaf at time t+1 (Y) on those obtained from numbers of females per leaf at time t (X)

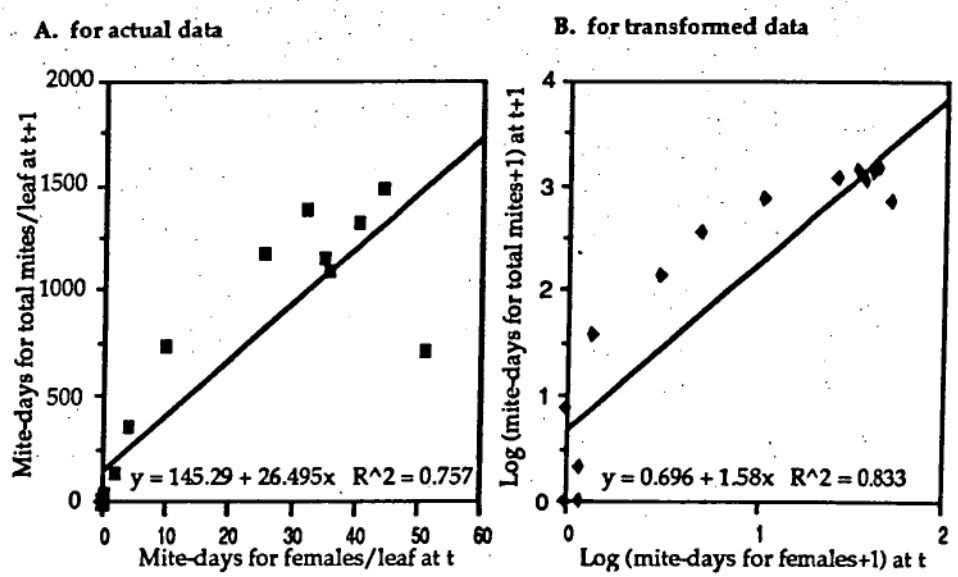


Fig. 3.19. Linear regression of total numbers of mites per leaf at time t+2 (Y) on numbers of females per leaf at time t (X).

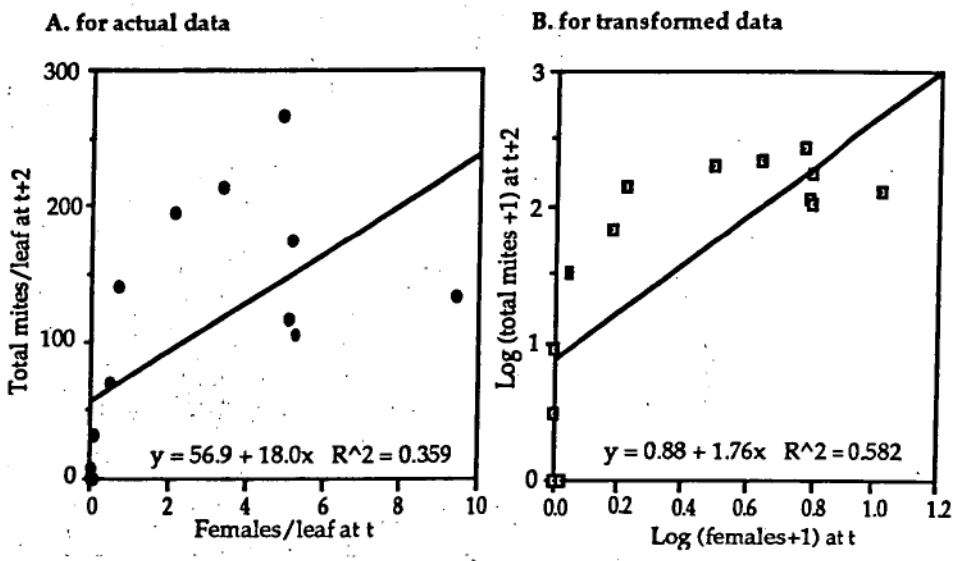


Fig. 3.20. Linear regression of mite-days obtained from total numbers of mites per leaf at time t+2 (Y) on those from numbers of females per leaf at time t (X).

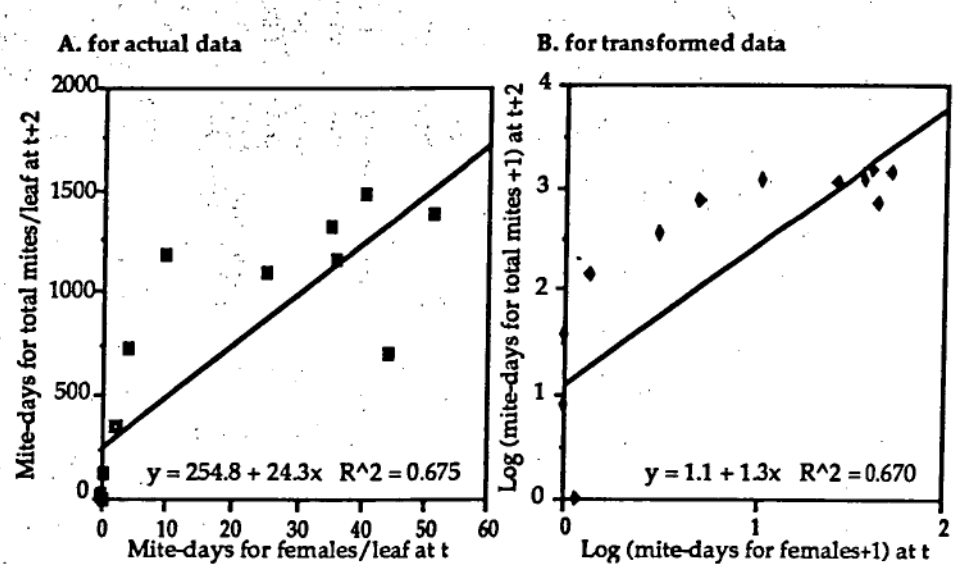
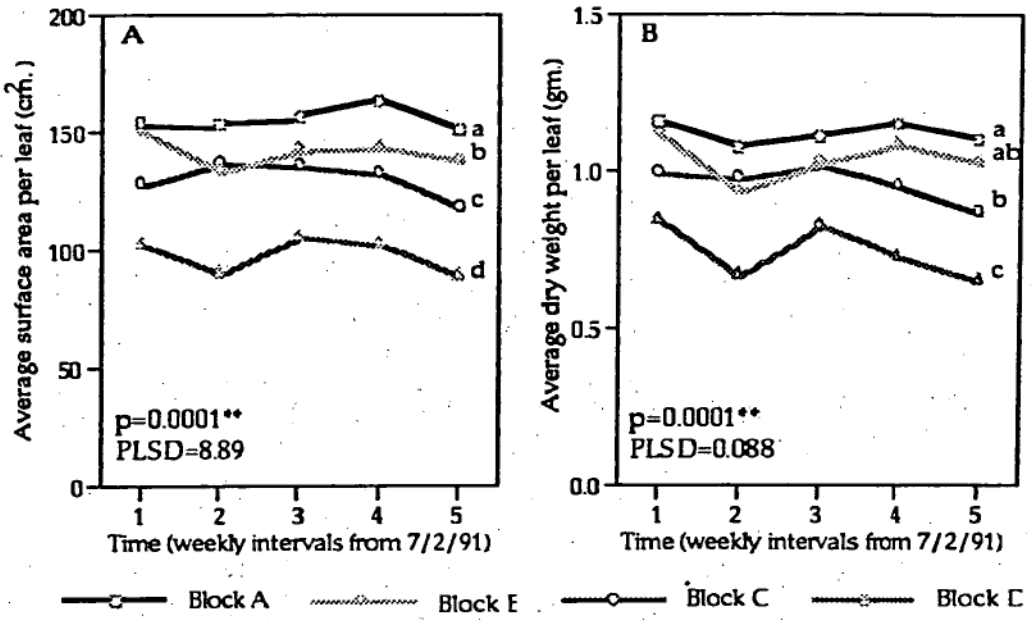
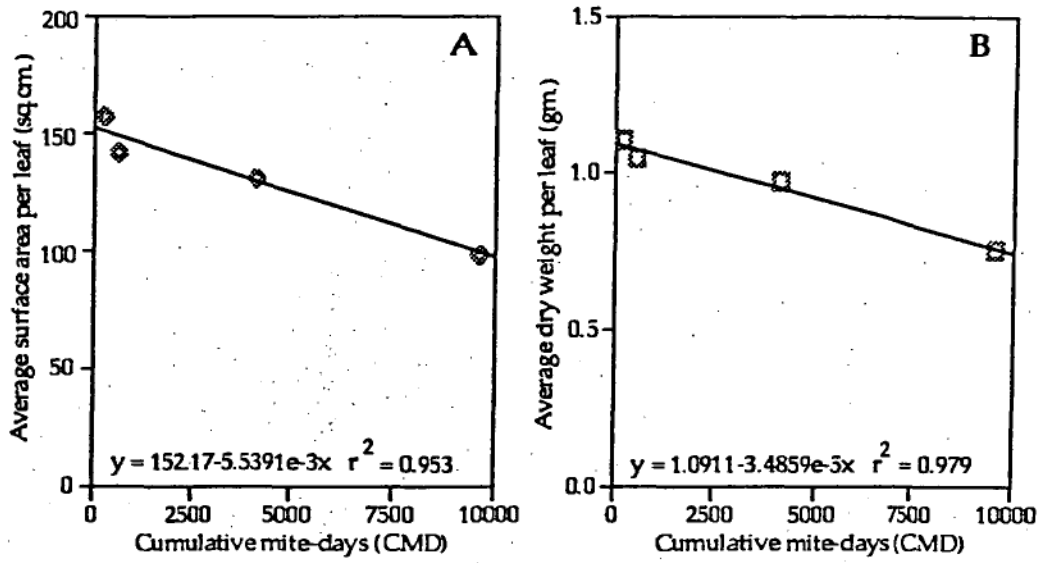


Fig. 3.21. Differences in average leaf area (A) and dry weight (B) of hops among blocks at various time intervals during the 1990/91 growing season. (Significance indicated by different letters).



The relationship between the average surface areas of foliage and the cumulative mite-days in each block, as shown in Fig. 3.22A, clearly indicates that the regression of leaf surface areas against cumulative mite-days was highly significant ($p < 0.01$). The blocks with high cumulative mite-days had smaller leaf surface areas than those with low cumulative mite-days. A similar result was also obtained for the dry weights of foliage (Fig. 3.22B).

Fig. 3.22. Linear regressions of surface areas and dry weights of leaves (Y) on cumulative mite-days in each block (X) during the 1990/91 growing season.



3.3.2 Growing season 1991/92 The seasonal accumulation of mite-days in each block is presented in Fig. 3.23. From this figure, it was found that the cumulative mite-days of total mite populations during this season were 241.50, 2431.80, 15590.15, and 22816.70 mite-days for Blocks A, B, C, and D, respectively. Eggs converted to mite-days ranged from 58.30 to 83.30% of total mite-days; immatures ranged from 13.60 to 23.80%; males ranged from 0.01 to 11.10%; and females ranged from 2.20 to 6.80%. Again, linear regressions of total mite populations on mites at each stage in terms of both actual mite-days and tranformed mite-days revealed that females and eggs were the stages most commonly found in the mite population (Fig. 3.24 and 3.25).

Fig. 3.23. Seasonal accumulation of mite-days in each block during the 1991/92 growing season.

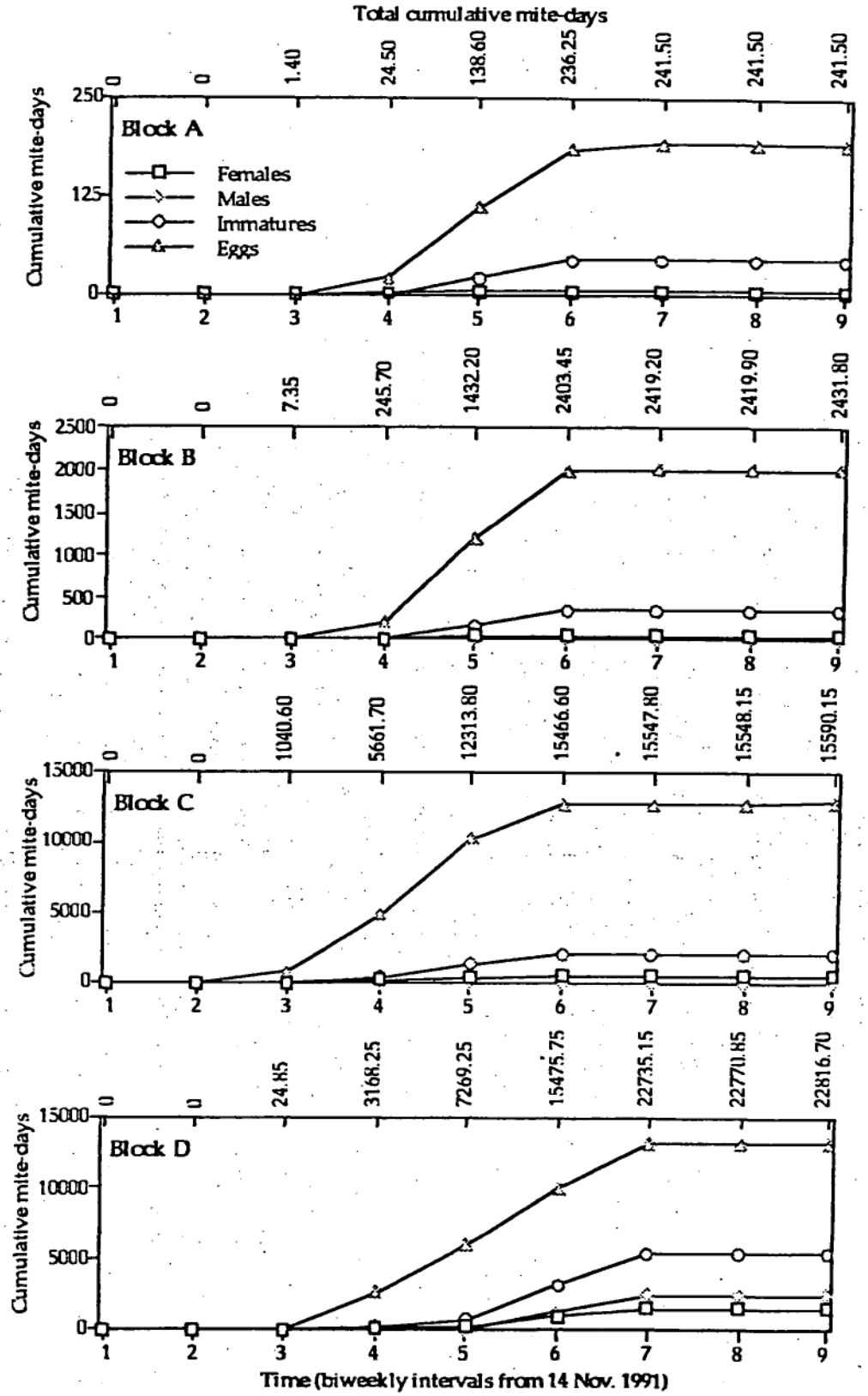


Fig. 3.24. Linear regressions of mite-days obtained from total numbers of mites (Y) on those obtained from numbers of mites in various stages (X) during the 1991/92 season.

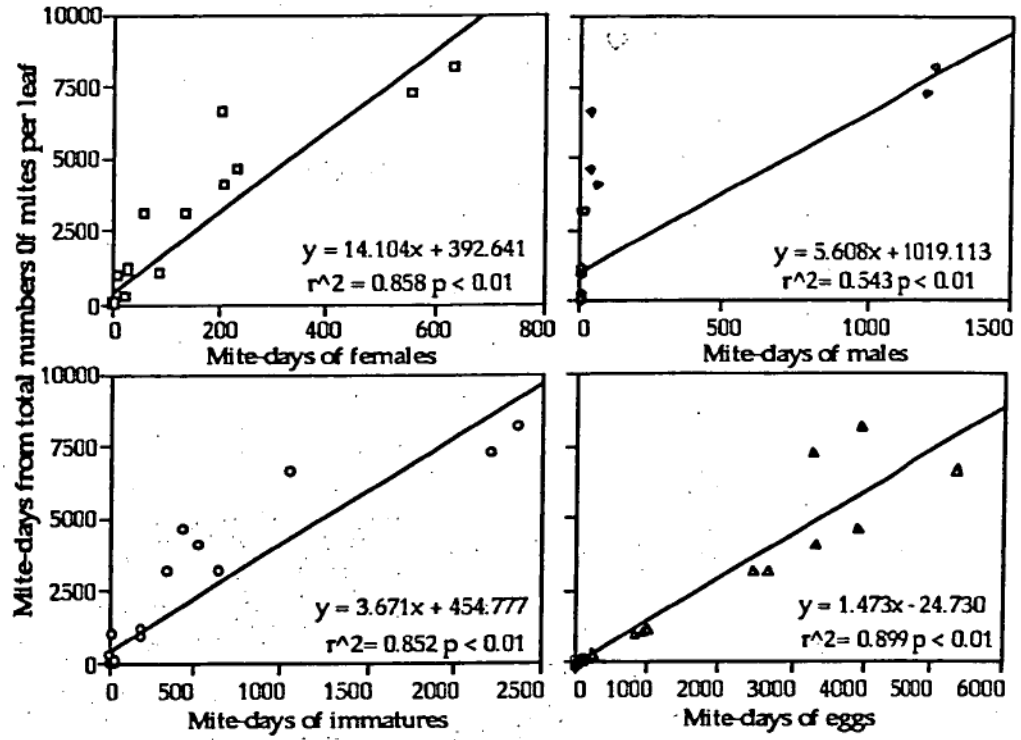
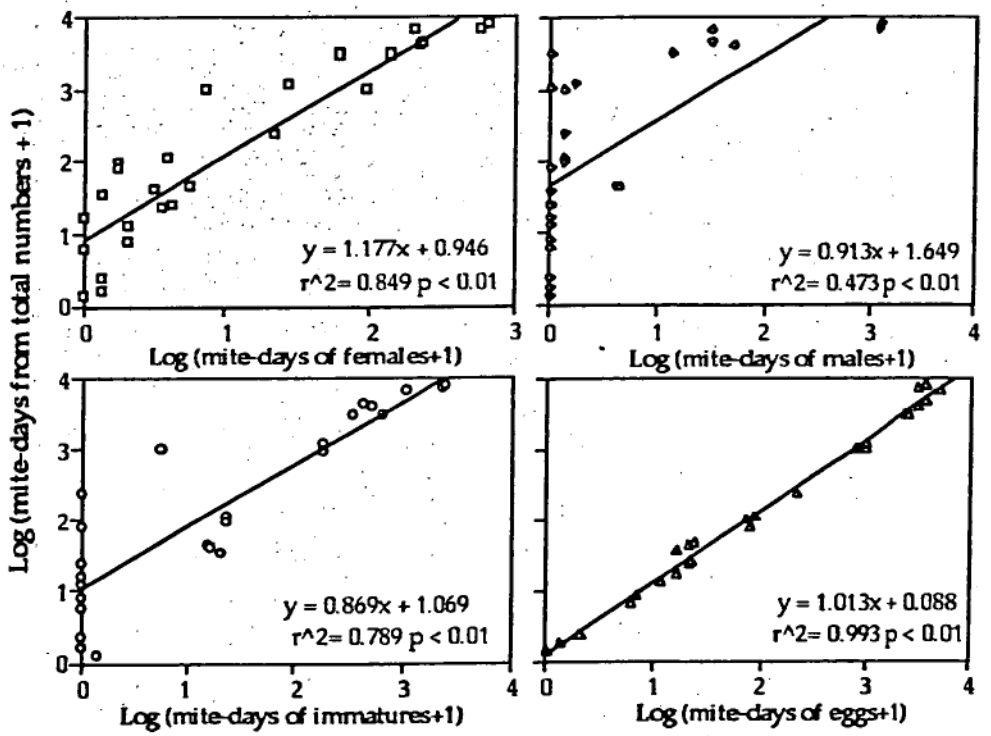


Fig. 3.25. Linear regressions of transformed mite-days obtained from total numbers of mites (Y) on those obtained from numbers of mites in various stages (X) during the 1991/92 season.



There were no significant differences in the surface areas and dry weights of leaves among blocks during this season (Fig. 3.26). The number of cumulative mite-days was again significantly related to the surface areas and dry weight of leaves (r^2 = 0.942 and 0.996, respectively; Fig. 3.27).

Fig. 3.26. Differences in average leaf area (A) and dry weight (B) of hops among blocks at various time intervals during the 1991/92 growing season.

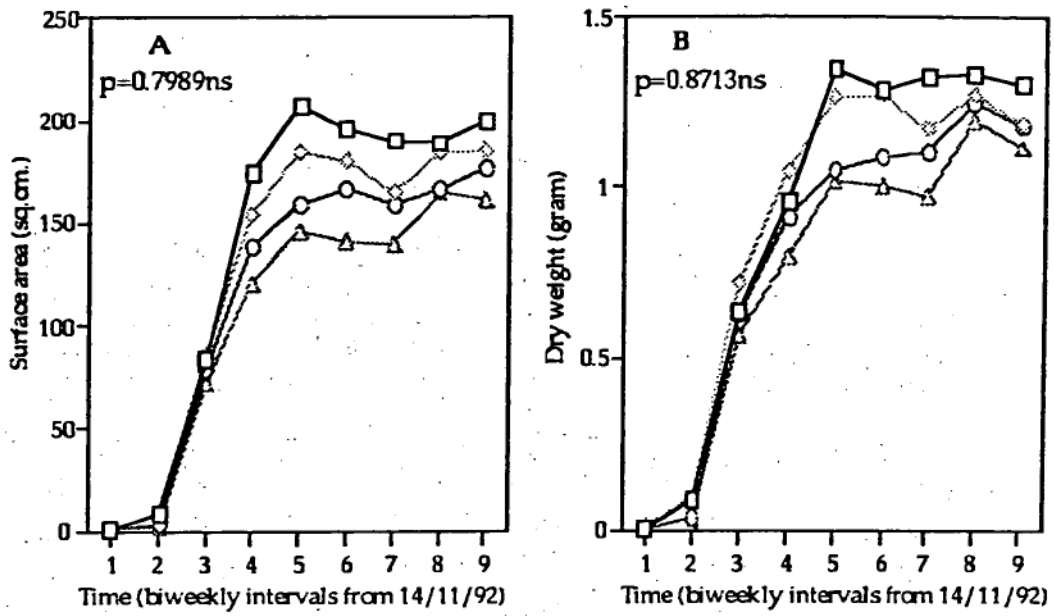
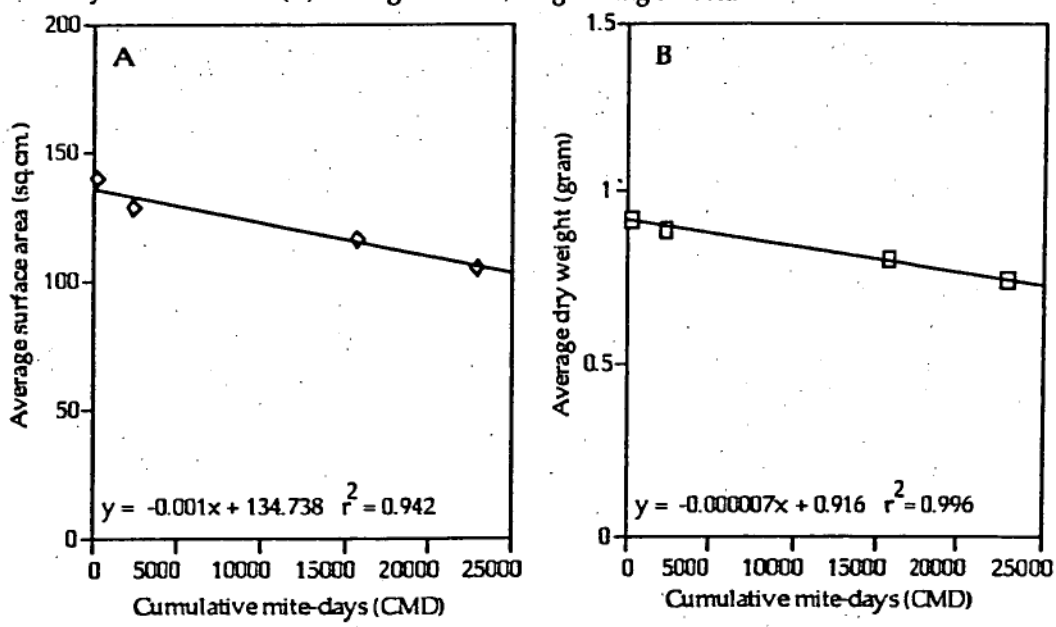


Fig. 3.27. Linear regressions of surface areas and dry weights of leaves (Y) on cumulative mite-days in each block (X) during the 1991/92 growing season.



3.3.3.3. Growing season 1992/93 The pattern of cumulative mite-days in all blocks was similar to that in the previous season (Fig. 3.28). Populations of all stages of TSSM in each block failed to develop after the miticide application and the mean population level stabilized over the remainder of the season. Regression analyses of total mite-days on mite-days for each stage were similar to those mentioned earlier (Fig. 3.29 and 3.30).

According to the leaf area data in the 1990/91 season, the product of leaf length and width at the widest point was found to correlate significantly with the surface area of leaves ($p < 0.01$; Fig. 3.31). A linear regression model was obtained and subsequently used to estimate leaf areas in this study.

Statistical analyses of the surface areas and dry weights of leaves collected from the fourth node of the plants during the early season revealed that average surface areas and dry weights of uninfested hop leaves did not differ significantly between blocks ($p \geq 0.05$; Fig. 3.32).

No significant differences in surface areas and dry weights of 1.8-m mainstem leaves among these blocks were detected when the data was pooled over the season (Fig. 3.33A and B). There was a significant linear regression of the surface areas and dry weights of leaves on the cumulative mite-days ($r^2 = 0.895$ and 0.738, respectively; Fig. 3.34).

Fig. 3.35 shows the cumulative mite-days recorded for each block over the 3-year study. In the first year, mite populations, the smallest being on treated hops in Block A and the largest on untreated hops in Block D, are clearly illustrated in this figure. The boundary areas, i.e. Block B and C, showed intermediate situations. In the second year, during the early part of the season mites accumulated most quickly in Block C followed by Block D. After miticides were applied, almost no increase in mite populations was observed in all blocks and especially in

Fig. 3.28. Seasonal accumulation of mite-days in each block during the 1992/93 growing season.

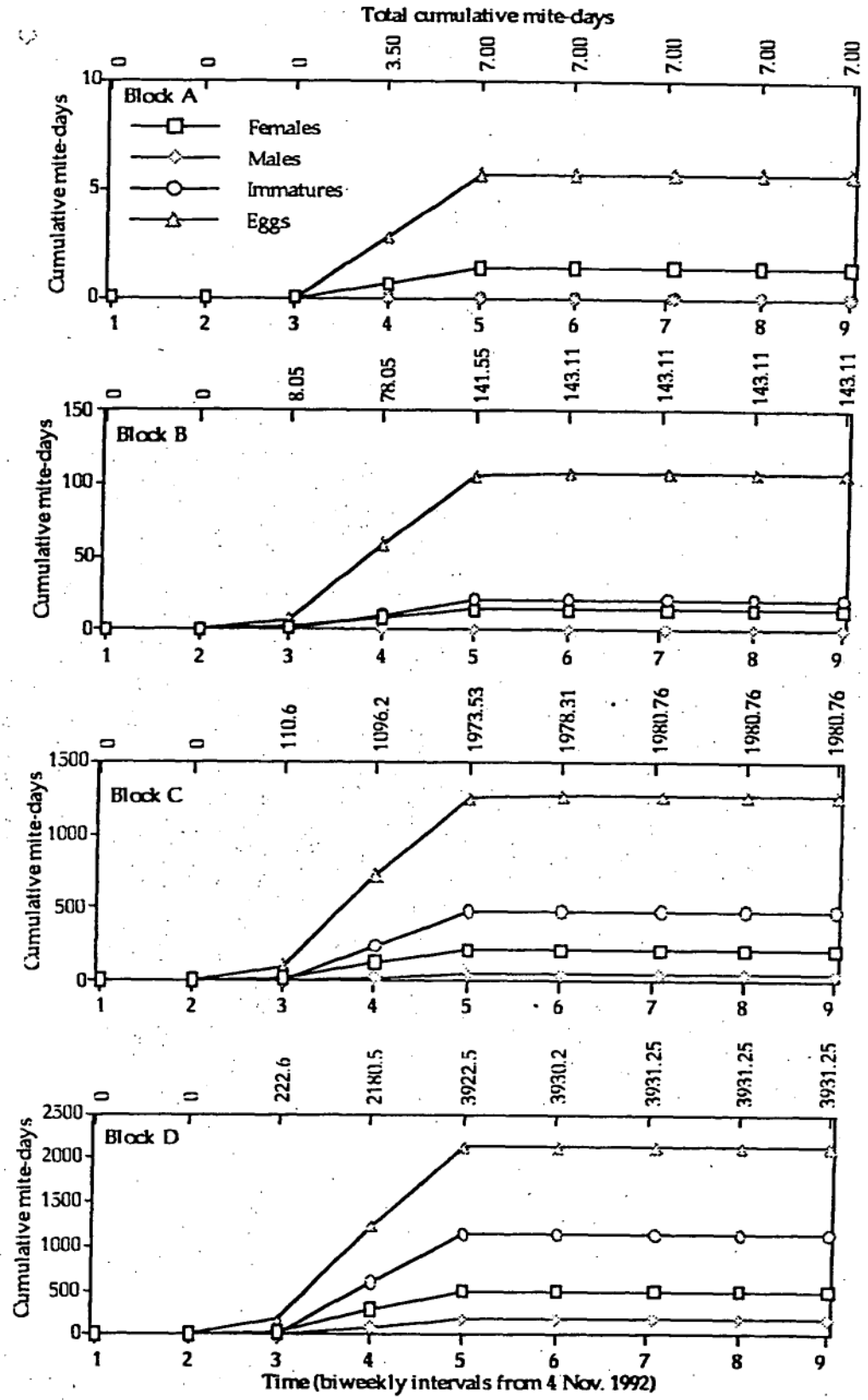


Fig. 3.29. Linear regressions of mite-days obtained from total numbers of mites (Y) on those obtained from numbers of mites in various stages (X) during the 1992/93 season.

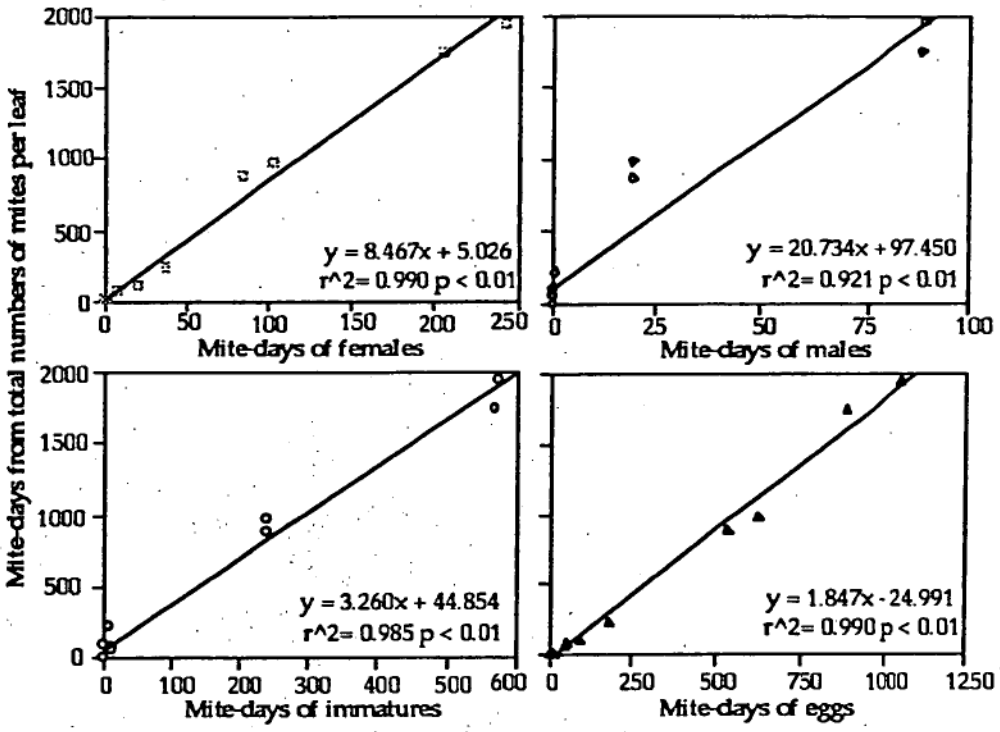


Fig. 3.30. Linear regressions of transformed mite-days obtained from total numbers of mites (Y) on those obtained from numbers of mites in various stages (X) during the 1992/93 season.

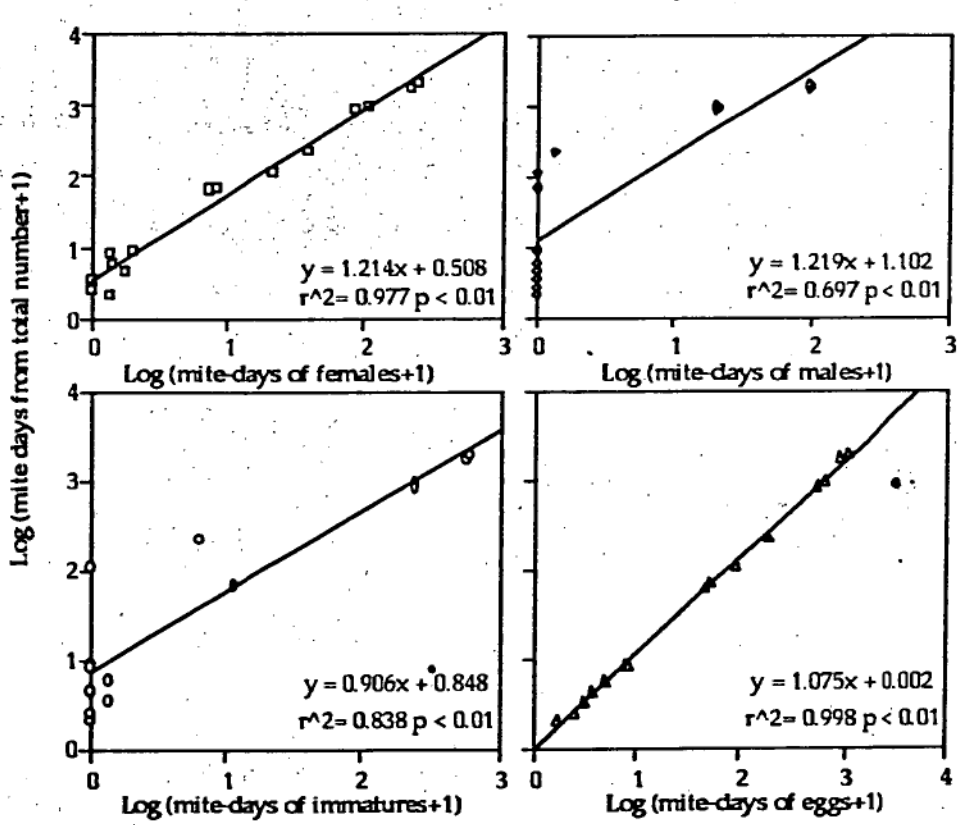


Fig. 3.31. Relationship between leaf area and the product of leaf length and width at the widest point.

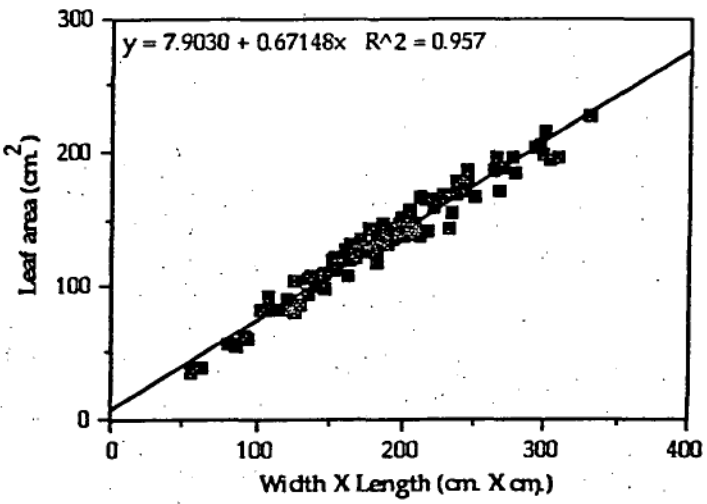


Fig. 3.32. Surface area and dry weight of leaves collected from the fourth node of hop mainstems during the 1992/93 growing season.

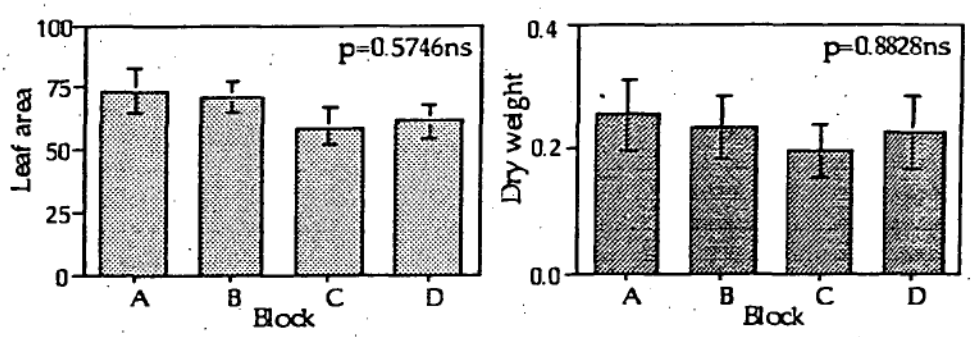


Fig. 3.33. Differences in average leaf area (A) and dry weight (B) among block at various time intervals during the 1992/93 growing season.

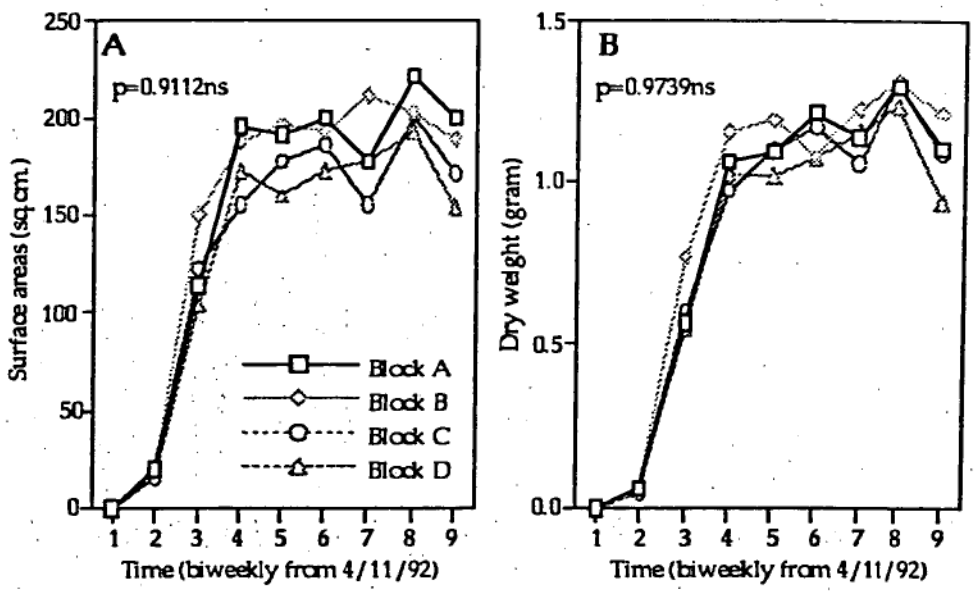


Fig. 3.34. Linear regressions of surface area and dry weight of leaves (Y) on cumulative mite-days in each block (X) during the 1992/93 growing season.

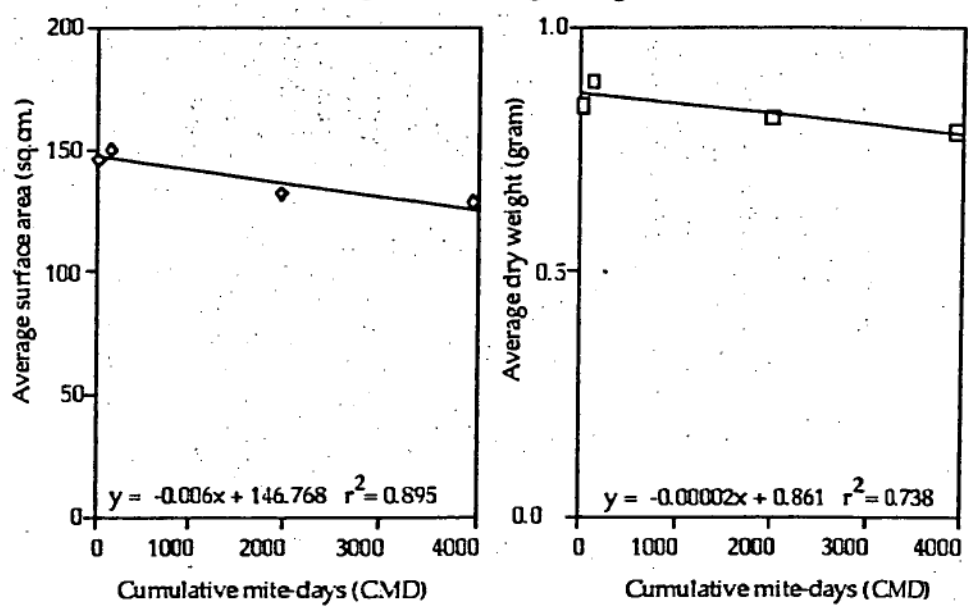
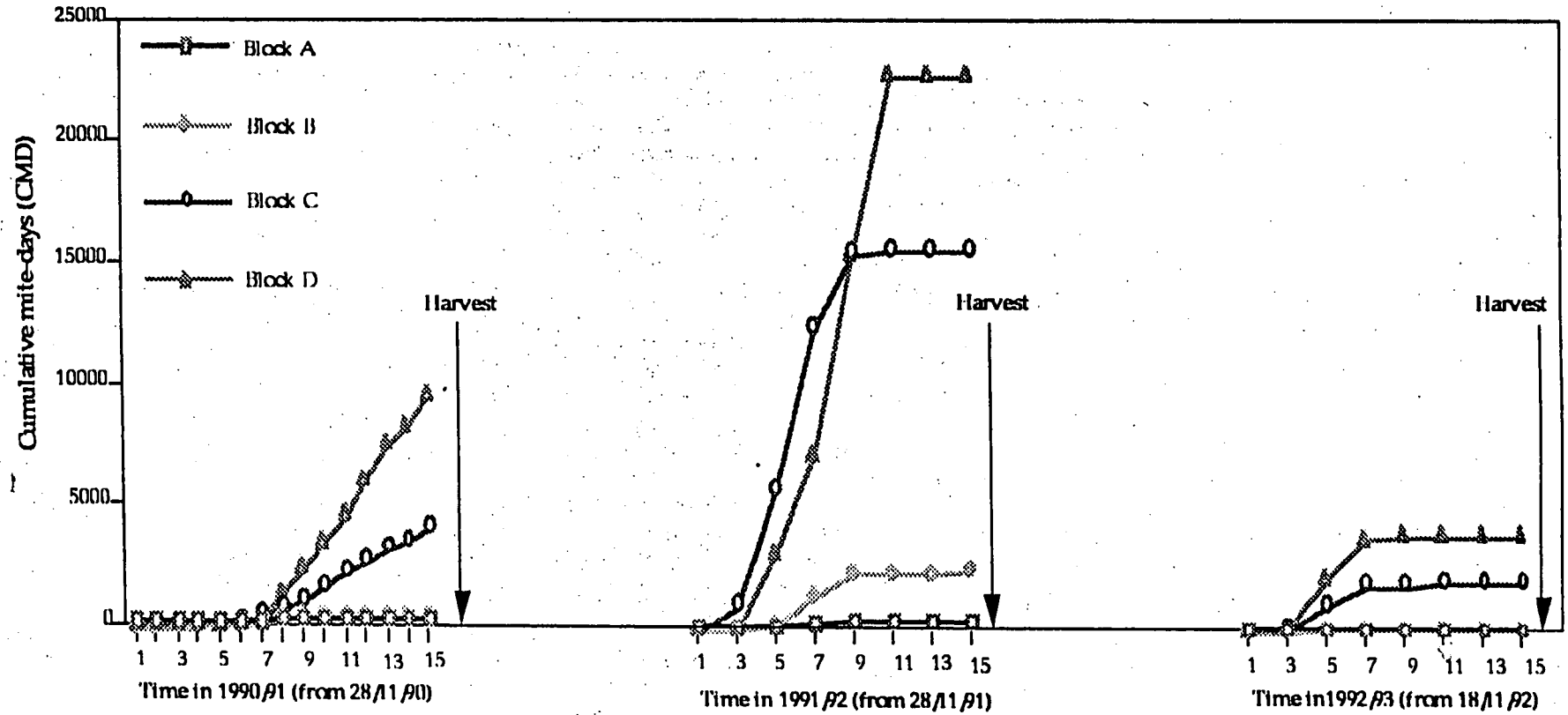


Fig. 3.35. Cumulative mite-days at the height of 1.8 m. in each block over the 3-yr study (1990/91, 1991/92, and 1992/93).



Block A. However, the mean population levels over the entire period in treated blocks were higher than those of the first year, indicating that the absence of chemical restraints in the 1990/91 season led to a severe infestation of mites in the following year. In the final year, i.e. the 1992/93 season, the infestion of TSSM in all blocks was less than that of the two previous year since miticides had been sprayed over the entire area in the preceding year. This also indicates that an outbreak of TSSM can occur despite the employment of intensive chemical control.

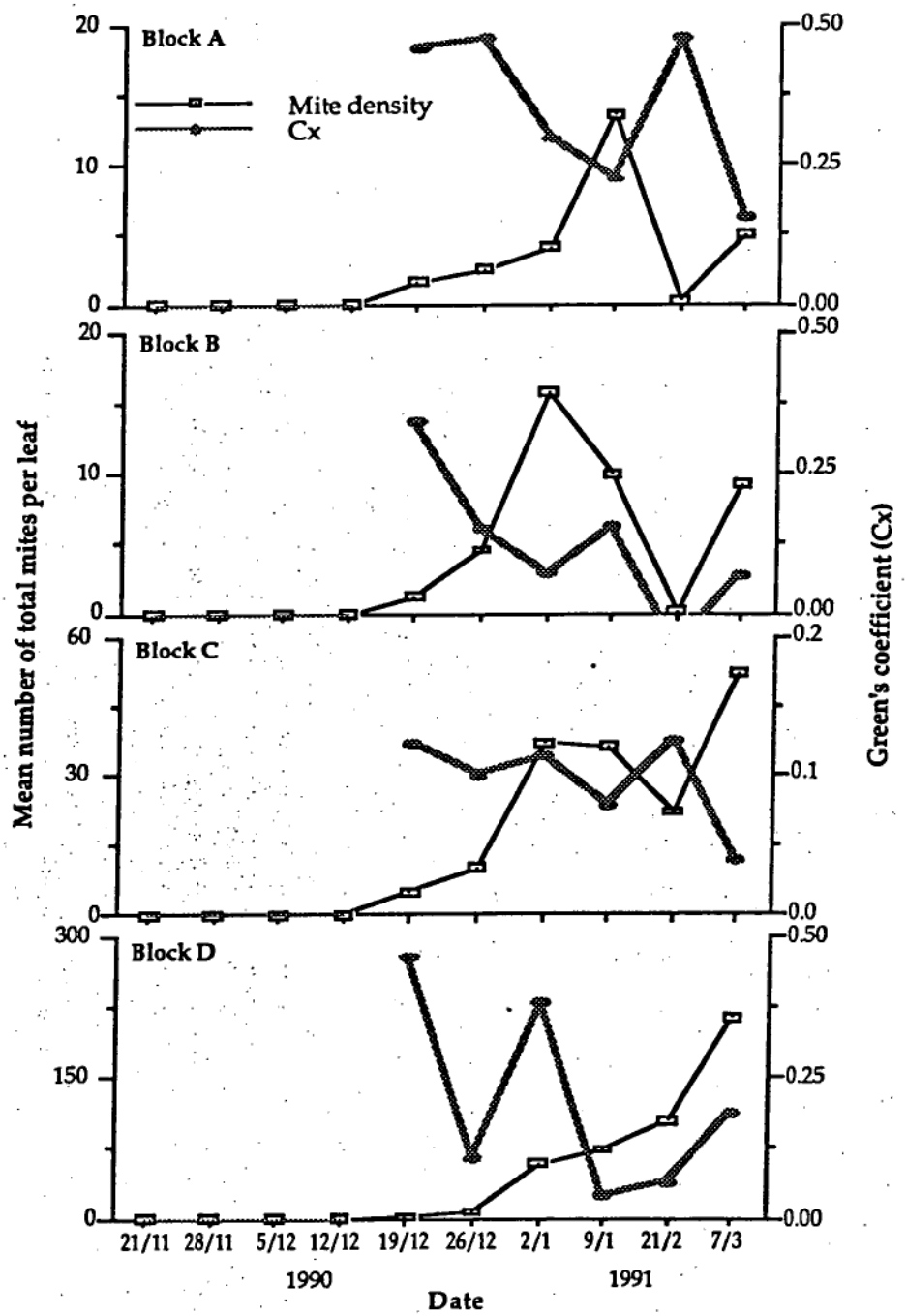
3.3.4. Spatial distribution Since the application of miticides in the 1991/92 and 1992/93 affected mite distribution in all blocks, only the data from mite populations during 1990/91 growing season was employed. Aggregation indices obtained from the variance-to-mean ratio and Green's coefficient, C_x, were in general agreement (Table 3.4). The populations of adult females in all blocks were uniformly distributed between hop plants during early summer (19/12/90) and became aggregated as the season progressed. After spraying with miticides, the dispersion of the females in treated blocks (A and B) ranged again from uniform to aggregated. For adult males, immatures and eggs, the dispersion was found to be aggregated throughout the study period. In each block, the average values of both indices were greater for eggs than for the population as a whole. Hence, eggs were the most highly aggregated stage. When all stages of mites were considered, their distribution in each block, except Block B on 21 February, was aggregated.

Changes in the pattern of aggregation during the growing season are presented in Fig. 3.36. Mite populations were most aggregated, i.e. C_x was highest, during the early growing season when the number of TSSM per leaf was lowest. The values of C_x dropped sharply when mite populations increased. This indicates that as the number of mite-infested plants increased mite dispersion became more random.

Table 3.4. Distribution of TSSM in each block during 1990/91 growing season.

Date	Block	Variance-mean ratio					Green's coefficient				
	(n=20)	Females	Males	Immatures	Eggs	Total	Females	Males	Immatures	Eggs	Total
19/12/90	A	0.95	-	-	13.75	14.70	-0.0526	-	-	0.4555	0.4567
	B	0.89	-	-	8.17	8.82	-0.0526	-	-	0.3584	0.3402
	C	0.98	-	-	11.41	12.32	-0.0025	-	-	0.1225	0.1231
	D	0.95	-	-	17.65	18.60	-0.0526	-	-	0.4626	0.4630
26/12/90	A	0.95	-	-	22.20	23.13	-0.0526	-	-	0.4711	0.4709
	B	1.09	1.00	4.68	10.68	14.35	0.0175	0.0000	0.1752	0.1614	0.1500
	C	1.05	-	-	20.04	21.04	0.0048	-	-	0.1002	0.0997
	D	1.16	-	-	16.96	18.09	0.0175	-	-	0.1057	0.1061
2/1/91	A	1.52	-	8.55	19.90	24.95	0.2583	-	0.9438	0.2739	0.2957
	B	2.36	-	14.52	16.50	22.87	0.2274	-	0.1852	0.0665	0.0697
	C	4.32	-	24.88	79.18	83.77	0.1276	-	0.1769	0.1367	0.1126
	D	1.89	-	9.69	444.93	446.18	0.0740	-	0.2414	0.3974	0.3815
9/1/91	A	2.33	-	32.11	55.33	60.93	0.1388	-	0.3419	0.3313	0.2236
	B	1.60	-	16.28	25.77	31.36	0.2982	-	0.3057	0.1720	0.1533
	C	5.14	3.89	29.87	34.40	29.87	0.1534	0.3216	0.2139	0.0612	0.0788
	D	6.05	20.04	39.01	32.85	60.29	0.0971	0.2139	0.0603	0.0447	0.0399
21/2/91	A	0.95	-	-	2.00	2.42	-0.0526	-	-	1.0000	0.4737
	B	0.95	-	-	-	0.95	-0.0526	-	-	-	-0.0526
	C	1.78	4.76	31.44	23.73	55.53	0.0277	0.1214	0.1253	0.1697	0.1242
	D	5.40	15.62	50.21	112.93	138.29	0.0531	0.0599	0.0530	0.1320	0.0652
7/3/91	A	1.79	-	-	14.79	15.89	0.1579	-	-	0.1533	0.1551
	B	1.05	1.00	2.39	14.75	13.61	0.0048	0.0000	0.1388	0.0854	0.0685
	C	8.78	6.23	19.13	18.89	41.65	0.0695	0.0488	0.0366	0.0566	0.0393
	D	79.98	61.30	227.34	489.19	799.00	0.1381	0.1256	0.1545	0.2777	0.1865

Fig. 3.36. Relationship between Green coefficients and mite densities in each block.



3.3.5. Vertical distribution

3.3.5.1. Growing season 1990/91 The within-plant distribution of TSSM and their predators over three foliage heights of hops was examined in Block D during the last week of sampling. As can be seen from Fig 3.37, the greatest percentages of TSSM in various stages and their predators were found on upper leaves. Of the total number of mites from sample leaves, 66.4% were recorded on upper leaves, 21.6% on middle leaves, and 12.0% on lower leaves. This indicates that the mites moved up the hop plants and concentrated on the upper portions of the host. Over 60% of the total *Stethorus* spp. and predatory mite populations were detected on upper leaves. On middle leaves, the percentage of *Stethorus* spp. was less than on lower leaves, whereas the percentage of predatory mites was higher than on lower leaves. This result suggested a competitive relationship between *Stethorus* spp and predatory mites, particularly in an area with low-density prey populations.

According to the nonparametric Kruskal-Wallis test, the mean number of eggs did not vary significantly among different foliage heights ($p \geq 0.05$, Table 3.5). There were highly significant differences in mean numbers of immatures and adult females ($p < 0.01$) as well as significant differences in adult males among different foliage heights ($p < 0.05$).

The average surface area and dry weight per leaf at each foliage height is presented in Fig. 3.38. The lower leaves had the smallest surface areas and dry weights. For upper leaves, the surface areas were larger than those of middle leaves, whereas the dry weights were less than those of middle leaves, indicating that the old-growth foliage from the middle portion of the hop plant had a greater leaf biomass per unit area than the younger growth from the upper portion.

Fig.3.37. Percentages representative of various stages of TSSM and its major predators at different levels within plants.

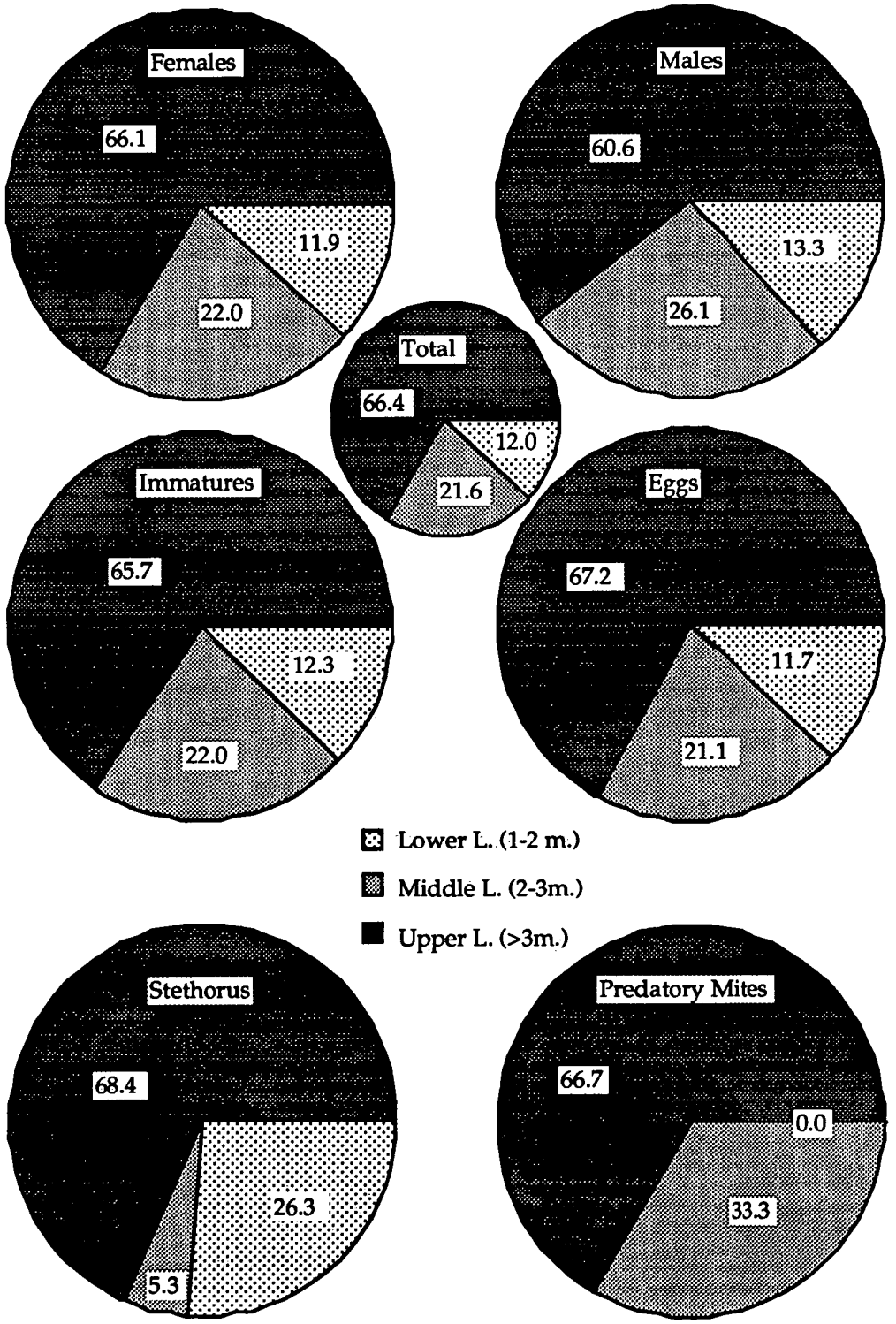
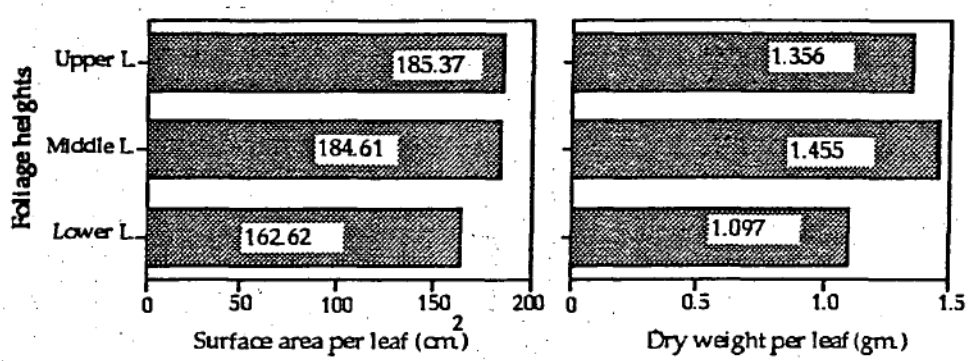


Table 3.5. Mean numbers of mites per leaf among different foliage heights.

Foliage heights (n=16)	Stages (Means±S.E.)			
	Eggs (p=0.0565ns)	Immatures (p=0.0003**)	Adult males (p=0.0323*)	Adult females (p=0.0002**)
Upper (>3m.)	99.44 ± 35.44	44.06 ± 15.44	6.81 ± 2.59	4.50 ± 1.12
Middle (2-3m.)	31.25 ± 7.79	14.75 ± 2.91	2.94 ± 0.92	1.50 ± 0.66
Lower (0-2m.)	17.37 ± 7.36	8.25 ± 3.14	1.50 ± 0.35	0.81 ± 0.21

Fig. 3.38. Average surface area and dry weight of leaves at each foliage height.



The densities of mites of various stages, expressed as the mean numbers of mites/cm.^{2}, are presented in Table 3.6. These results were obtained using the same statistical procedure as was used to analyse the mean number of mites per leaf (Table 3.5). The mean numbers of eggs and adult males per unit area did not differ significantly among different foliage heights ($p \geq 0.05$). There were highly significant differences in immatures and adult females among different foliage heights ($p < 0.01$). Similar results were found when the densities of eggs, immatures and adult mites were expressed as mean numbers of mites per gram leaf biomass (Table 3.7).

Table. 3.6. Mean numbers of mites per cm^2 among different foliage heights.

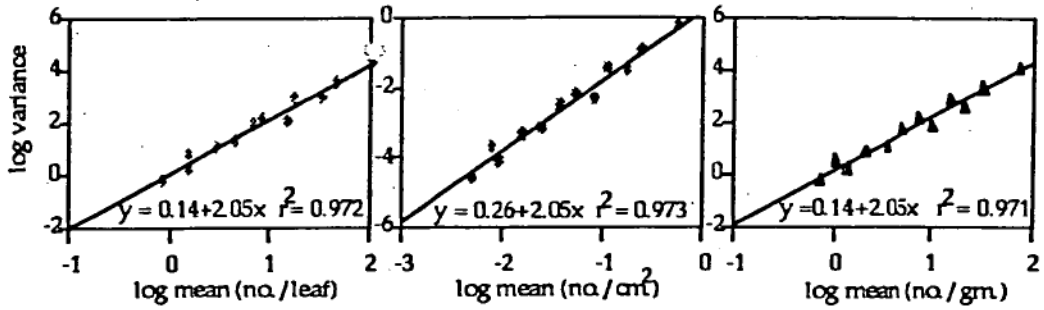
Foliage heights (n=16)	Stages (Means±S.E.)			
	Eggs (p=0.1053ns)	Immatures (p=0.0007**)	Adult males (p=0.0997ns)	Adult females (p=0.0012**)
Upper (>3m.)	0.536 ± 0.191	0.238 ± 0.083	0.037 ± 0.014	0.024 ± 0.006
Middle (2-3m.)	0.169 ± 0.042	0.080 ± 0.016	0.016 ± 0.005	0.008 ± 0.004
Lower (0-2m.)	0.107 ± 0.045	0.051 ± 0.019	0.009 ± 0.002	0.005 ± 0.001

Table. 3.7. Mean numbers of mites per gram among different foliage heights.

Foliage heights (n=16)	Stages (Means±S.E.)			
	Eggs (p=0.1189ns)	Immatures (p=0.0013**)	Adult males (p=0.0589ns)	Adult females (p=0.0004**)
Upper (>3m.)	73.33 ± 26.14	32.49 ± 11.39	5.02 ± 1.91	3.32 ± 0.83
Middle (2-3m.)	21.48 ± 5.35	10.14 ± 2.00	2.02 ± 0.63	1.03 ± 0.45
Lower (0-2m.)	15.84 ± 6.71	7.52 ± 2.86	1.37 ± 0.32	0.74 ± 0.19

A one-way analysis of variance with Fisher's protected least significant difference test (PLSD) was subsequently used to separate means of mite densities in each foliage stratum. Since the slope (b) values of the regression equations of log variance versus log mean values in each comparison (as shown in Fig. 3.39) are more than 1, the log (x+1) transformation of data was employed in the analyses (Southwood, 1978).

Fig. 3.39. Relationship of log variance to log mean values of mites between different foliage heights.



From Table 3.8 it can be seen that the differences in the transformed mean numbers of mites per leaf among different foliage heights agree with the results obtained from the nonparametric procedure for untransformed data, except that significant differences in eggs densities were detected ($p < 0.05$). It was also evident that the numbers of eggs, immature and adult mites on upper leaves were significantly higher than on lower leaves. Additionally, there were significant differences between the density of immatures on middle and upper leaves, adult females on middle and upper leaves, and immatures on lower and middle leaves.

Table. 3.8. Differences in mite densities per leaf between different foliage heights.

Foliage heights (n=16)	Stages (Log mean (x+1)±S.E.)			
	Eggs (p=0.0372*)	Immatures (p=0.0001**)	Adult males (p=0.0188*)	Adult females (p=0.0001**)
Upper (>3m.)	1.47 ± 0.20b	1.43 ± 0.11c	0.68 ± 0.10b	0.64 ± 0.07b
Middle (2-3m.)	1.21 ± 0.15ab	1.08 ± 0.09b	0.45 ± 0.09ab	0.26 ± 0.08a
Lower (0-2m.)	0.83 ± 0.16a	0.70 ± 0.12a	0.33 ± 0.07a	0.21 ± 0.05a

Means followed by same letter not significantly different at alpha = 0.05 (PLSD)

Analyses of variance using transformed mean numbers of mites per cm.^{2} indicated that there were significant differences in eggs and immatures among different foliage heights ($p < 0.05$, Table 3.9). Highly significant differences were found in adult female densities ($p < 0.01$). The mean numbers of adult males did not differ significantly among different foliage heights ($p \geq 0.05$). However, significant differences in adult males were apparent between lower and upper leaves. For eggs, immatures and adult females, the mean numbers of mites on upper leaves were significantly higher than on both lower and middle leaves.

Table. 3.9. Differences in mite densities per cm.^{2} between different foliage heights.

Foliage heights (n=16)	Stages (Log mean (x+1)±S.E.)			
	Eggs (p=0.0283*)	Immatures (p=0.0105*)	Adult males (p=0.0676ns)	Adult females (p=0.0035**)
Upper (>3m.)	0.147 ± 0.045b	0.082 ± 0.023b	0.015 ± 0.005b	0.010 ± 0.003b
Middle (2-3m.)	0.064 ± 0.015a	0.033 ± 0.006a	0.007 ± 0.002ab	0.003 ± 0.002a
Lower (0-2m.)	0.040 ± 0.015a	0.020 ± 0.007a	0.004 ± 0.001a	0.002 ± 0.001a

Means followed by same letter not significantly different at alpha = 0.05 (PLSD)

For transformed mean numbers of mites per gram leaf biomass, there were highly significant differences in numbers of immature and adult female mites/gm. among different foliage heights ($p < 0.01$, Table 3.10). Significant differences in adult males were detected also($p < 0.05$). The mean numbers of eggs did not differ significantly ($p \geq 0.05$). Significant differences in eggs and adult males were apparent between lower and upper leaves. For immatures and adult females, the mean numbers of mites on upper leaves were significantly higher than on both lower and middle leaves.

Table. 3.10. Differences in mite densities per gram between different foliage heights.

Foliage heights (n=16)	Stages (Log mean (x+1)±S.E.)			
	Eggs (p=0.0699ns)	Immatures (p=0.0004**)	Adult males (p=0.0358*)	Adult females (p=0.0002**)
Upper (>3m.)	1.360 ± 0.192b	1.302 ± 0.105b	0.59 ± 0.094b	0.544 ± 0.068b
Middle (2-3m.)	1.080 ± 0.144ab	0.935 ± 0.083a	0.37 ± 0.077ab	0.212 ± 0.066a
Lower (0-2m.)	0.801 ± 0.159a	0.671 ± 0.121a	0.31 ± 0.062a	0.201 ± 0.049a

Means followed by same letter not significantly different at alpha = 0.05 (PLSD)

Even though the data was analysed in different ways, the results for adult females remained consistent, indicating that this stage provided the most accurate estimater for statistical analyses.

When the same statistical procedures were repeated with the mean numbers of total mites and their predators, it was found that the vertical distribution patterns of total TSSM were more similar to those of the corresponding densities of predatory mites than those of *Stethorus* spp. (Fig.3.40). For example, there were significant differences in population densities of TSSM and predatory mites between lower and upper leaves, whereas no significant differences in the densities of *Stethorus* spp. between lower and upper leaves were detected.

3.3.5.2. Growing season 1991/92 The within-plant distribution of TSSM of various stages prior to the miticide application during this season is presented in Fig. 3.41. During the first three occasions of sampling, the majority of the mite population at each stage was on lower leaves. On the fourth occasion, most of the males and immatures were still detected on lower leaves, whereas the females and eggs were mostly found on middle leaves. Because of the stripping of the lower leaves, no leaves at this foliage height were collected during the remainder of the

Fig. 3.40. Densities of TSSM and its major predators at different plant foliage heights.

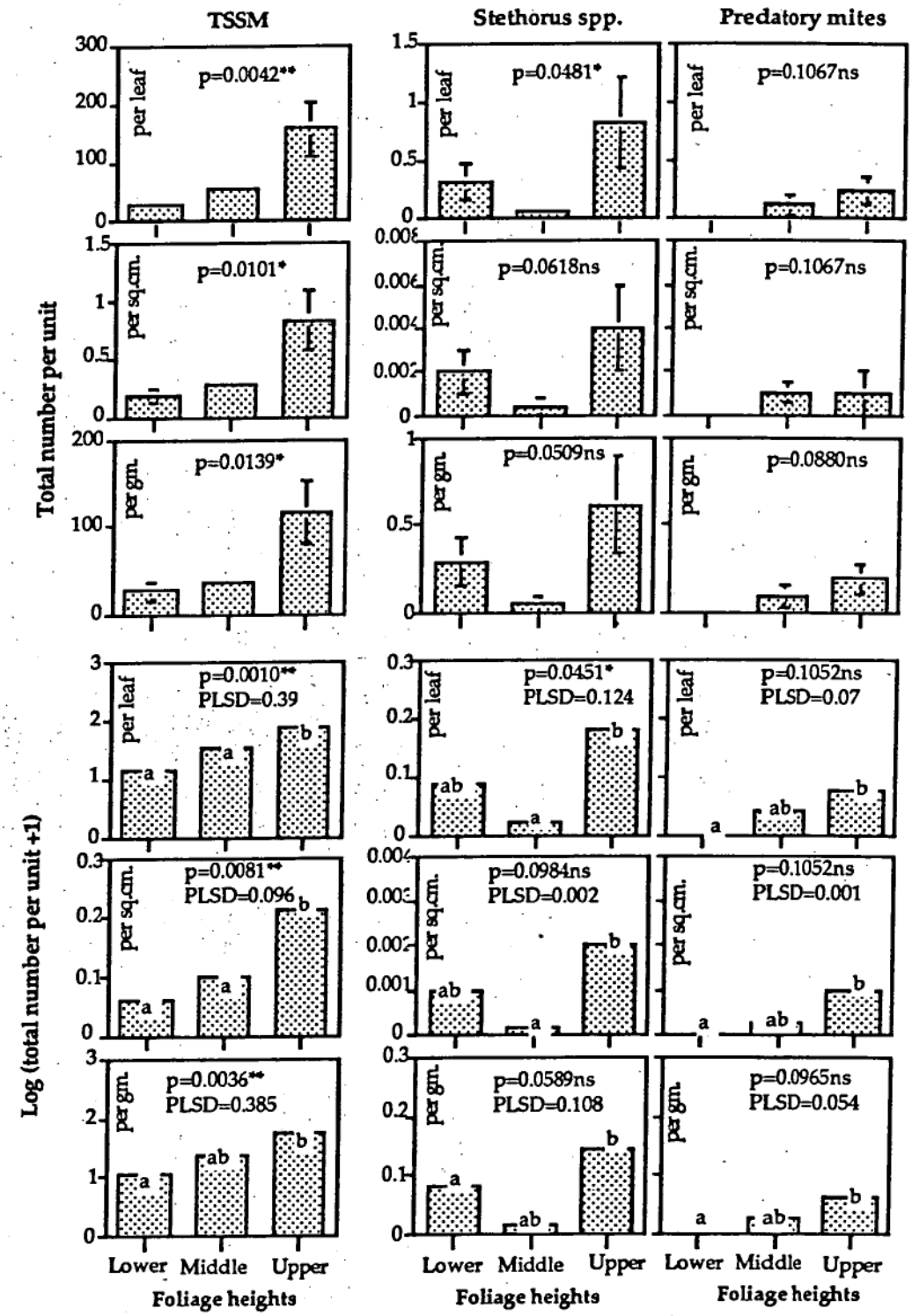
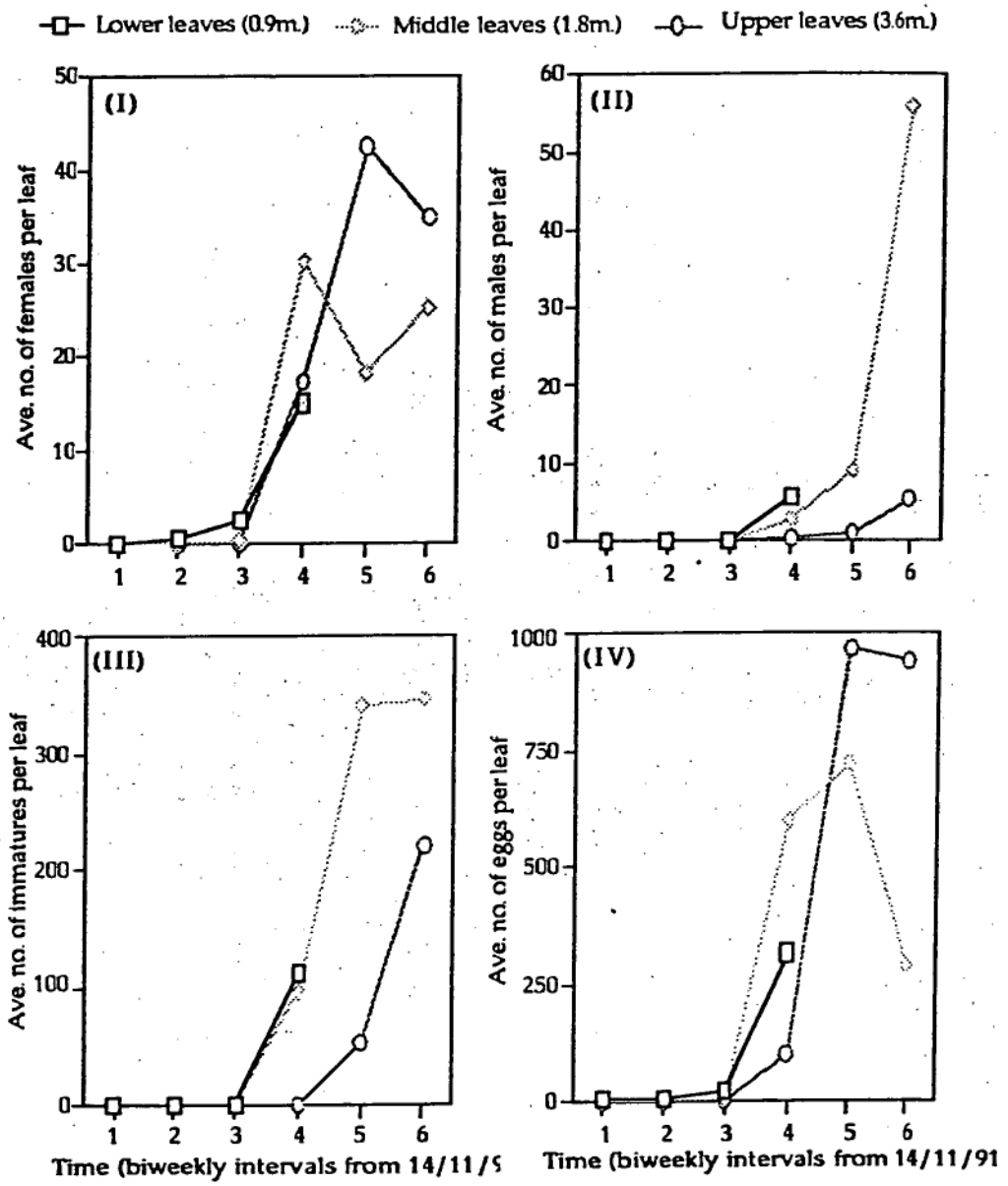


Fig. 3.41. Mean numbers of TSSM at various stages in different foliage heights during the 1991/92 growing season: (I) Females; (II) Males; (III) Immatures; and (IV) Eggs.



study. For the final two occasions of sampling, males and immatures were most numerous on middle leaves, whereas the majority of females and eggs were on upper leaves. This indicates that mites at each stage were found on the lower leaves early in the season then progressed up the plant as it grew, and that the migration of males and immatures was slower than that of females.

When the total number of mites of various stages were combined together, similar patterns of upward movement were obtained (Fig. 3.42I). Mite populations on lower leaves comprised from 86.33 to 100% of the total population during the first three occasions of sampling. On the fourth occasion of sampling (26 December), the percentages of the total population were 34.73, 56.22, and 9.05% for mites on the lower, middle and upper leaves, respectively. This indicates that mites became less abundant on lower leaves and the majority of mites were on middle leaves by the end of December. As the plants continued to grow, TSSM became more abundant on upper leaves; the percentage of mites on the upper leaves was 49.27% on the fifth occasion of sampling (9 January), whereas this had risen to 62.54% on the sixth occasion (23 January).

The frequency of mites at each foliage height was related to changes in average surface areas and dry weights of leaves (Fig. 3.42 I, II, and III). The majority of mites were found on lower leaves, when the foliage at this height had the largest surface area and dry weights. Similar results were also obtained for middle and upper leaves. This indicated that leaf size could be associated with the movement of mite populations.

The pattern of increase and decline for the mite densities per unit area and per unit dry weight in each stage between different foliage heights is presented in Fig. 3.43 and 3.44. The density of females and eggs on each foliage height increased during the first four occasions of sampling followed by a rapid density decline, while the males and

Fig. 3.42. Average numbers of total mites per leaf (I) and surface areas (II) and dry weights (III) of leaves among different foliage heights during the 1991/92 growing season.

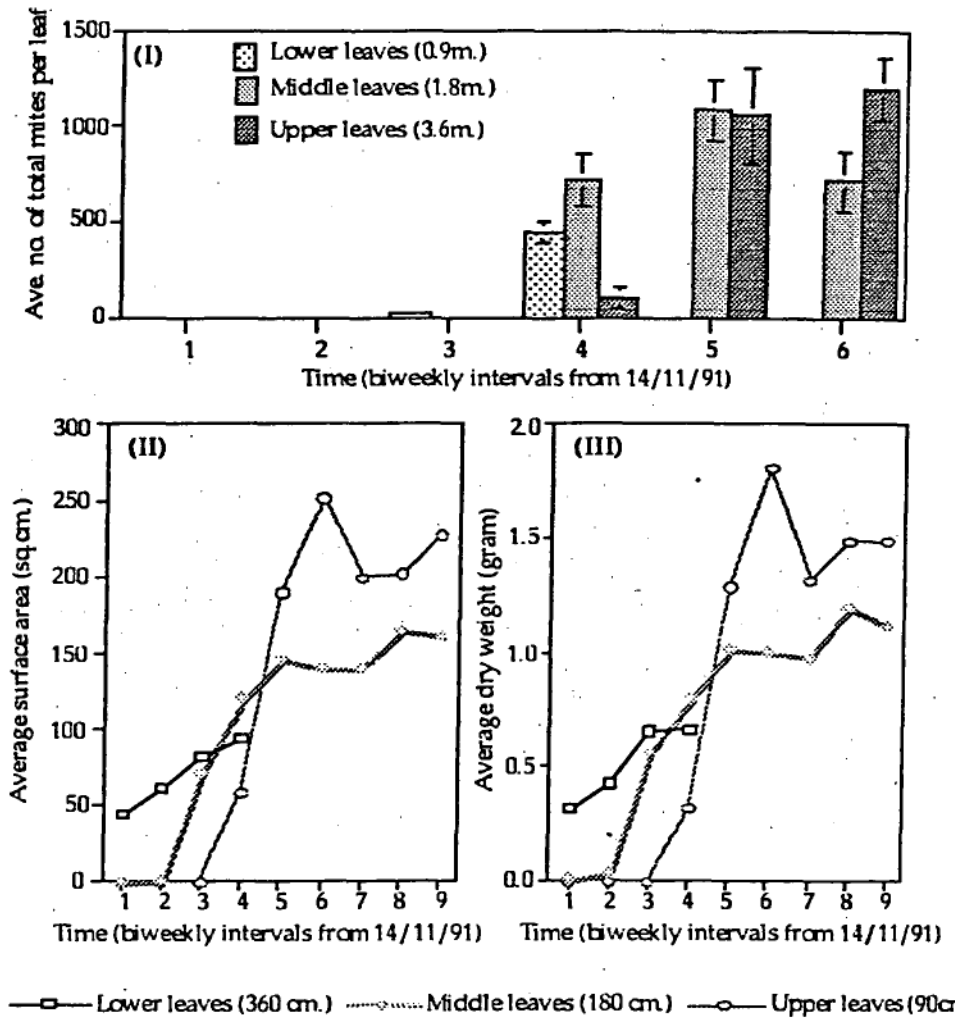


Fig. 3.43. Mean numbers of TSSM per cm.^{2} among different foliage heights during the 1991/92 growing season: (I) Females; (II) Males; (III) Immatures; (IV) Eggs; and (V) Total mites.

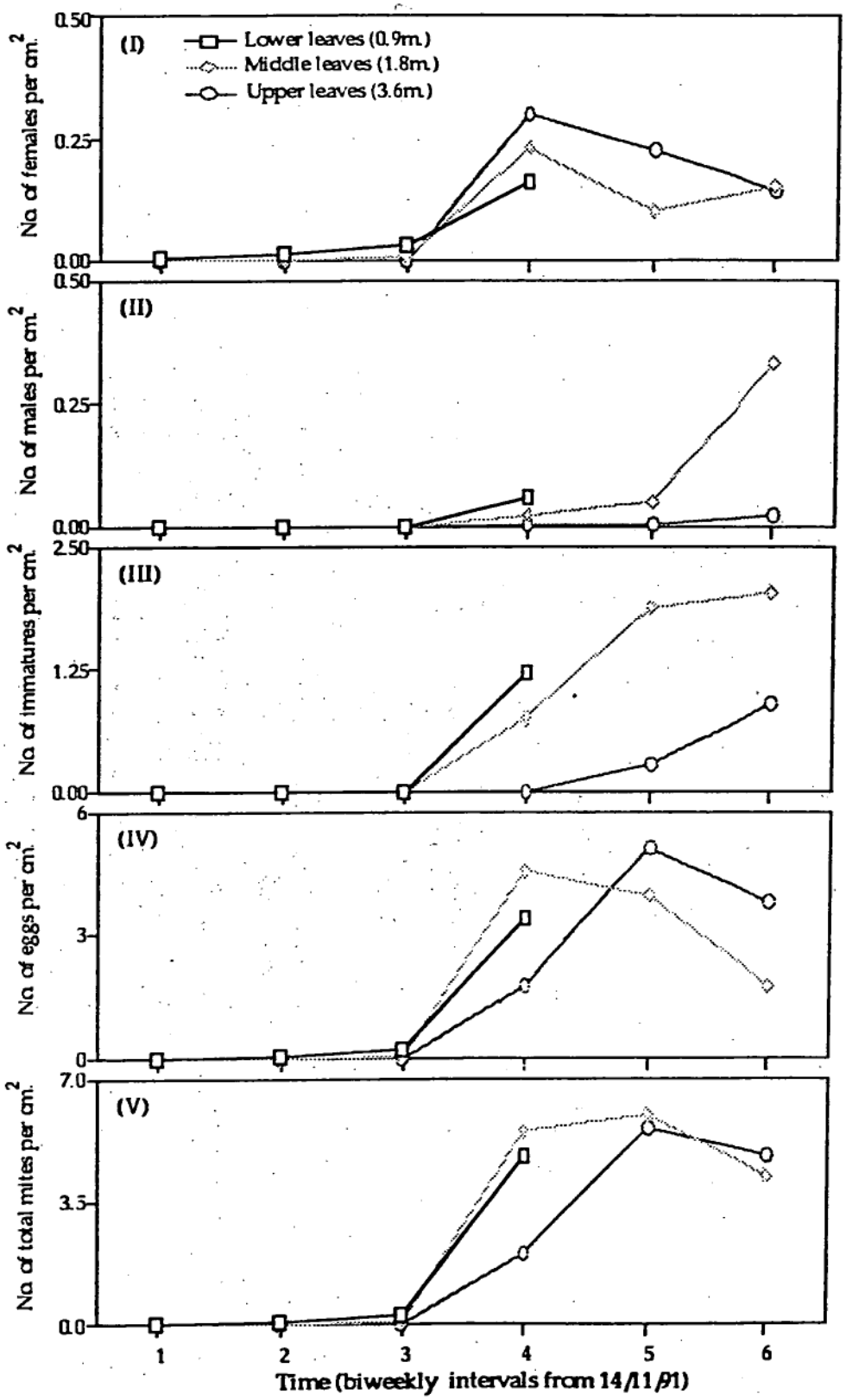
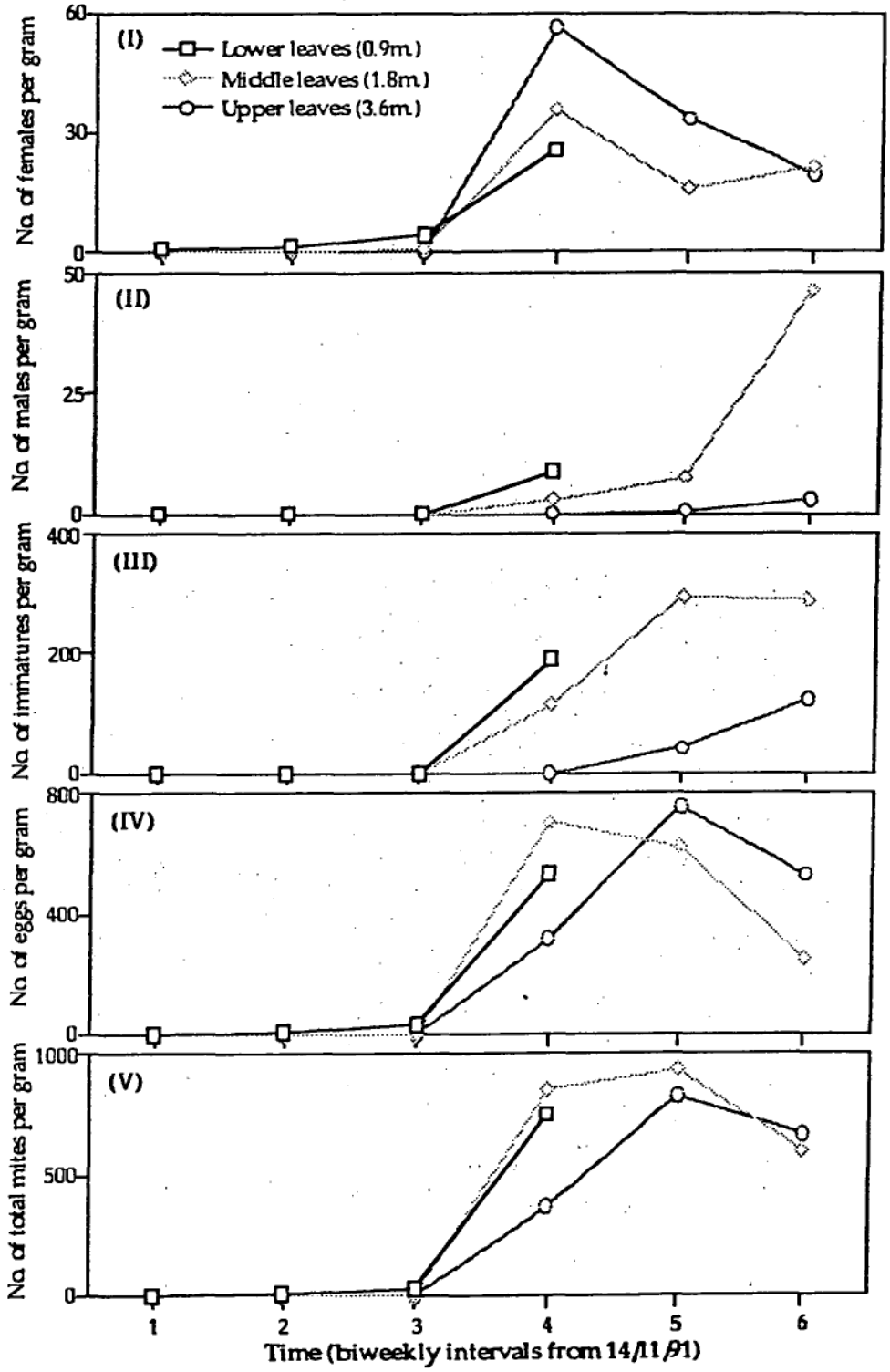


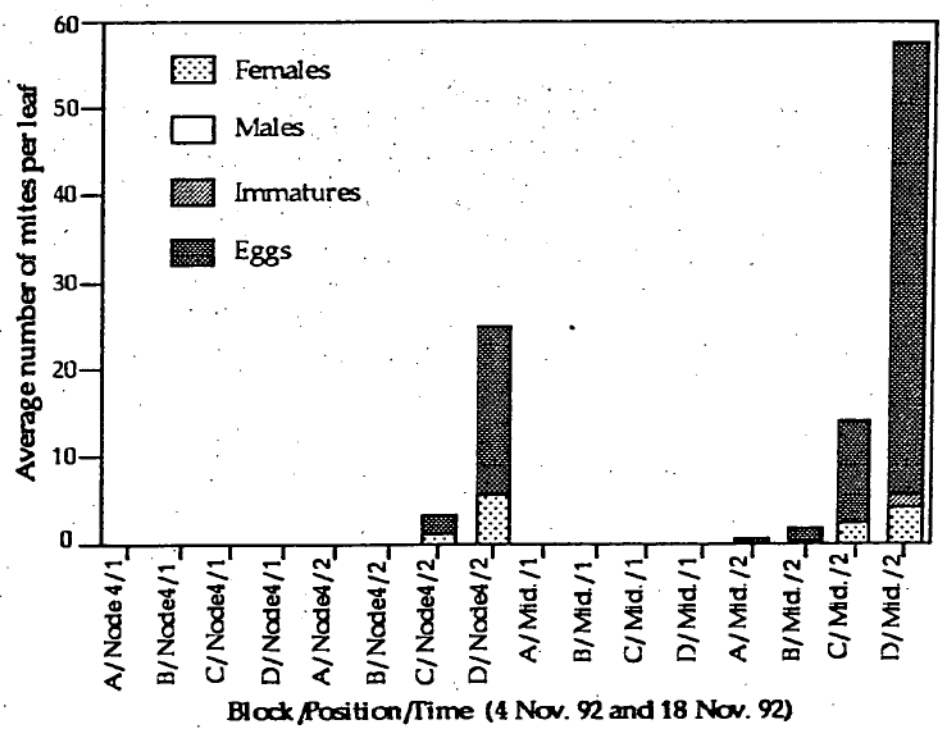
Fig. 3.44. Mean numbers of TSSM per gram leaf biomass among different foliage heights during the 1991/92 growing season: (I) Females; (II) Males; (III) Immatures; (IV) Eggs; and (V) Total mites.



immatures continually increased throughout the study period. However, females on middle height leaves were denser on the final occasion of sampling due to the reduction in leaf surface area. For total mites, the population density in each foliage height increased until the fifth occasion of sampling and declined on the final occasion of sampling. This result indicates that the upward distribution of TSSM within hop plants, especially females and eggs, lowers the density of mites at the lower heights and results in higher densities at the upper heights.

3.3.5.3. Growing season 1992/93 Early in the season, the mite populations of all stages were relatively abundant on lower leaves in the middle region of the plant, whereas on upper leaves at the fourth node of plants, populations were very low (Fig. 3.45). Obviously, eggs were the predominant stage in both foliage strata during this period.

Fig. 3.45. Average mite densities in various stages on leaves from the fourth node and the middle region of hop plants in each block on the first and second sampling occasion during the 1992/93 season.



3.4. DISCUSSION

3.4.1. Seasonal abundance

This study demonstrated a generalised pattern of growth and decline in TSSM populations on commercial hops during the growing season. The normal pattern of population change on the 1.8-m mainstem leaves, as shown in untreated areas, indicated that the mites peaked after hops had formed the visible bases of inflorescences and peaks were generally followed by a population decline due to mite migration and plant maturity. For treated areas, an application of miticides upset the normal pattern of infestation development; mites of all stages were depleted. In both areas, the adult females observed at the end of season began to change from the green summer form to the bright-orange overwintering form in response to seasonal changes, i.e. daylength, temperature and plant quality. Among these variables, daylength has been proved to be the major factor for the regulation of diapause in TSSM (Veerman, 1985). In general, overwintering mites on hops are produced when daylength is less than fourteen hours (Moreton, 1964). Thereafter, TSSM overwinters in the hollow cavities of hop twigs in the litter around hop rootstocks (Cao, 1989) and the numbers of female progeny from overwintered mites have an influence on seasonal population development in the following season (Cone et al., 1986).

The relationship between TSSM population size and the proportion of leaves infested in the untreated area showed that all the leaves sampled at the height of 1.8 m. could be infested when the average number of mites per leaf was more than 100. This relationship is a key to the development of a monitoring program for TSSM on hops based on presence-absence sampling, which has been developed effectively for pests of cotton and brussels sprouts (Wilson and Room, 1983; Wilson et al., 1983).

In the treated areas, it was found that TSSM continued to infest the hop plants and were detected at low levels several times after the miticide application. According to van de Vrie (1985b), there are two possible sources of TSSM reinfestation; (1) reproduction of mites which escaped control on the host plant and (2) mites from secondary host plants within the area or in close proximity. Since TSSM has a wide range of host plants, their reinfestation is related to other host plants. Cao (1989) observed that overwintered TSSM moved from thistle to nearby growing hops during the early part of growing season.

In addition, the application of miticides is known to be one of various factors affecting the abundance of spider mites (Huffaker et al., 1969). The suppression of mite populations in treated areas over the 3-yr study provides evidence to support this concept. The miticide application contributed to initial infestation levels of mites on treated and untreated hops in the following season. The initial infestation largely determines the potential for TSSM populations to develop early (Wilson and Morton, 1993). For example, naturally-occurring populations of TSSM in treated areas of the 1990/91 season were low in the early season of 1991/92, whereas those in untreated areas were relatively abundant. Similar results were obtained by Terauds (1989) who indicated that the absence of chemical restraints for some growing seasons in apples caused a large build-up of pests in the following season.

It is widely believed that the application of some pesticides enhances the intrinsic power of increase of the mites, and may cause outbreaks, regardless of the presence of mite predators (van de Vrie et al., 1972). Carey (1982a) suggests that mite populations treated with pesticides may attain a 1.4- to a 4.2- fold difference in population size compared to an untreated population after 2 generations and a 1,300-fold potential difference after 10 generations. Further, Mansour (1990) observed that the

tetranychid mite populations were larger and the phytoseiid populations smaller in sprayed apple orchards, whereas mite populations in unsprayed orchards were very small. The results of the present study indicate that the average numbers of predators were too small to influence the population of TSSM on commercial hops. This appears to be related to the application of miticides in the previous season.

Natural enemies found in all 3 yrs of the study were *Stethorus* spp. and phytoseiid mites, ranging from 0.1 to 1.0 per leaf. Terauds (1989) reported that *Stethorus vagans* and *Stethorus nigripes* were the most important natural controls of pest mites in Tasmania. According to Cao (1989), the effect of *Stethorus* spp. on TSSM populations in hop yards was less significant than that of the native phytoseiid mite, *Amblyseius longispinosus* Evans, which actively depleted TSSM in the early stages of overwintering and in the spring immediately after overwintering. However, the numbers of this phytoseiid mite were not sufficient to suppress the subsequent build up of TSSM populations. In contrast, the introduced phytoseiid mite, *P. persimilis* , has been proved to be effective in controlling TSSM populations, but this predator cannot survive the cold winter conditions of Tasmania.

In the present investigation it was also noted that variation in damage of hop plants could affect mite populations reinfested after spraying miticides. Heavily damaged plants became less suitable for survival and oviposition, while slight damage resulted in the plants being more suitable. This may be due to inducible resistance in hop plants for mite infestations. The results from this study confirm the earlier reports for several herbivore-plant associations (Karban and Carey, 1984; Hildebrand et al., 1986; Karban and Myers, 1989).

In addition, the results of this study indicated that eggs were the predominant stage for most of the season, and that the stage-specific

percentages changed as the season progressed. Carey (1982a) proposed that a stable stage distribution for TSSM is approximately 66% eggs, 26% immatures and 8% adults and that natural mite populations are often quite close to this stable stage distribution. At the peak density of mite populations in untreated areas during the 1990/91 season, the percentage of eggs, immatures, and adult mites averaged approximately 60%, 27%. and 13%, respectively, not too different from the distribution just described.

The decrease in the proportion of eggs during the latter part of the season was probably related to the lack of nutrients in the aging plant, a factor in the induction of diapause. Trichilo and Leigh (1985) suggest that the availability of leaf nutrients, as affected by plant age, may influence mite population growth rates. Mitchell (1973) also reported that any factors that affect leaf quality resulted in changes in TSSM egg production. In addition to nutrients, Krainacker and Carey (1991) indicated that the proportion of eggs in the mite population was positively correlated with the proportion of females in an adult population in which the sex ratio became less female biased as mite populations per plant increased.

The relatively high growth rates of TSSM populations on young leaves, especially on young plants (Watson, 1964), suggests a species capable of capitalizing on ephemeral resources, such as hop plants. It has been pointed out by Sabelis (1985a) that r_m-selected tetranychid populations eventually collapse because the life span of their host is short, their host is overexploited, other hervivores competitively exclude them, they are attacked by natural enemies or pathogens, or reduced by inclement weather. In Tasmania, where both the pest and the host plant are exotic species, there is no evidence that other herbivores, natural enemies or pathogens are significant factors in limiting population

growth rates of these mites. This leaves host plant effects and inclement weather as possible factors.

3.4.2. Climatic effects

The dynamics of mite populations on field hops may have been influenced by climatic conditions, including temperature, humidity, rain, light and wind. Very little precise information is available showing the quantitative impact of climatic factors involved in population dynamics of spider mites (van de Vrie et al., 1972). The present study addresses only temperature and rain.

The results of this study indicated that mite populations increased as the accumulation of heat units progressed; however the effects of other seasonal factors, such as day length and declining nutrient status caused population decline late in the season. Abundant rainfall during some parts of the season could have been responsible for the retardation of some mite infestations. It was also observed that mite populations developed more quickly during the periods of little or no rainfall and high temperatures.

Mite outbreaks are favoured by hot, dry weather (Neve ,1991); for this reason, TSSM infestation is a serious problem of hop production in Australia. Cao (1989) suggested that climatic factors play a very important role in the development of both TSSM and hops due to the differences in the initial development of mite populations and the growth of hop plants. Kac (1963) studied the influence of temperature on the population dynamics of TSSM on hops in former Yugoslavia and found that the effects of high February temperatures on overwintering mites created the potential for high-density populations during summer. Cold wet weather possibly caused considerable mortality of overwintering mites and greatly reduced any build-up in spring (Cranham, 1985).

Simpson and Connell (1973) analysed population data for mites in soybean fields over a seven-year period and found that low precipitation

was more highly correlated with mite densities than was high temperature in the field. The effect of free water in retarding population build-up has been reported by Herne (1968), and confirms common field experience of the suppression of mite outbreaks by rainfall.

In general, heavy rains might be expected to create severe losses, particularly in spider mites that inhabit the upper surfaces of leaves and are not heavy webbers, and the effect may be intensified if heavy rains occurred with turbulent wind, which would also tend to expose the lower surface of the foliage (van de Vrie et al., 1972). TSSM usually feeds on the lower surfaces of hop leaves (Neve, 1991) and constructs a complicated web (Saito, 1985); for this reason, rains may have little influence on this species. Linke (1953) reported that the beating force of rainfall on plant leaves does not entirely explain the decrease in TSSM populations on hops in Germany during rainy periods and that the webs protect TSSM and entire colonies on hop leaves from being blown off by winds and wetted by rains. In his experiments, rainfall was simulated by immersing infested hop leaves in water for 2-4 hr daily. However, such a technique seemingly does not simulate characteristics of rainfall which would cause dislodgement from impact (Simpson and Connell, 1973). Klubertanz et al. (1990) also demonstrated that precipitation applied with a rainfall simulator was not found to significantly affect mite intensity in soybean plots.

Thermal degree-day (DD) summation has been widely used for more than a century as a means of predicting time of harvest, and for scheduling planting dates of crops (Wang, 1960). It is also utilized in programs for disease and weed control, pest control, analysis of biological control, and agricultural loss assessment (Worner, 1988).

3.4.3. Feeding damage

Feeding damage can be estimated by calculating the number of mite-days (Hoy, 1985). It is generally recognized that mite-days, which provide accurate estimates of the mean population level of mites over the period of infestation of pest, are more useful than determining whether numbers are greater or less than a practicular mean number of mites per leaf (Jones, 1990).

The results of this study reveal the effect of different densities of TSSM on hop foliage: the surface areas and dry weights of leaves in the area with high seasonal mite-day accumulations were less than those in the area with low seasonal mite-day accumulations. As reported earlier, inverse relationships between cumulative mite-days and surface areas as well as dry weights of leaves were detected in all three years of the study. However, there were significant differences in surface areas and dry weights of leaves between blocks only in the 1990/91 season, whereas those in the 1991/92 and 1992/93 seasons did not differ significantly. This may have resulted from early miticide applications which resulted in the recovery of leaves during the latter part of the season.

Atlthough feeding damage in terms of relationships between cumulative mite-days and yields has been examined on several crops, including apples (Hoyt et al., 1979), strawberries (Oatman et al., 1981; 1982), almonds (Welter et al., 1984), red raspberries (Raworth, 1989), and hops (Cao, 1989), a detailed study of the impact on plant foliage, especially on hop leaves has not yet been conducted. According to Peters and Berry (1980a), mite-induced foliar damage weakens the hop plants, and feeding injury on the cones reduces market value of the crop. Tomczyk and Kropczynska (1985) suggested that changes in dry matter and leaf area of plants may be observed as a consequence of plant injury caused by spider mites. Reductions in leaf area associated with spider mite injury have

been reported for almonds (Summers and Stocking, 1972) and peppermint leaves (DeAngelis et al., 1983a).

According to Unwin (1971), TSSM causes significant damage to foliage and reduction in yield on a wide variety of host plant. The mites feed by rasping and piercing surface tissue of leaves (Davis, 1961; Anonymous, 1965). Liesering (1960) found that, during feeding, TSSM punctured and extracted the contents from 18-22 parenchymal and palisade cells per minute. Mechanical injury and desiccation of the leaf tissue is indicated by a characteristic leaf mottling, yellowing and withering. Symtoms will vary somewhat on different plants (Cant, 1960; Fenner, 1962).

The increasing water stress caused by mite feeding may have a effect on surface areas and dry weights of hop leaves. Water stress almost immediately elicits a reduction in cell division and enlargement, the basic growth processes (Kramer, 1983); for this reason, smaller plant and plant parts result.

The effect of mite feeding damage may contribute to a reduction in the following year's crop. For instance, Lienk et al. (1956) found that a 64.8 percent reduction in apple yield occurred in the year following infestation with TSSM and *Metatetranychus ulmi*.

The results of relationships between total mite numbers and numbers of mites at each stage in terms of both mite-days and transformed mite-days indicate that the estimate of the actual mite-days of all stages of mites from only the mite-days of any stage results in significant linear regression. However, it was noted that adult females were found more commonly in total mite populations than were the other destructive stages. For this reason, the numbers of mite-days for the female stage alone may be more meaningful than those from the other stages. In agricultural acarology, the female is the stage preferred

for counting because the adult female is the largest stage and the only stage seen with the naked eye, and its proportion in the total population is generally small (Cao, 1989). Furthermore, adult females are usually used to estimate the population that contributes to leaf injury (De Angelis et al., 1982) and the significant linear regression relationships between this stage and total mite numbers have been found by Jones and Parrella (1984) for *Panonychus citri* on lemons, Mollet and Sevacherian (1984) for *T. cinnabarinus* on cotton, Perring et al. (1987) for *T. urticae* on cantalope and Coa (1989) for *T. urticae* on hops. The results of this study also indicate that feeding damage may be predicted using the relationship between females at time t and total mites at time t+1 in terms of both the number of mite-days and the original number of mites and that best estimate of total damaging populations was obtained seven days after female estimate.

3.4.4. Spatial distribution

The results from this study revealed changes in TSSM dispersion patterns during the growing season. The populations of adult females were uniformly distributed between hop plants during the early part of the growing season and became aggregated as the season progressed. For adult males, immatures and eggs, the dispersion was found to be aggregated throughout the study period. Eggs were the most highly aggregated stage. When the number of all stages of mites was considered, the distribution was aggregated throughout the study period and this is in agreement with the observations made by So (1991) for TSSM on roses. Jones (1990) suggested that knowledge of the between-plant dispersion is necessary to determine the number of plants per plot to sample.

According to Green's coefficient, mite dispersion became more random as the number of mite infested plants increased. The dispersion

of TSSM in this study was similar to what Pickett and Gilstrap (1986) and Krainacker and Carey (1990) reported in spider mites infesting corn.

In this study, the impact of miticides on the distribution of TSSM was also found and this is similar to the finding by Trumble (1985) that insecticides created changes in the population dispersion of TSSM which invalidated sampling plans based on data from untreated fields. A very minor effect of miticides on TSSM populations infesting cotton was also reported by Wilson and Morton (1993). However, this is in contrast to the result from Mollet et al. (1984) who found no such effects for *T. cinnabarinus* (Boisduval) on cotton.

3.4.5. Vertical distribution

The results from this study indicated that mites in each stage were found on the lower leaves early in the season but then progressed up the plant as it grew and that approximately 66% of total mite populations in early March before harvest were detected on the upper leaves, whereas only 12% of the total were found on the lower leaves. Similar results were demonstrated by Sites and Cone (1985), who noted that TSSM were primarily found on the lower half of the hop plants during the early season and the majority of the mites were found on the upper half of the plants in late season. Cao (1989) suggested that the within-plant distribution patterns of TSSM on hops vary with time and mite stage.

The vertical dispersal of TSSM was described by Foott (1964) and Unwin (1971) as follows: in early spring, the overwintering females seek out oviposition sites on the new season's foliage and exhibit a negatively geotactic orientation; following generations disperse throughout the remainder of the plant; and in late summer, the diapausing generation reacts positively geotactically and migrates downwards towards the lower part of the plant and beyond. This is in agreement with the observation

made by Cao (1989) that the mites moved downwards along hop vines to seek overwintering refuges in early to mid-March.

This study also found that the migrations of males and immatures were slower than those of females and that the upward distribution of TSSM, especially females and eggs, within hop plants shifted the subsequent density of active mites from the lower to the upper foliage. Mitchell (1973) demonstrated that TSSM females migrated before movement of the other mobile life stages. Perring et al. (1987) found that the distribution of eggs corresponded to location of the females on the plant and TSSM females moved away from the area in response to increasing mite density. However, intraplant-dispersal results from a tendency for a portion of the pre-reproductive females to emigrate from the leaf on which they developed, regardless of population density on that leaf (Hussey and Parr, 1963). The positive phototactic response of mites in the dispersal phase under conditions of high density and plant damage also results in mites moving up the plant and concentrating around the periphery of their host (Kennedy and Smitley, 1985). Collins and Margolies (1991) observed that TSSM females exhibited an aerial dispersal posture that helped them become airborne, and allowed them to disperse long distances under crowded conditions and deteriorating resource quality. Boyle (1957) considered that TSSM is normally disseminated by wind carriage at all life cycle stages under field conditions. In terms of leaf age, TSSM tend to be more fecund on young leaves (Henneberry, 1962; Watson, 1964; Oloumi-sadeghi et al., 1988). Carey (1982b) suggested that the age of leaves on the mainstem are always constant: all of the primary leaves below a particular node will be older, and all above it younger. Spider mites have been reported to disperse upward toward younger, presumably more nutritious leaves (Hollingsworth and Berry, 1982; Rodriguez et al., 1983). Changes in both

leaf microenvironment and food resources as mite infested plants age is strongly involved in these mite behavioural changes (Rodriguez and Rodriguez, 1987).

Furthermore, it was found that actual counts of adult females provided accurate estimates for statistical analysis, although the data were transformed when considering various types of mite densities. The results indicated that significant differences in densities of adult females between foliage heights were consistent, whereas those of the other stages were intermediate.

In a more recent study, Krainacker and Carey (1990) related the within-plant distribution of TSSM on field corn to sampling and reported that early season sampling should focus solely on the number of females on the lowest foliage while mid-season sampling should concentrate on the foliage in the middle of the plant. This is similar to the results as stated earlier.

This study provides an additional piece of evidence to support the concept which suggests that an understanding of the role of dispersal in the population dynamics of TSSM will enhance the population management of this agriculturally important mite species, allowing both more efficient and more effective management over the long term.

CHAPTER 4 DIFFERENCES IN SUSCEPTIBILITY OF HOP GENOTYPES TO INFESTATIONS BY TSSM

4.1. INTRODUCTION

The increasing problems with strains of TSSM resistant to chemical control in commercial hop yards have focused attention upon non-chemical ways of controlling these phytophagous mites. According to Trichilo and Leigh (1985), increased plant resistance to mites could reduce the need for miticides and thereby result in slower development of pesticide resistance in mites, less damage to natural enemies, reduced levels of chemicals in the environment, and a more economically produced crop.

Several attempts have been made in the past to assess hop genotypes for resistance to TSSM. Mayberry (1968) observed that the fecundity of TSSM was affected by different hop genotypes. Regev and Cone (1975) indicated that hop varieties grown both in the field and in the glasshouse differed in susceptibility to TSSM. Peters and Berry (1980a) confirmed varietal differences in susceptibility to the mites under glasshouse conditions and also obtained information indicating highly significant differences in developmental rates of TSSM reared on different hop varieties. Leszcynski et al. (1988) subsequently demonstrated differences in intrinsic rates of increase between mites on different hop cultivars.

The purpose of the present study is two fold: to evalulate levels of susceptibility and/or tolerance of a range of hop genotypes to TSSM infestations, and to conduct preliminary studies on the mechanisms of resistance involved.

4.2. MATERIALS AND METHODS

4.2.1. Artificial infestations

4.2.1.1. Sources of plant material: The rootstocks of 26 hop genotypes, as shown in the following list, were selected from a collection made by Australian Hop Marketers Pty Ltd.

No.	Code	Genotype	Parent (F. * M.)
1	M1	A-86-21	Hallerian*Open
2	M2	AB-82-64	J78*Open
3	M3	B-86-13	YF-81-80*Open
4	M4	EG-86-23	YD-81-102*YM-81-22
5	M5	EP-86-20	YR-81-113*29/70/54
6	M6	EQ-86-30	YR-81-113*YD-81-50
7	M7	E-85-20	21055*Open
8	M8	G-87-60	J-83-46*Open
9	M9	J-83-5	YS-81-37*Open
10	M10	LA-85-68	J78*29/70/SH
11	M11	L-86-17	LQ-82-38*Open
12	M12	MD-86-11	96-76-44*28/68/65
13	M13	N-86-27	AB-82-33*Open
14	M14	S-87-9	TA-84-50*Open
15	M15	TA-85-22	(4*J78)*64037M
16	M16	TB-82-5	(4*J78)*18/67/20
17	M17	TC-85-26	(4*J78)*29/70/54
18	M18	TD-85-35	(4*J78)*YB-81-77
19	M19	TD-86-1	(4*J78)*YA-81-61
20	M20	TE-86-11	(4*J78)*YD-81-50
21	M21	TF-84-15	(4*J78)*YM-81-22
22	M22	TG-86-19	(4*J78)*AF-81-148
23	M23	TH-86-10	(4*J78)*TC-81-12
24	M24	X-86-20	L-83-14*Open
25	M25	Aquila	American cultivar
26	M26	Huller Bitterer	German cultivar.

4.2.1.2. Mite culture: TSSM were reared on dwarf bean plants in an isolated chamber maintained at an average temperature of 25°C and a 16:8 (L:D) photoperiod.

4.2.1.3. Under glasshouse conditions: Two experiments were conducted to investigate the effect of hop genotype on mite population build-up.

In the first experiment (free choice), all 26 genotypes were planted into pots aligned in a completely randomized pattern on a glasshouse floor. Duplicate plants of each genotype were studied at an average temperature of 25°C with natural lighting conditions. The study commenced on October 9, 1990 when the hop plants were 45 days old. Each plant was artificially infested with 10 adult female mites onto one of its mature leaves. Six weeks after release, the number of all developmental stages of mites except eggs on each of four leaves, two in the middle region and two on the top of each plant, was counted on 4 occasions at weekly intervals. Damage caused to plants by mites was also observed on the final occasion of sampling and plants were scored on a scale of 1 to 5 where 1 = no leaf yellowing and 5 = leaves dry (after Al-Abbasi and Weigle, 1982). In addition, size measurements of 10 each of eggs, adult females, and adult males on the plants of each genotype were made using an eyepiece micrometer.

In the second experiment (no choice), the hop rootstocks of the 26 genotypes kept in the cool room at 4°C were set out in the glasshouse to grow on January 17, 1993. Five weeks later, two teneral female mites from the culture were placed into and allowed to oviposit in a small plastic leaf cage (Hughes et al., 1966) designed to provide some basic requirements, i.e. having easy removable lids for observation, light weight, good ventilation, convenient installation, ability to withstand variable climate, and low cost. The materials used for making the cages were: polyurethane foam, plastic tubing, 'lil' pins, fine nylon mesh, Kwik Grip adhesive, nail varnish, acetate sheet, and sponge. The cage body was comprised of a 1 cm. section of tubing (ca. 1.8 cm. diam.) with one smooth

surface end and the other glued with a sponge strip. Two nails were embedded in opposite sides of the tubing. The cage lid was made with a disc of acetate sheet (ca. 2.3 cm. diam.) and in it a hole (ca. 1.0 cm. diam.) was drilled for ventilation. A fine nylon mesh was glued over the ventilation hole using Kwik Grip adhesive. The acetate strips were cut to form rings which were used to assist the lids to fit snugly to the cage bodies. The backing plates were composed of polyurethane foam divided into the same dimensions (3.0 X 3.0 X 0.6 $cm.^3$). The cages were affixed to the underside of the fifth or sixth node (from the terminal) mainstem leaf of plants by pushing the pins, coated with nail varnish to prevent rust, through leaf tissue into the backing plates. Furthermore, pure lanolin was applied to the inner surface of the cages to prevent mites escaping from them. One week after release, the cages (including the leaves) were removed from the plants and the number of mites of all stages were counted under a binocular microscope (20X). This procedure was repeated four times for each hop genotype.

In addition, the number of leaves on each plant, surface areas of mature leaves, plant heights, numbers of tillers and lengths of the first four internodes from terminal shoots were also recorded for each genotype when the plant was six weeks old. The leaf surface area was determined by using a linear regression model that estimates area from measures of leaf length and width at the widest point: leaf area ($cm.^2$) = 7.903 + 0.67148 (width x length) $r^2 = 0.957$; n=93.

4.2.1.4. Under field conditions: An experimental plot was established at Horticultural Research Centre, University of Tasmania. Twelve hop genotypes were selected, based on the results of the first experiment reported in 1.3 (free choice), to represent varying levels of mite susceptibility from highly to slightly susceptible. The genotypes studied were M2, M4, M9, M10, M11, M14, M15, M18, M21, M23, M25 and

M26. The rootstocks of these genotypes were planted on October 9, 1991, in a randomized complete block design with six replications. Inter-row and inter-plant spacing at 1.0 m. x 0.7 m. was employed. Two strings supported from a 5-m. high trellis were tied down at each hill, and 2 vines were trained up each string. A total of 72 plants was used in the experimental plot. Twelve weeks after planting, mite-infested bean plants were placed uniformly among the experimental plants. Eleven weeks later, four leaves, two upper (3.6 m.) and two middle (1.8 m.) leaves on each plant, were collected at random and the number of all stages of mites was counted. The leaf surface areas were also measured by using a planimeter (Paton Electronic Planimeter, Paton Industries Pty Ltd.). At the end of the season, the hop cones were harvested and the numbers of cones as well as cone weights were determined for each genotype.

In the 1992/93 growing season, no naturally-occurring TSSM were detected on hop plants in this experimental plot even though the hop plants had reached the top of the trellis. Subsequently, the area was divided into three equal parts designated blocks A, B, and C (Fig. 4.1). Duplicated plants of the same genotype were grown in each block. All of the hop plants in Block A were inoculated with TSSM on January 5, 1993, whereas no mites were released in Blocks B and C. For this reason, hop plants in Blocks A, B, and C were regarded as infested, boundary, and uninfested plants, respectively. Inoculation was carried out by attaching one bean leaf disc which contained 10 teneral female mites from the culture to each plant. Eight weeks after release, two upper (3.6 m.) and two middle (1.8 m.) leaves on each plant were collected at random and the number of mites counted. The remaining steps of this procedure were similar to those in the previous season.

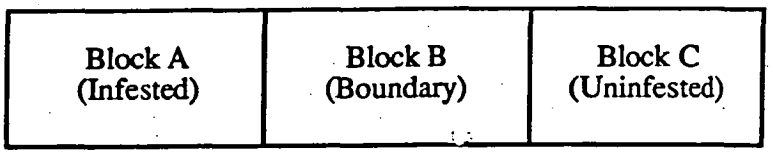


Fig. 4.1. Layout of the experimental plot at Horticultural Research Centre.

4.2.2. Natural infestations

4.2.2.1. Under glasshouse conditions: Cuttings from hop plants, of 26 genotypes, used in the first experiment (free choice) of 1.3 were propagated and grown from September 19, 1990. Duplicate plants were used for each genotype. After 20 weeks, the young plants were removed into the glasshouse in which TSSM populations had already been established. Consequently, the plants became infested naturally with TSSM from the glasshouse population. This technique was similar to that used by Shanks and Barritt (1984). Twelve weeks later, the total number of mites (except eggs) on each of the six leaves, three in the middle region, and three on the top of each plant was counted. Surface areas of leaves were measured using a planimeter. In addition, the damage ratings of hop genotypes were also observed in a similar manner to that described previously.

4.2.2.2. Under field conditions

4.2.2.2.1. Hop yard No. 1 at Bushy Park: In this hop yard, the following genotypes were studied: M1, M2, M3, M4, M5, M6, M7, M8, M9, M10, M11, M12, M13, M14, M15, M16, M17, M18, M19, M20, M21, M22, M23, and M24. Data on varietal differences in natural mite infestation were monitored in the three growing seasons, i.e. 1990/91, 1991/92 and 1992/93.

4.2.2.2.1.1. Growing season 1990/91: The leaves were sampled at weekly intervals from November 21, 1990 to February 27, 1991. One

mainstem leaf at a height of 1.8 m. was taken randomly from each plant on each sampling date and a total of 4 leaves was collected for each genotype. Leaf samples were examined under a binocular microscope (20X) and the numbers of mite eggs, immatures and adults were separately counted. This hop yard was sprayed with miticides in early January, 1991.

4.2.2.2.1.2. Growing season 1991/92: The leaves were sampled at fortnightly intervals from November 28, 1991 to March 5, 1992. As in the previous growing season, 4 leaves were sampled at a height of 1.8 m.. In addition, samples for each genotype on the final three sampling occassions consisted of one leaf which was collected at a height of 3.6 m. from the ground. Surface areas of mature leaves were measured using the planimeter. Dry weights of leaves, plant heights and growth habits of the above-ground parts of hop plants for each genotype were also recorded and it appeared that no miticides were applied to the hop plants throughout this season.

4.2.2.2.1.3. Growing season 1992/93: The leaves were sampled at fortnightly intervals from November 4, 1992 to February 24, 1993. On the first two occasions of sampling, sample leaves were collected at the fifth node from the terminal shoot of hop plants. A total of 4 leaves was taken from each genotype. The remaining steps of the procedure were similar to those in 1990/91 growing season.

4.2.2.2.2. Hop yard No. 2 at Bushy Park: In hop yard No.2, the cultivars M25 (Aquila) and M26 (Huller Bitterer) were studied. The methods used were similar to those in hop yard No. 1, except that the phytoseiid mites were released in 1990/91 season and the miticides were applied in both 1991/92 and 1992/93 seasons.

4.2.3. Data analyses

All statistical analyses were carried out using Staview SE + Graphics software on a Macintosh computer. A one-way analysis of variance was used to detect differences in plant characteristics and mite responses. Means were separated by least significant difference analysis with an alpha level of 5%. A log (x+1) transformation was used when necessary. Nonparametric procedures were also performed using Mann-Whitney U test for two group tests and the Kruskal-Wallis test for 3 or more group tests. In addition, linear regressions were performed using the procedure of the Cricketgraph computer program.

4.3. RESULTS

4.3.1. Fluctuations of mite populations among hop genotypes

4.3.1.1 Artificial infestations under glasshouse conditions: The mean number of mites per leaf on hop genotypes tested in the first experiment (free choice) is presented in Table 4.1. Analysis of variance of the transformed data showed highly significant ($p < 0.01$) differences among genotypes on the first, second, and fourth sampling date (Fig. 4.2). It was apparent that M4 had consistently fewer mites whereas M26 had consistently more mites on all sampling dates. Most of the other genotypes were intermediate between the high and low levels exhibited by these two genotypes. When the total number of mites counted on all 4 dates were considered together, highly significant differences ($p < 0.01$) in mean numbers were also detected among hop genotypes (Fig. 4.3). This clearly revealed that the least preferred genotype was M4, and the most preferred was M26.

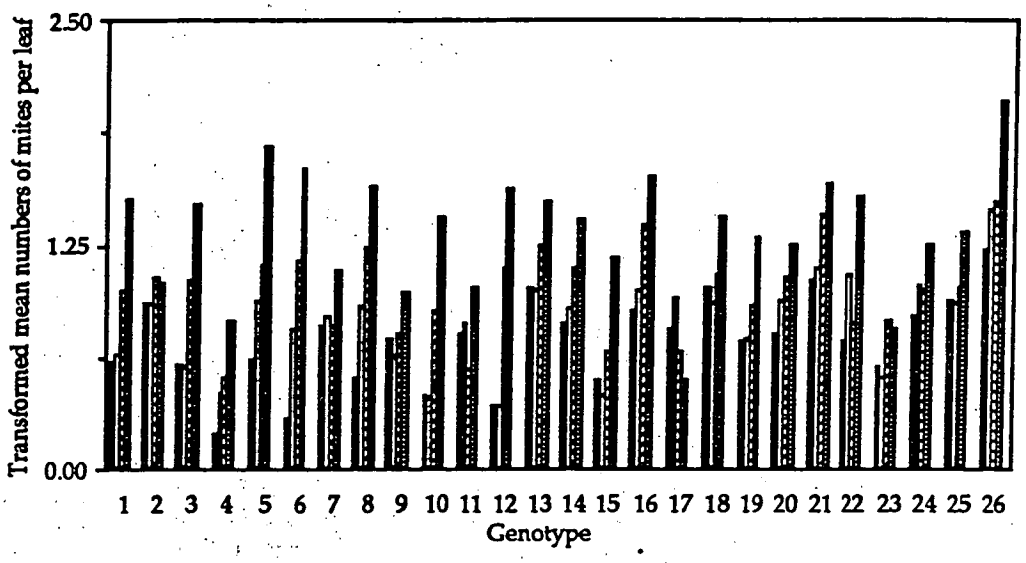
In addition, it was found that the mean egg sizes ranged from 0.14 to 0.15 mm., mean female sizes ranged from 0.36 to 0.60 mm., and mean male sizes ranged from 0.24 to 0.36 mm.. No differences in the sizes of

eggs, adult males, and adult females were noted between different genotypes.

Table 4.1. Mean numbers of mites on each genotype infested artificially under glasshouse conditions.

Genotype	Numbers of mites per leaf (mean ± SE)			
	1st. sampling date	2nd. sampling date	3rd. sampling date	4th. sampling date
M1	48.25 ± 15.50	51.25 ± 10.74	130.75 ± 15.76	480.00 ± 96.08
M2	146.50 ± 38.74	145.00 ± 37.53	242.00 ± 76.14	183.25 ± 34.86
M3	57.75 ± 22.50	43.75 ± 10.59	215.25 ± 119.70	697.75 ± 285.57
M4	12.25 ± 8.34	31.25 ± 12.51	52.25 ± 27.29	146.50 ± 72.99
M5	95.00 ± 68.26	151.00 ± 60.71	346.75 ± 163.24	1075.25 ± 264.75
M6	15.50 ± 7.86	70.00 ± 13.52	320.00 ± 141.86	696.50 ± 208.05
M7	122.50 ± 46.84	124.50 ± 24.03	124.75 ± 43.99	325.00 ± 179.16
M8	50.50 ± 37.81	115.00 ± 42.56	203.00 ± 42.44	438.00 ± 79.46
M9	55.00 ± 13.67	53.75 ± 26.86	62.50 ± 19.86	116.50 ± 47.54
M10	33.50 ± 17.78	28.50 ± 12.82	172.00 ± 108.33	443.50 ± 164.23
M11	82.25 ± 37.62	75.75 ± 10.61	120.50 ± 111.51	400.00 ± 224.96
M12	23.25 ± 13.12	18.25 ± 2.90	264.50 ± 154.93	589.25 ± 183.33
M13	84.75 ± 21.83	90.00 ± 31.85	149.25 ± 36.00	258.25 ± 49.18
M14	110.00 ± 44.38	113.75 ± 22.07	244.00 ± 78.59	489.50 ± 235.52
M15	35.00 ± 8.16	25.25 ± 3.64	71.75 ± 37.98	289.00 ± 139.78
M16	110.75 ± 55.86	198.75 ±137.64	258.50 ± 61.33	529.50 ± 159.51
M17	126.75 ± 58.80	153.50 ± 44.93	78.25 ± 41.96	39.75 ± 11.90
M18	170.25 ± 65.37	128.50 ± 31.48	223.75 ± 102.82	433.25 ± 118.46
M19	105.75 ± 46.08	118.00 ± 52.70	170.75 ± 70.45	462.00 ± 146.63
M20	91.00 ± 28.88	181.75 ± 86.84	242.00 ± 104.13	355.50 ± 128.11
M21	176.50 ± 79.16	198.50 ± 69.58	346.75 ± 102.22	518.50 ± 135.60
M22	184.25 ±146.12	230.25 ± 56.97	155.25 ± 68.46	635.50 ± 153.97
M23	48.25 ± 17.86	41.50 ± 13.96	93.00 ± 18.63	79.50 ± 9.91
M24	88.50 ± 25.71	127.00 ± 28.73	110.00 ± 18.27	211.75 ± 42.41
M25	148.50 ± 43.19	154.25 ± 57.98	207.00 ± 102.22	393.75 ± 141.64
M26	247.00 ± 46.78	414.75 ± 25.96	469.00 ± 63.22	1752.75 ± 288.30
p-value	0.1060ns	0.0001**	0.1322ns	0.0001**
PLSD	137.19	130.66	241.51	450.21

Fig. 4.2. Comparison of transformed mean numbers of mites per leaf between different genotypes at different sampling time.



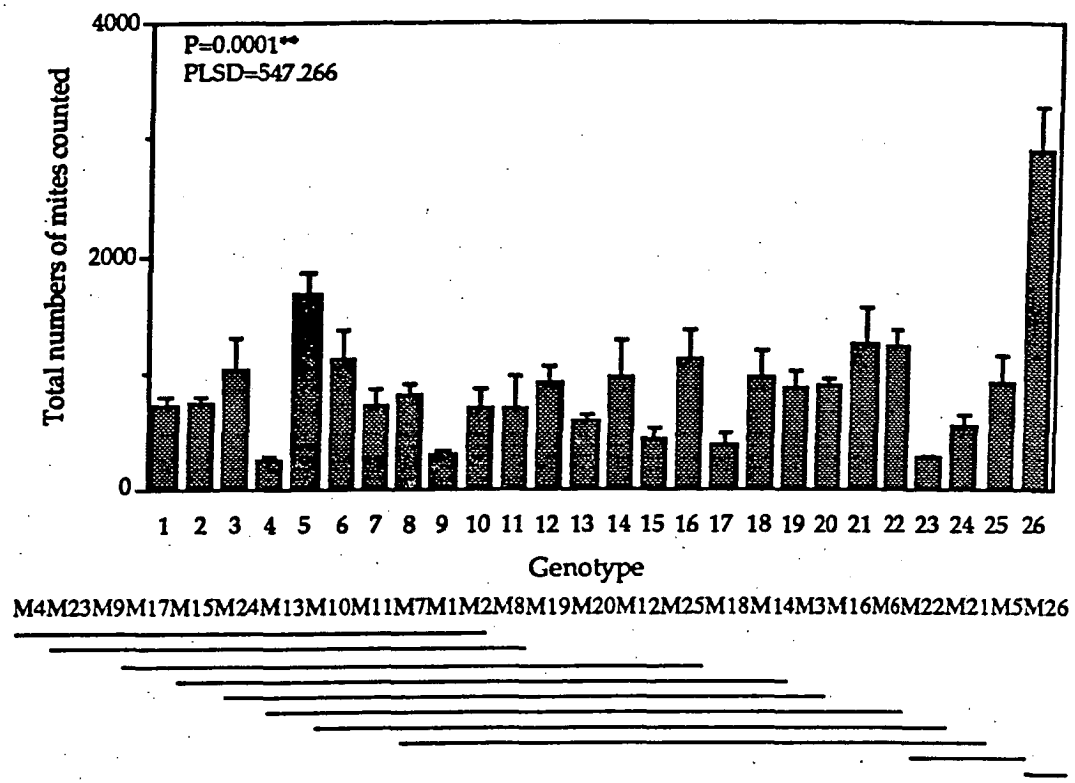
Sampling 1 p=0.0068** (Fisher PLSD = 0.729)
M4M6M10M12M8M5M3M15M23M1M9M11M16M19M22M24M20M17M13M14M7M25M21M2M18M26

Sampling 2 p=0.0001** (Fisher PLSD = 0.523)
M10M12M4M15M23M9M3M1M6M13M9M11M19M16M14M5M25M24M7M18M20M17M2M21M22M26

Sampling 3 p=0.0749ns
M11M4M15M9M17M10M23M22M7M24M19M1M13M25M3M6M5M18M12M20M2M14M8M16M21M26

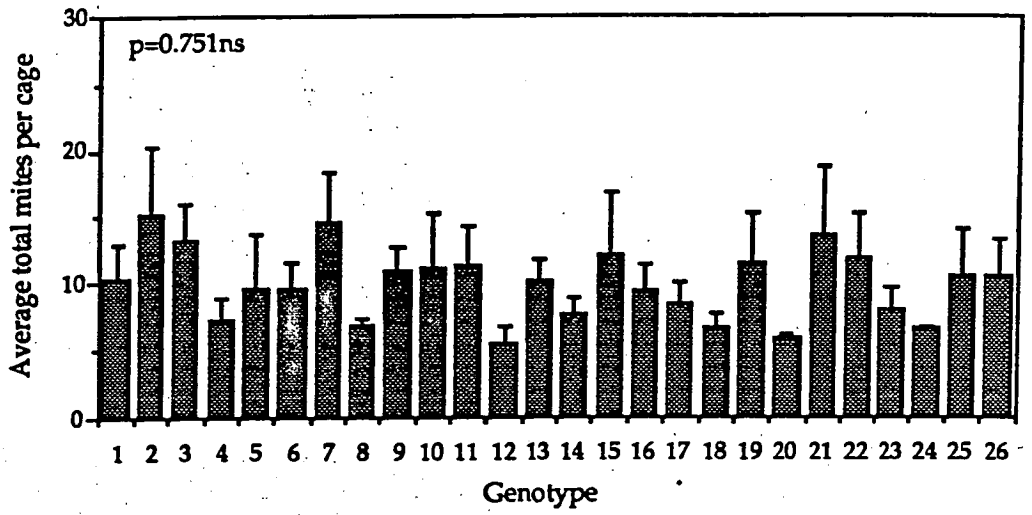
Sampling 4 p=0.0001** (Fisher PLSD = 0.545)
M17M23M4M11M9M2M24M15M7M13M20M25M19M10M14M18M3M8M1M16M21M12M22M6M5M26

Fig. 4.3. Total numbers of mites counted on each genotype in the first artificial infestation experiment under glasshouse conditions.



In the second experiment (no choice), numbers of mites in leaf cages did not differ significantly among genotypes ($p \geq 0.05$; Fig. 4.4). This indicated that TSSM could survive equally on all genotypes used in these studies. The average number of mites varied from 5.5 to 15.0 with M2 having the highest mean value.

Fig. 4.4. Mean numbers of mites on each genotype in the second artificial infestation experiment under glasshouse conditions.



4.3.1.2. Artificial infestations under field conditions: When twelve genotypes selected from the first experiment in the glasshouse were infested with mites from bean plants and evaluated in the field during the 1991/92 growing season, there were highly significant differences in mean numbers of mites per cm.^{2} among genotypes (Table 4.2). After 11 weeks, M26 had the highest mite density followed by M2. M4 had the lowest density compared with other genotypes, which showed an intermediate situation.

Table 4.2. Mean numbers of mites on each genotype grown at the Horticultural Research Centre.

Genotype	Susceptibility obtained from the results of glasshouse experiment	Average numbers of mites per cm^2 (Mean ± SE)	
		1991/92 season p=0.0028** PLSD=0.65	1992/93 season p=0.7616ns PLSD=0.094
M4	The least	0.055 ± 0.044	0.059 ± 0.012
M23	↓	0.084 ± 0.073	0.017 ± 0.006
M9		0.582 ± 0.531	0.026 ± 0.019
M15		0.213 ± 0.109	0.064 ± 0.013
M10		0.079 ± 0.045	0.061 ± 0.042
M11		0.167 ± 0.079	0.078 ± 0.047
M2		0.852 ± 0.351	0.017 ± 0.012
M25		0.077 ± 0.031	0.007 ± 0.006
M18		0.056 ± 0.016	0.086 ± 0.076
M14		0.098 ± 0.045	0.056 ± 0.037
M21		0.217 ± 0.153	0.033 ± 0.025
M26	The highest	1.323 ± 0.418	0.019 ± 0.012

However, analysis of variance of the data for 1992/93 growing season showed no significant differences ($p \geq 0.05$) in mean numbers of mites per cm^2 among hop genotypes infested with the same number of mites on leaf discs (Table 4.2). The mite number per cm^2 varied from 0.007 to 0.086 per cm^2 with M18 having the highest density.

4.3.1.3. Natural infestations under glasshouse conditions: Highly significant differences ($p < 0.01$) in mean numbers of mites per leaf were found among hop genotypes infested naturally in the glasshouse (Table 4.3). M26 had the highest density compared to the other hop genotypes, followed by M20. The least infested genotypes were M2, M4, M7, M8, M9, M14, and M16. When the mite density was transformed to numbers of mites per cm^2, similar results were also obtained.

Table 4.3. Mean numbers of mites on each genotype infested naturally under glasshouse conditions.

Genotype	Average number of mites per leaf (p=0.0062**)	Average number of mites per cm^2 (p=0.0003**)
M1	32.33 ± 9.39 bcde	6.14 ± 1.79 ab
M2	4.17 ± 1.64 a	0.84 ± 0.33 a
M3	18.67 ± 8.68 abc	3.01 ± 1.40 ab
M4	6.00 ± 2.49 a	0.82 ± 0.34 a
M5	14.33 ± 8.39 abc	2.40 ± 1.40 ab
M6	10.17 ± 3.74 abc	1.81 ± 0.67 ab
M7	6.50 ± 2.63 a	1.19 ± 0.48 a
M8	4.33 ± 2.01 a	0.80 ± 0.37 a
M9	7.67 ± 3.95 a	1.38 ± 0.71 ab
M10	25.33 ± 13.78 abcd	5.11 ± 2.78 ab
M11	24.17 ± 8.52 abcd	3.92 ± 1.38 ab
M12	17.83 ± 6.01 abc	3.22 ± 1.09 ab
M13	8.00 ± 2.13 ab	2.35 ± 0.62 ab
M14	4.50 ± 1.91 a	0.80 ± 0.34 a
M15	22.50 ± 4.53 abcd	3.28 ± 0.66 ab
M16	7.17 ± 2.46 a	1.57 ± 0.54 ab
M17	12.67 ± 3.14 abc	2.53 ± 0.63 ab
M18	13.33 ± 2.85 abc	2.16 ± 0.46 ab
M19	20.17 ± 5.71 abcd	4.00 ± 1.13 ab
M20	43.83 ± 20.66 de	6.97 ± 3.29 bc
M21	23.50 ± 10.40 abcd	5.18 ± 2.29 ab
M22	33.17 ± 7.68 cde	5.27 ± 1.22 ab
M23	18.50 ± 8.40 abc	4.30 ± 1.95 ab
M24	11.00 ± 5.23 abc	1.83 ± 0.87 ab
M25	12.83 ± 2.55 abc	2.62 ± 0.52 ab
M26	53.17 ± 24.91 e	17.07 ± 8.00 c

Means with the same letter in a column are not significantly different (P>0.05) using Fisher PLSD.

4.3.1.4. Natural infestations under field conditions Two measurements were used to evaluate differences in susceptibility of hop

genotypes to TSSM. These were the average number of mites on upper (3.6 m.) and middle (1.8 m.) leaves and the numbers of mites on leaves of the same age.

In hop yard No.1, there were significant differences ($p < 0.05$) in average numbers of mites per sq.cm on leaves at the two foliage heights among hop genotypes on all sampling dates (Table 4.4). Among all genotypes studied, M13 was found to have significantly higher mite densities than the rest ($p < 0.05$) on the first sampling date (February 2, 1992). There was no statistically significant difference in mite densities among the genotypes studied after deletion of M13 ($p \geq 0.05$). On the second and third sampling date (February 20, and March 5, 1992), it was found that significant differences in mite densities between hop genotypes had increased, indicating that mites showed a preference to feed on some genoytypes. In terms of the total number of mites counted on all three sampling dates, M13 had the highest mite density, followed by M2, M7, and M12 with M1, M19, M4, M10, M16, M15, M17, and M24 recording the lowest number of mites. When mean numbers of mites per $cm.^2$ on leaves at the same age were used to evaluate for susceptibility during 1992/93 season, similar results were also obtained (Table 4.5). It was found that M12 and M13 had significantly higher total mites counted on both sampling dates than did the other genotypes. M2, M6 and M5 also had higher total mite counts. Nevertheless, total numbers of mites on the remaining genotypes did not differ significantly from each other.

In hop yard No.2, a comparison of average numbers of mites on the 2 foliage heights indicated that M25 had consistently fewer mite densities than M26 during 1991/92 season (Fig. 4.5). This reveals that mites showed a lower degree of preference for M25 than to M26. However, no mites were detected on leaves at the fifth node below the terminal shoot of both genotypes in the early season.

Table 4.4. Mean density of TSSM on leaves of 24 genotypes in hop yard No.1 during 1991/92 season. (all leaves collected at 1.8 and 3.6 m. heights)

Genotype	Average number of mites per cm.^{2}			Total
	6/2/92	20/2/92	5/3/92	
M1	0.000 a	0.015 a	0.014 a	0.029 a
M2	0.111 a	0.852 de	0.696 cd	1.659 i
M3	0.270 a	0.223 abc	0.550 bcd	1.042 fghi
M4	0.000 a	0.050 a	0.075 ab	0.124 abc
M5	0.000 a	0.169 ab	0.495 abcd	0.665 bcdefg
M6	0.063 a	0.510 bcd	0.612 cd	1.185 fghi
M7	0.200 a	0.313 abcd	1.002 d	1.515 hi
M8	0.000 a	0.082 a	0.737 bcd	0.819 cdefgh
M9	0.150 a	0.233 abcd	0.636 bcd	1.019 efghi
M10	0.000 a	0.036 a	0.195 abc	0.231 abcd
M11	0.034 a	0.278 abcd	0.299 abcd	0.611 bcdefg
M12	0.300 a	0.078 a	1:156 d	1.535 ghi
M13	2.172 b	1.062 e	2.969 e	6.203 j
M14	0.035 a	0.204 abc	0.974 d	1.212 fghi
M15	0.003 a	0.092 ab	0.211 abc	0.306 abcde
M16	0.072 a	0.044 a	0.166 abc	0.282 abcd
M17	0.001 a	0.071 a	0.432 abcd	0.504 abcdef
M18	0.261 a	0.553 cde	0.324 abcd	1.139 fghi
M19	0.000 a	0.004 a	0.087 ab	0.091 ab
M20	0.393 a	0.058 a	0.628 bcd	1.079 efghi
M21	0.053 a	0.108 ab	0.639 cd	0.800 defghi
M22	0.051 a	0.216 abc	0.557 bcd	0.824 defghi
M23	0.010 a	0.141 ab	0.837 d	0.988 fghi
M24	0.000 a	0.176 abc	0.331 abcd	0.507 abcdef
p-value (Transformed data)	0.0280*	0.0004**	0.0001**	0.0001**

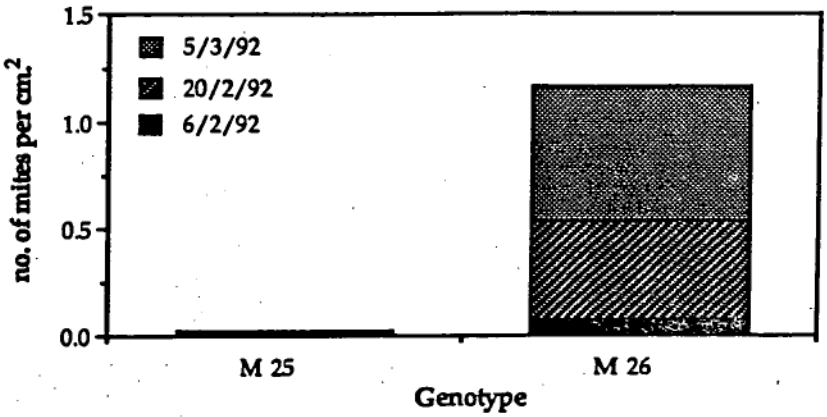
Means with the same letter in a column are not significantly different (P>0.05) using Fisher PLSD.

Table 4.5. Mean density of TSSM on leaves at node No.5 of 24 genotypes in hop yard No. 1 during 1992/93 season.

Genotype	Average number of mites per cm^2		Total
	4/11/92	18/11/92	
M1	0.000 a	0.000 a	0.000 a
M2	0.022 a	0.883 d	0.905 c
M3	0.011 a	0.040 ab	0.050 a
M4	0.000 a	0.013 a	0.013 a
M5	0.084 b	0.403 bc	0.486 b
M6	0.023 a	0.464 c	0.487 b
M7	0.007 a	0.043 ab	0.050 a
M8	0.006 a	0.033 ab	0.038 a
M9	0.000 a	0.052 ab	0.052 a
M10	0.000 a	0.089 abc	0.089 a
M11	0.010 a	0.146 abc	0.156 ab
M12	0.083 b	1.435 e	1.518 d
M13	0.112 b	1.402 e	1.514 d
M14	0.000 a	0.015 ab	0.015 a
M15	0.000 a	0.003 a	0.003 a
M16	0.010 a	0.014 ab	0.024 a
M17	0.000 a	0.098 abc	0.098 a
M18	0.000 a	0.043 ab	0.043 a
M19	0.006 a	0.000 a	0.006 a
M20	0.000 a	0.000 a	0.000 a
M21	0.000 a	0.000 a	0.000 a
M22	0.000 a	0.004 a	0.004 a
M23	0.000 a	0.329 abc	0.329 ab
M24	0.000 a	0.053 ab	0.053 a
p-value	0.0006**	0.0001**	0.0001**
PLSD	0.059	0.389	0.382

Means with the same letter in a column are not significantly different (P>0.05) using Fisher PLSD.

Fig. 4.5. Total number of mites per cm.^{2} of leaves counted in hop yard No. 2 during the 1991/92 season.



4.3.2. Leaf-feeding damage (Tolerance test)

4.3.2.1. Glasshouse studies: This test was performed by pooling the data of damage ratings in the first of the two artificial infestation experiments and that of damage ratings in the natural infestation under glasshouse conditions. According to ANOVA, these genotypes showed highly significant differences ($p < 0.01$) in susceptibility to the pest (Table 4.6). The genotype M4 and M9 were the least susceptible, while the genotypes M21 and M26 were the most susceptible (Plate 4). All other genotypes were intermediate.

4.3.2.2. Field studies: In hop yard No. 1, the seasonal accumulation of mite-days per leaf for adult females, adult males, immatures, motiles, eggs, and total mites on each genotype in 1990/91, 1991/92, and 1992/93 growing seasons is illustrated in Fig. 4.6, 4.7, and 4.8, respectively. According to the Kruskal-Wallis test, pooling all data for the season over the 3-yr study showed no significant differences ($p \geq 0.05$) in accumulated mite-days among genotypes in this hop yard (Fig. 4.9). On average M2, M6, M9, M12, and M13 were highly preferred genotypes, whereas M1, M4, M10, M16, and M19 were least preferred.

Table 4.6. Damage ratings at 42 days after infestation of hop cultivars in replications 1 and 2 and at 84 days after infestation of those in replications 3 and 4 under glasshouse conditions.

Genotype	Damage rating (1-5)				Average p=0.0006** PLSD=0.971
	Artificial infestations		Natural infestations		
	Rep. 1	Rep. 2	Rep. 3	Rep. 4	
M1	2	2.5	3	3	2.625 bcd
M2	3	3	2.5	2	2.625 bcd
M3	3	2.5	3	5	3.375 de
M4	1	1	2	2	1.500 a
M5	4	3.5	3	3	3.375 de
M6	3	2.5	2	3	2.625 bcd
M7	3	2	3	3	2.750 bcd
M8	3	3	2	3	2.750 bcd
M9	2	2	2	2	2.000 ab
M10	2	2.5	3	4	2.875 bcd
M11	2	2.5	2	3	2.375 abc
M12	2.5	1.5	5	3	3.000 cd
M13	3	3	3	3	3.000 cd
M14	3	2.5	3	2	2.625 bcd
M15	3	2.5	3	3	2.875 bcd
M16	3.5	3	2	3	2.875 bcd
M17	2	3	3	3	2.750 bcd
M18	4	3	2	3	3.000 cd
M19	2	3	3	3	2.750 bcd
M20	3	2	3	5	3.250 cde
M21	4	4	5	5	4.500 f
M22	2	3	3	3	2.750 bcd
M23	3	2	3	3	2.750 bcd
M24	3	2	4	3	3.000 cd
M25	3	3	3	3	3.000 cd
M26	5	5	3	3	4.000 ef

Means with the same letter in a column are not significantly different (P>0.05) using Fisher PLSD.

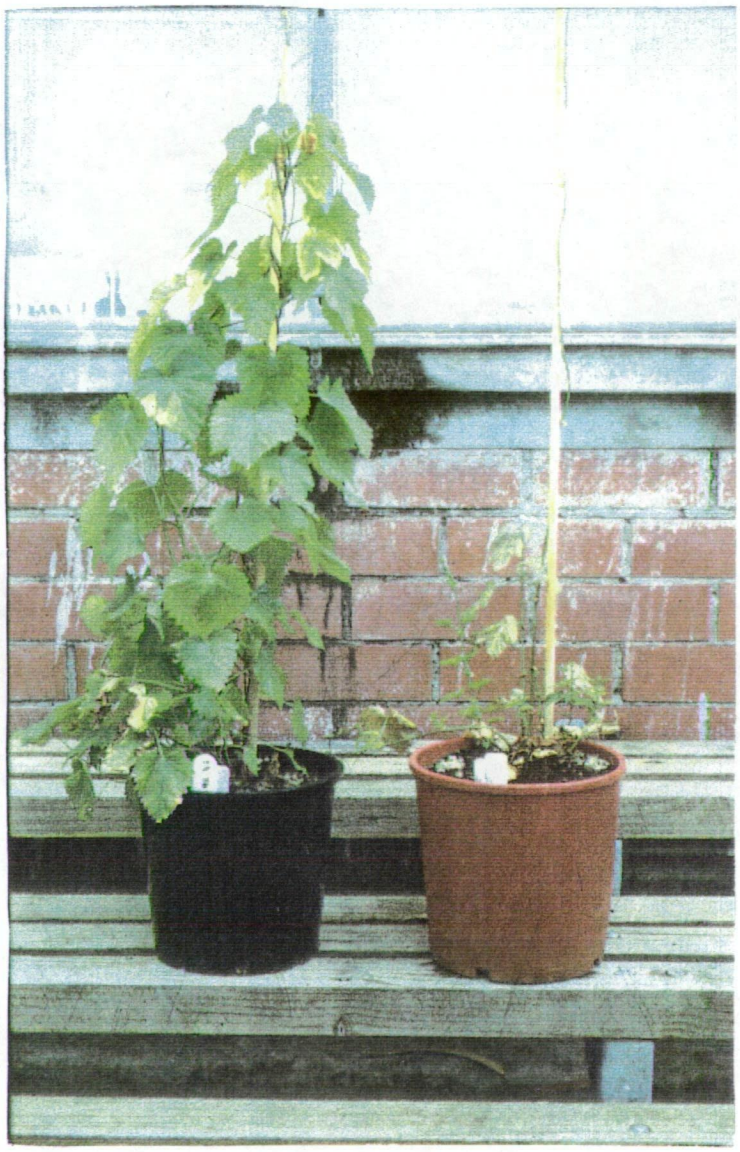


Plate 4. Hop plants infested by TSSM under glasshouse conditions:

M4 (left) and M26 (right).

Fig. 4.6. Cumulative mite-days on each genotype grown in hop yard No.1 during the 1990/91 season.

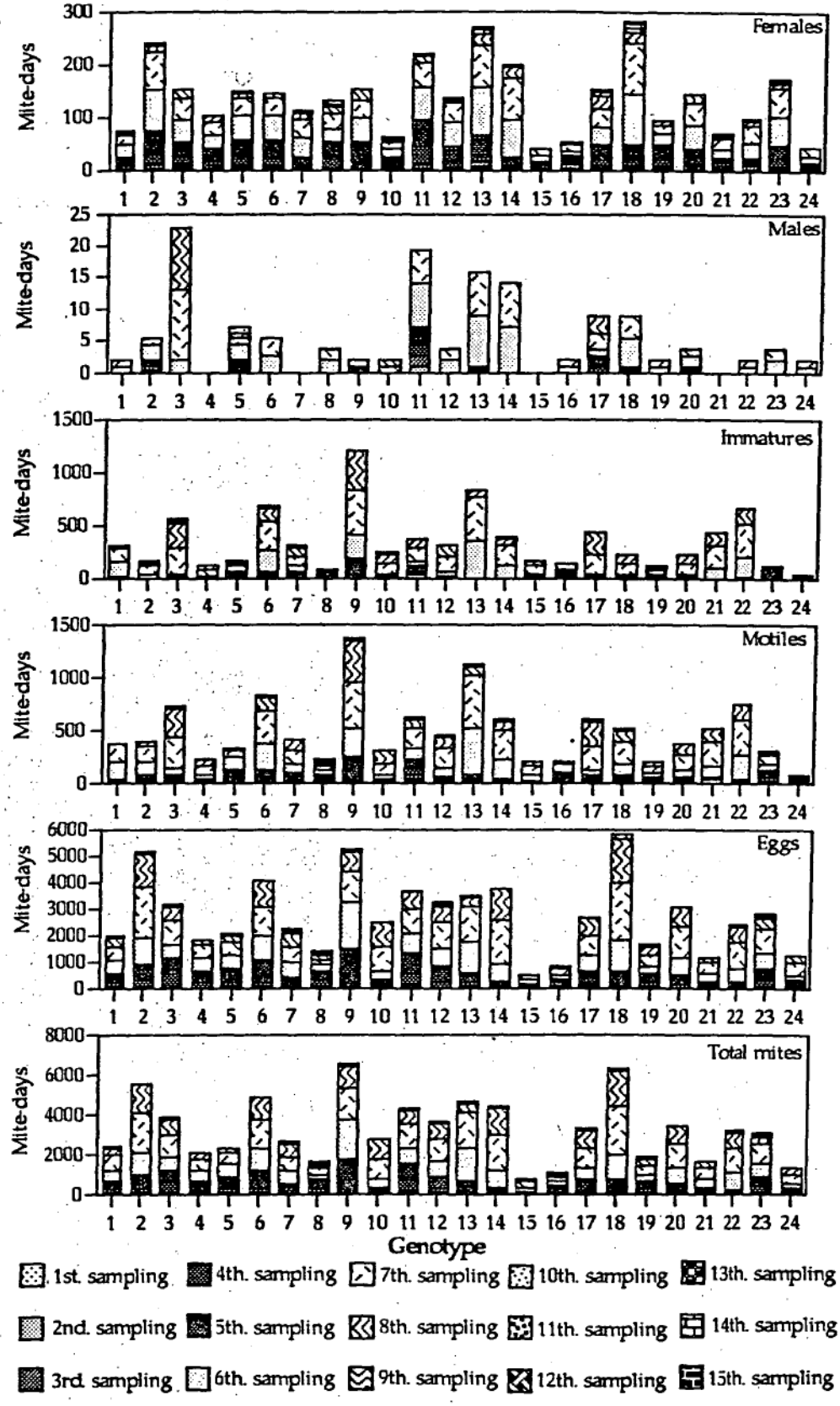


Fig. 4.7. Cumulative mite-days on each genotype grown in hop yard No.1 during the 1991/92 season.

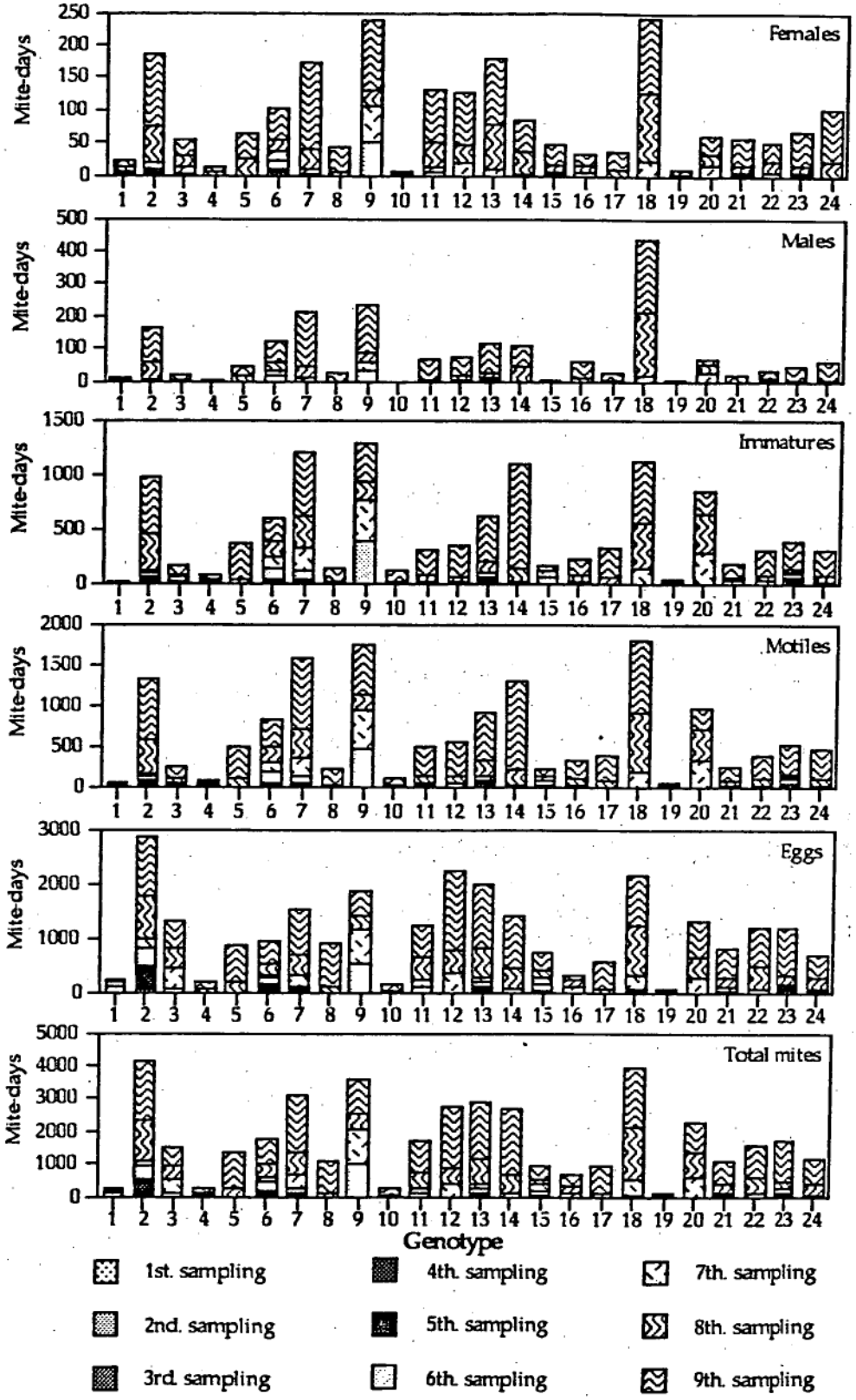


Fig. 4.8. Cumulative mite-days on each genotype grown in hop yard No.1 during the 1992/93 season.

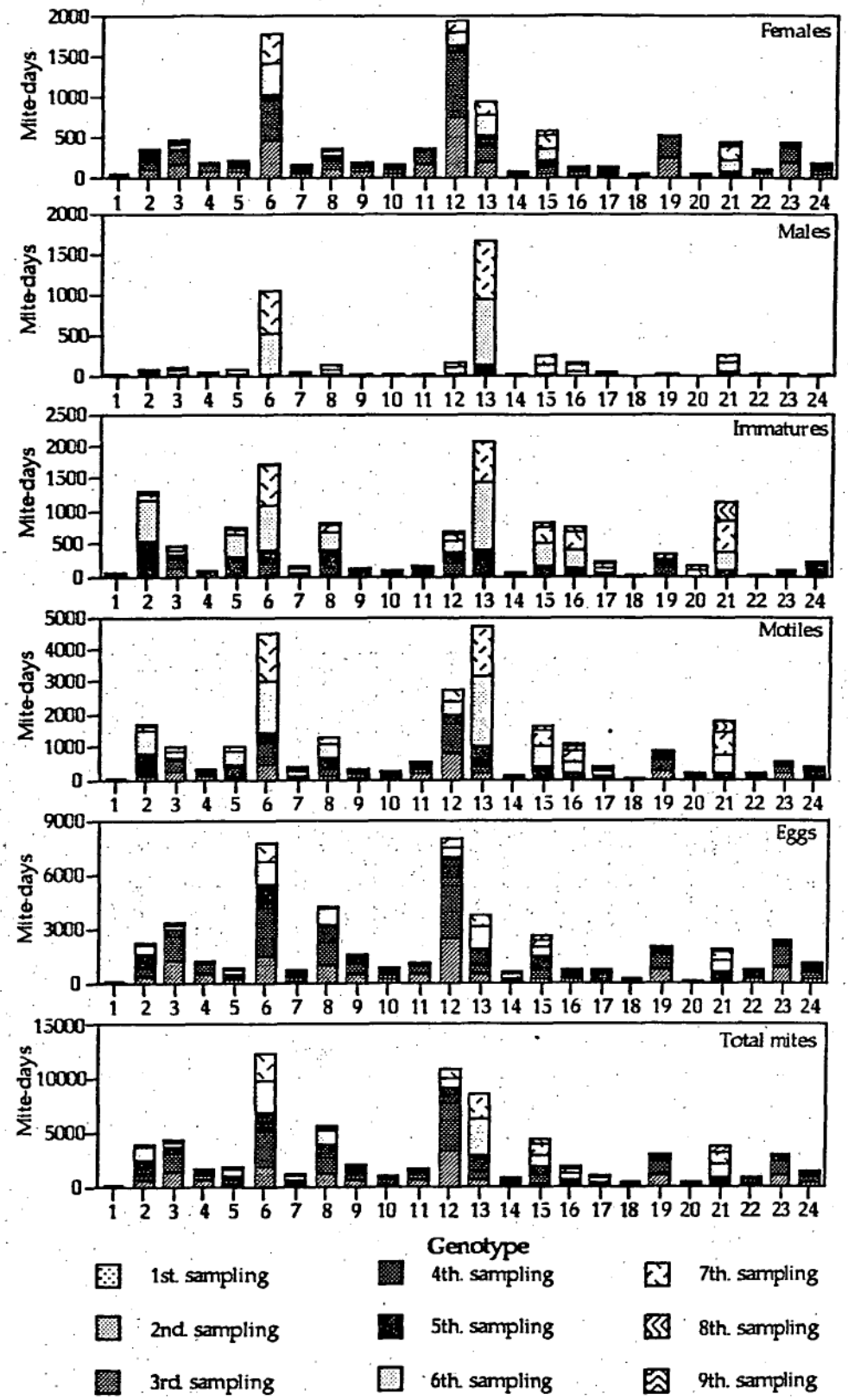
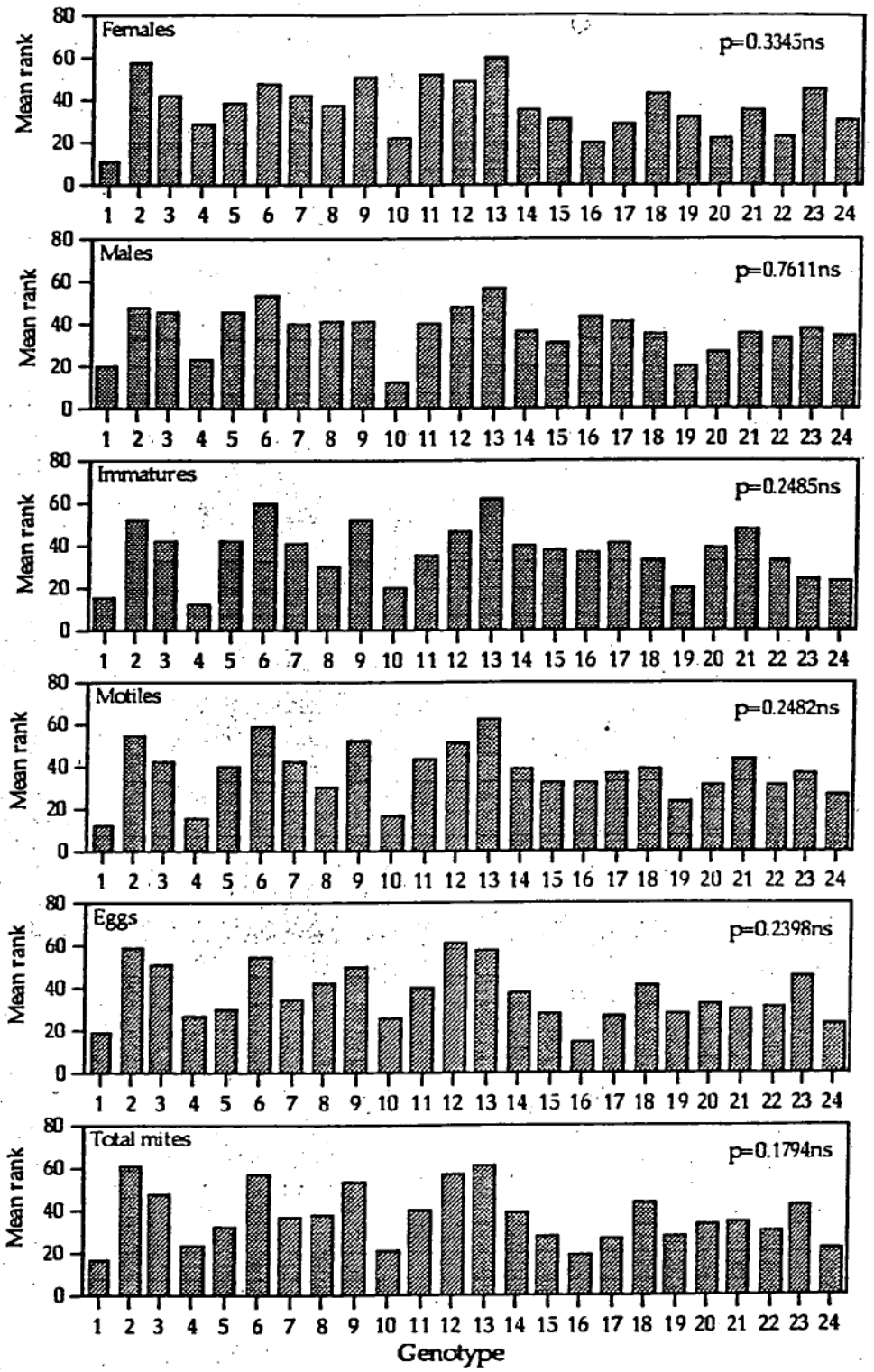


Fig. 4.9. Kruskal-Wallis mean ranks of cumulative mite-days for each genotype grown in hop yard No.1.



In hop yard No.2, the seasonal accumulation of mite-days per leaf for adult females, adult males, immatures, motiles, eggs, and total mites on M25 and M26 in each growing season is presented in Fig. 4.10, 4.11, and 4.12. According to the Mann-Whitney U test, there were significant differences ($p < 0.05$) in those accumulated mite-days between these genotypes (Fig. 4.13).

4.3.3. Plant characteristics

The following results were obtained for leaf areas, leaf numbers, tiller numbers and plant heights of hops in the glasshouse as well as surface areas and dry weights of leaves, plant heights and the growth habit of the above-ground parts of hop plants in the field.

4.3.3.1. Hops in the glasshouse: For all of the plant characteristics studied, there were no significant differences ($p \geq 0.05$) in length of internodes among different genotypes (Table 4.7), whereas highly significant differences ($p < 0.01$) in surface areas of mature leaves, numbers of leaves on hop plants, numbers of tillers and plant heights were found among genotypes (Table 4.8, 4.9, 4.10 and 4.11). It was apparent that leaf damage ratings of the hop genotypes were negatively correlated with their leaf areas, leaf numbers, tiller numbers and plant heights ($b = -0.35, -10.76, -0.97$, and -9.46, respectively); however, these relationships ($r^2 = 0.152, 0.093, 0.068$, and 0.02, respectively) were not statistically significant ($p \geq 0.05$; Fig. 4.14).

In addition, significant differences in plant heights between the least susceptible genotype M4 and the most susceptible genotype M26 demonstrated that M4 grew faster than M26 at the same points in time (Table 4.11). Leaf surface areas and the number of leaves on the plant also differed significantly between these genotypes (Table 4.8 and 4.9), whereas the number of tillers did not differ significantly (Table 4.10).

Fig. 4.10. Cumulative mite-days on each genotype grown in hop yard No.2 during the 1990/91 season.

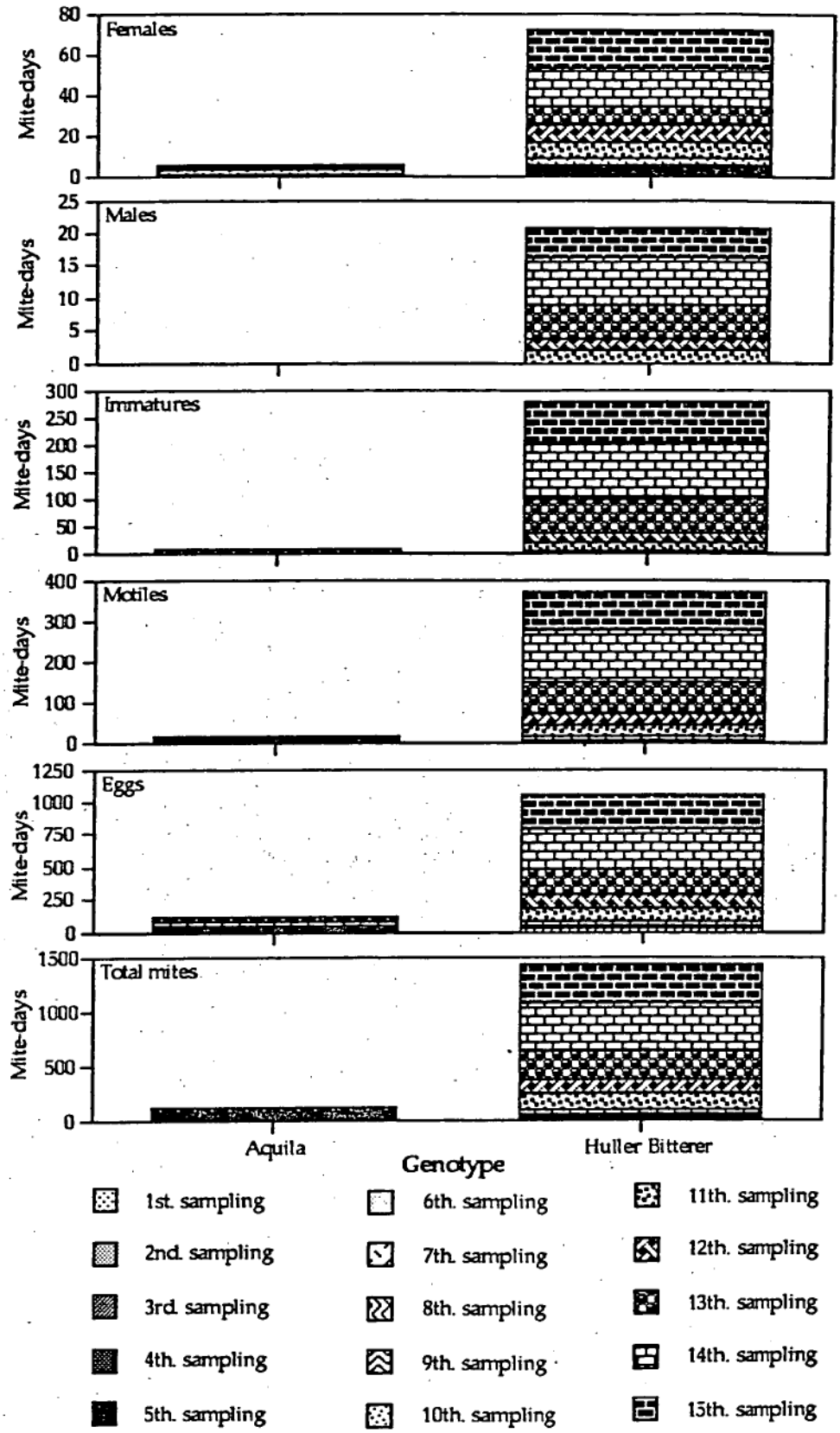


Fig. 4.11. Cumulative mite-days on each genotype grown in hop yard No.2 during the 1991/92 season.

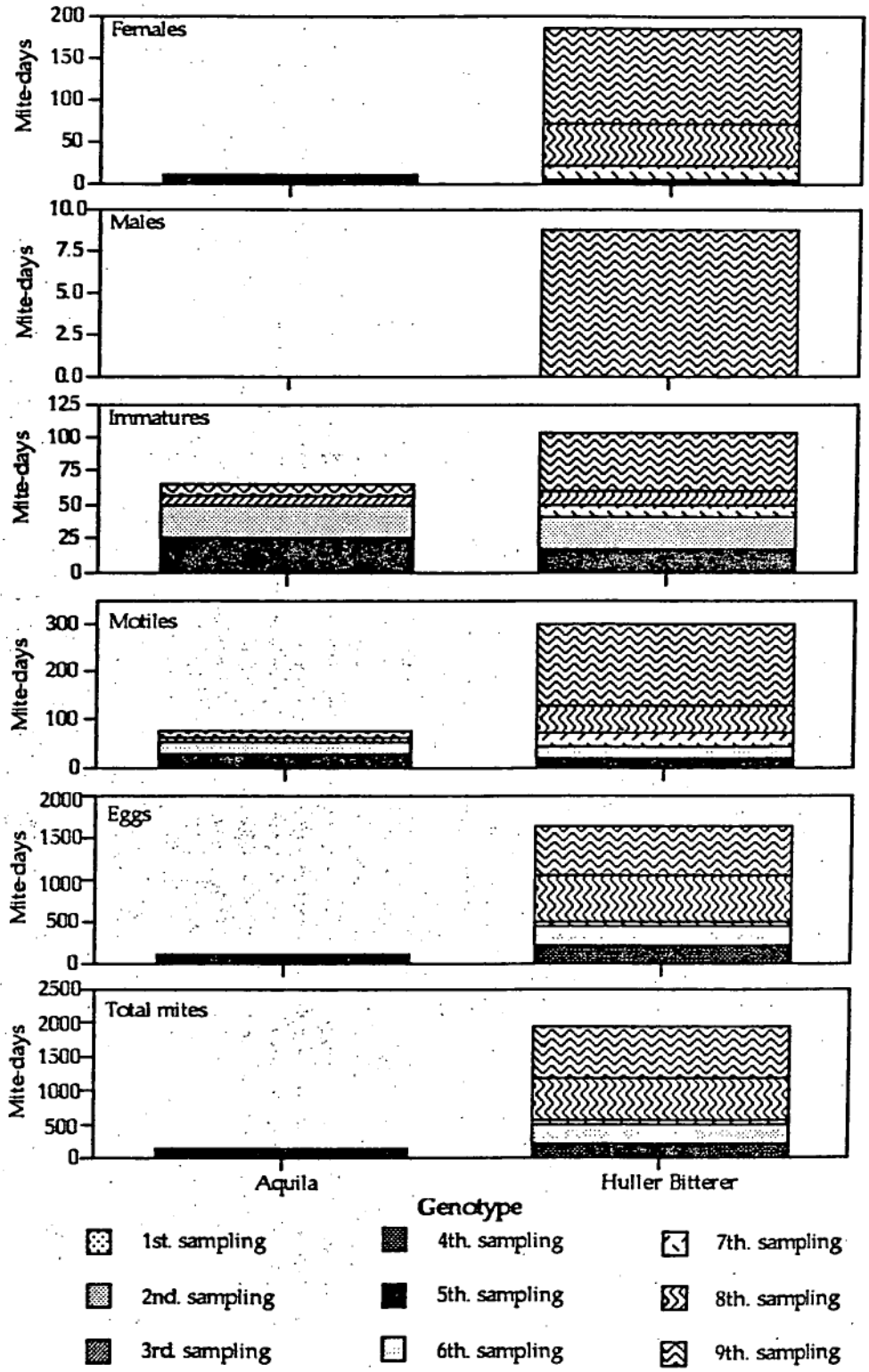


Fig. 4.12. Cumulative mite-days on each genotype grown in hop yard No.2 during the 1992/93 season.

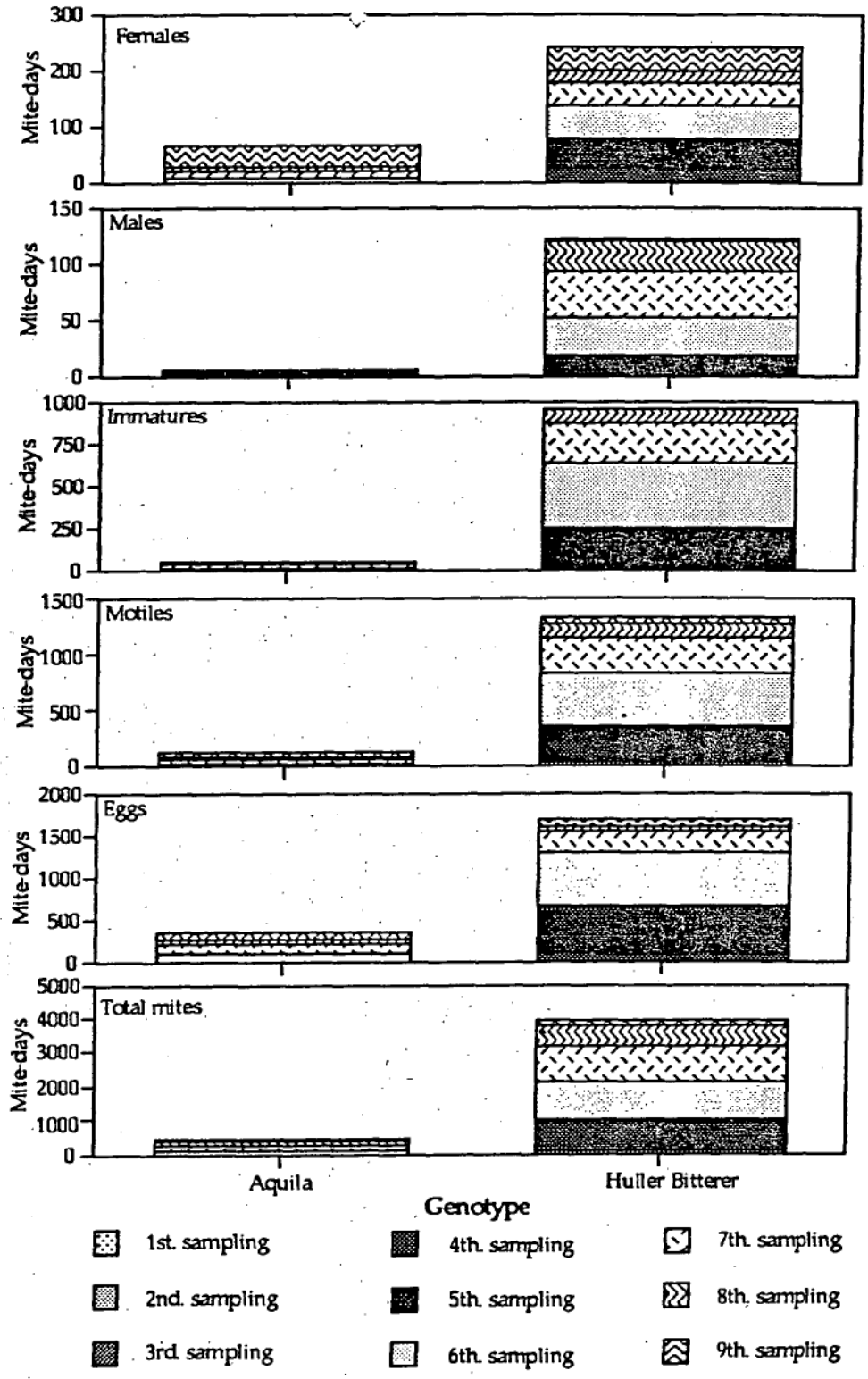


Fig. 4.13. Mann-Whitney mean ranks of cumulative mite-days for each genotype grown in hop yard No.2.

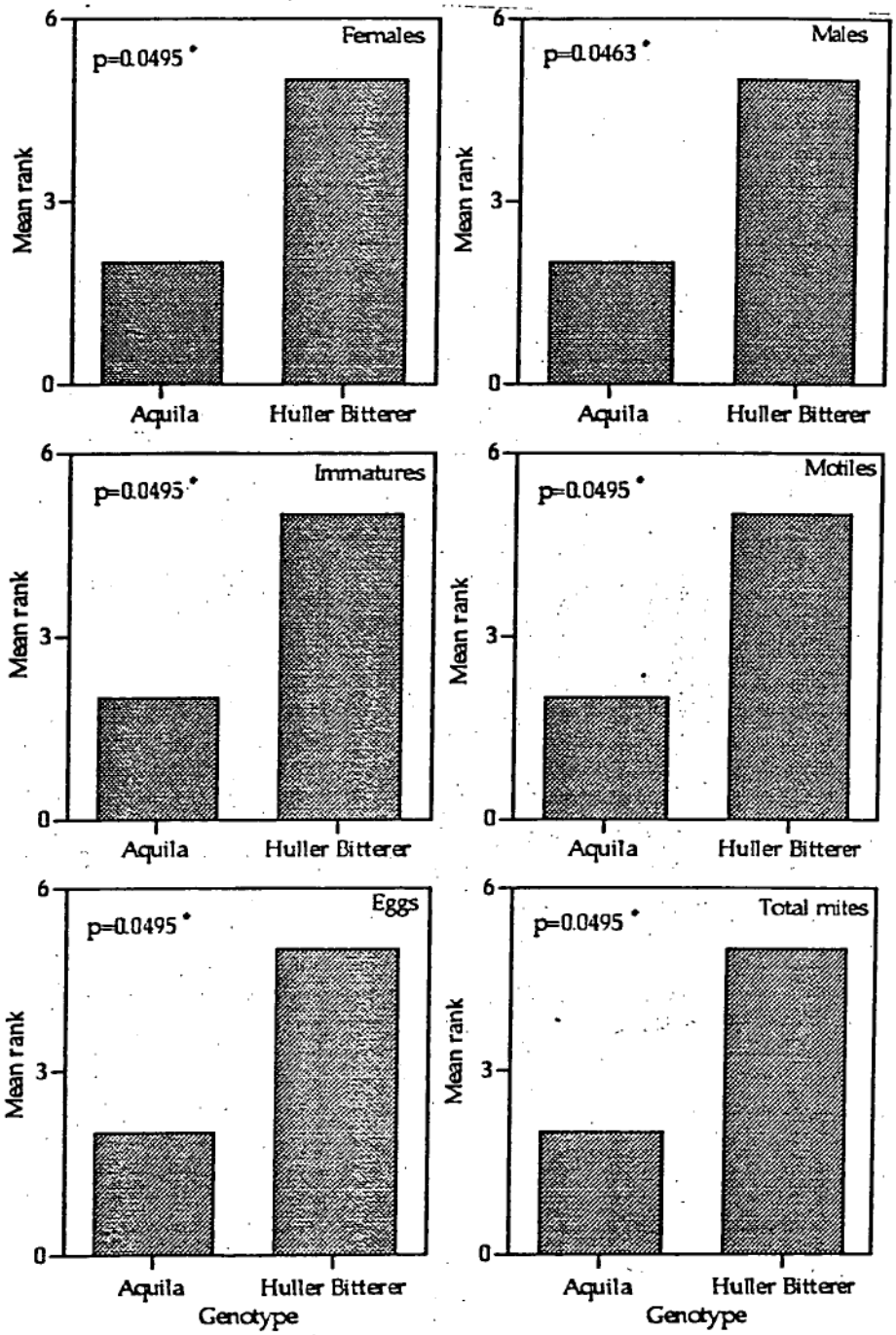


Table 4.7. Mean internode lengths of each hop genotype grown under glasshouse conditions, measured at 6 weeks after establishment.

Genotype	Internode lengths (cm.) means ± SE
M1	7.12 ± 1.85
M2	7.91 ± 0.64
M3	6.81 ± 1.98
M4	7.63 ± 0.33
M5	6.09 ± 0.24
M6	9.07 ± 0.19
M7	5.62 ± 1.72
M8	7.90 ± 1.03
M9	4.74 ± 0.68
M10	6.63 ± 1.73
M11	8.53 ± 0.59
M12	6.93 ± 1.28
M13	2.72 ± 0.63
M14	6.88 ± 2.13
M15	6.70 ± 1.57
M16	2.15 ± 0.16
M17	8.50 ± 1.01
M18	5.18 ± 1.08
M19	6.62 ± 2.07
M20	7.13 ± 2.46
M21	6.54 ± 1.70
M22	7.12 ± 1.66
M23	6.77 ± 1.21
M24	5.57 ± 0.66
M25	6.77 ± 2.24
M26	4.09 ± 1.45
p-value	0.161ns
PLSD	3.983

Table 4.8. Mean leaf areas of each hop genotype grown under glasshouse conditions.

Genotype	Leaf area ($cm.^2$) means ± SE
M1	4.72 ± 0.34 cdefghi
M2	4.71 ± 0.38 cdefghi
M3	4.36 ± 0.35 abcdefg
M4	4.80 ± 0.27 defghij
M5	3.91 ± 0.33 abc
M6	4.60 ± 0.38 bcdefghi
M7	4.97 ± 0.35 efghij
M8	5.14 ± 0.35 ghij
M9	4.46 ± 0.25 abcdefgh
M10	4.50 ± 0.30 bcdefgh
M11	5.01 ± 0.26 fghij
M12	4.36 ± 0.24 abcdefg
M13	3.67 ± 0.19 a
M14	4.21 ± 0.23 abcdef
M15	4.71 ± 0.31 cdefghi
M16	4.17 ± 0.17 abcde
M17	5.11 ± 0.30 ghij
M18	5.18 ± 0.31 hij
M19	4.15 ± 0.29 abcd
M20	4.71 ± 0.20 cdefghi
M21	4.11 ± 0.30 abcd
M22	5.39 ± 0.38 ij
M23	4.36 ± 0.27 abcdefg
M24	5.61 ± 0.29 j
M25	4.08 ± 0.28 abcd
M26	3.70 ± 0.17 ab
p-value	0.0001**
PLSD	0.819

Means with the same letter in a column are not significantly different (P>0.05) using Fisher PLSD.

Table 4.9. Mean numbers of leaves on plants of each hop genotype grown under glasshouse conditions.

Genotype	Number of leaves per plant means ± SE	
M1	63.0 ± 4.14	abcdef
M2	92.5 ± 8.33	efg
M3	51.8 ± 7.69	abcd
M4	74.8 ± 8.99	abcdefg
M5	53.3 ± 7.35	abcd
M6	81.5 ± 24.13	abcdefg
M7	50.3 ± 12.55	abc
M8	106.5 ± 16.13	g
M9	105.8 ± 16.31	g
M10	78.5 ± 16.52	abcdefg
M11	90.8 ± 19.75	defg
M12	60.5 ± 5.12	abcde
M13	46.5 ± 24.91	ab
M14	65.5 ± 12.09	abcdef
M15	70.8 ± 7.39	abcdefg
M16	42.5 ± 19.12	a
M17	84.3 ± 12.44	bcdefg
M18	83.3 ± 15.01	bcdefg
M19	47.3 ± 6.42	ab
M20	44.0 ± 8.78	a
M21	86.8 ± 12.46	cdefg
M22	70.0 ± 13.44	abcdefg
M23	101.0 ± 15.59	fg
M24	78.0 ± 21.09	abcdefg
M25	52.8 ± 3.25	abcd
M26	50.3 ± 7.78	abc
p-value	0.0095**	
PLSD	39.11	

Means with the same letter in a column are not significantly different (P>0.05) using Fisher PLSD.

Table 4.10. Mean number of tillers per plant of each hop genotype grown under glasshouse conditions.

Genotype	Number of tillers per plant means ± SE
M1	6.25 ± 0.48 cdefg
M2	6.50 ± 1.76 cdefgh
M3	4.25 ± 0.25 abcd
M4	7.25 ± 0.25 defgh
M5	5.50 ± 0.65 bcdef
M6	4.50 ± 0.65 abcd
M7	3.50 ± 0.29 abc
M8	9.50 ± 2.36 hi
M9	9.25 ± 1.75 ghi
M10	9.00 ± 2.04 ghi
M11	7.25 ± 1.11 defgh
M12	5.50 ± 1.19 bcdef
M13	2.25 ± 0.63 a
M14	6.75 ± 0.95 defgh
M15	7.25 ± 1.65 defgh
M16	2.75 ± 0.75 ab
M17	10.75 ± 1.60 i
M18	8.00 ± 1.08 efghi
M19	5.00 ± 1.00 abcde
M20	4.75 ± 0.75 abcd
M21	6.75 ± 1.25 defgh
M22	6.50 ± 0.50 cdefgh
M23	8.50 ± 0.87 fghi
M24	4.75 ± 0.75 abcd
M25	5.50 ± 1.41 bcdef
M26	5.50 ± 0.29 bcdef
p-value	0.0001**
PLSD	3.219

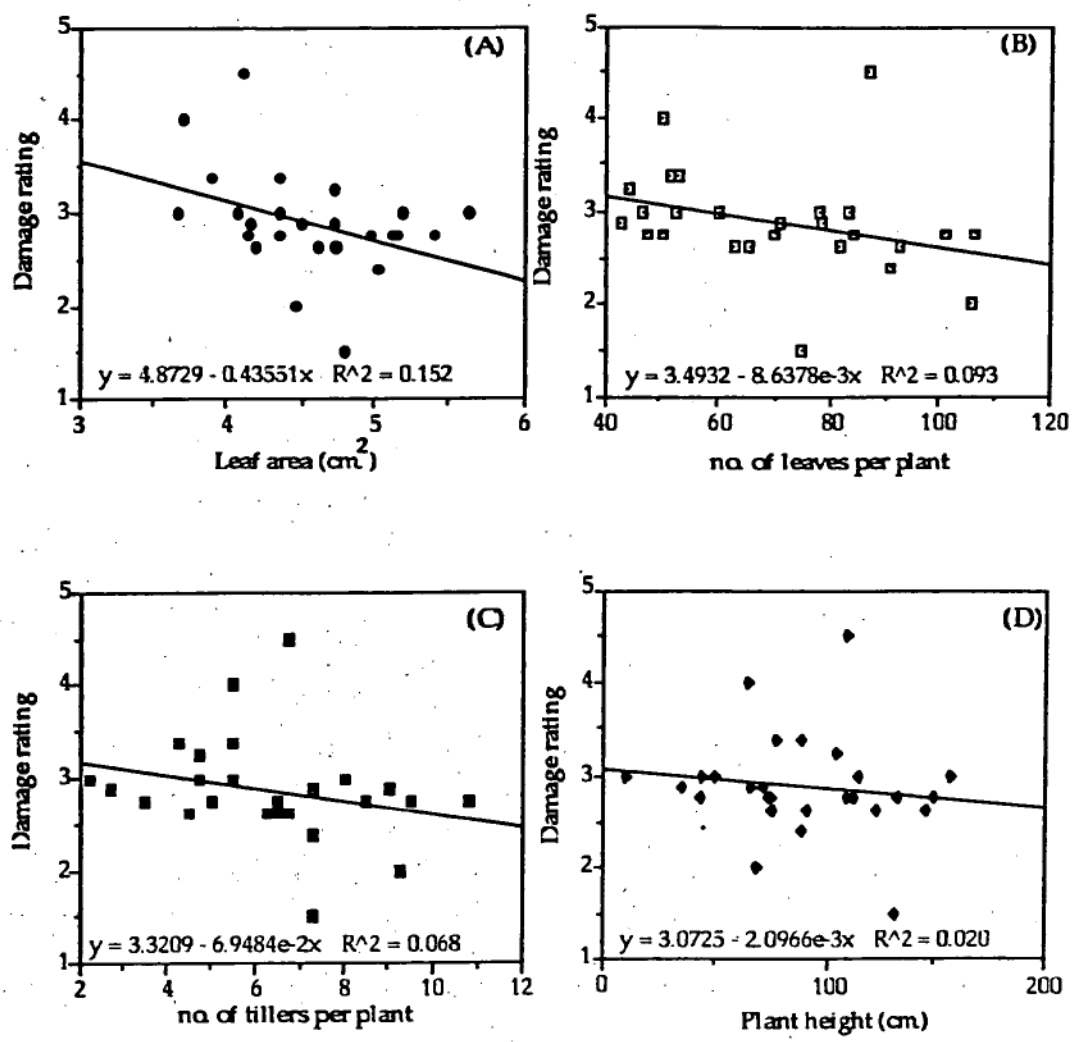
Means with the same letter in a column are not significantly different (P>0.05) using Fisher PLSD.

Table 4.11. Average plant height of each hop genotype grown under glasshouse conditions.

Genotype	Plant height (cm.) means ± SE
M1	90.2 ± 6.39 efghi
M2	146.3 ± 13.42 klm
M3	76.7 ± 13.33 cdefgh
M4	131.0 ± 2.65 jklm
M5	87.3 ± 31.99 defghi
M6	122.3 ± 15.34 ijklm
M7	131.7 ± 3.93 jklm
M8	43.7 ± 6.17 abc
M9	68.3 ± 4.26 bcdef
M10	71.3 ± 6.36 bcdef
M11	88.0 ± 24.03 defghi
M12	156.7 ± 12.02 m
M13	10.0 ± 5.51 a
M14	74.7 ± 3.18 cdefg
M15	65.7 ± 20.19 bcd
M16	35.2 ± 10.83 ab
M17	111.7 ± 8.33 hijk
M18	50.7 ± 5.81 bgd
M19	150.0 ± 15.01 lm
M20	104.0 ± 17.93 fghij
M21	108.7 ± 6.39 ghij
M22	108.3 ± 14.24 ghij
M23	74.3 ± 8.83 bcdefg
M24	44.3 ± 13.25 abc
M25	114.3 ± 7.17 ijkl
M26	65.0 ± 9.07 bcde
p-value	0.0001**
PLSD	36.69

Means with the same letter in a column are not significantly different (P>0.05) using Fisher PLSD.

Fig. 4.14. Relationships between leaf feeding damage and plant characteristics: leaf area (A), no. of leaves per plant (B), no. of tillers per plant (C), and plant height (D).



4.3.3.2 Hops in the field: There were highly significant differences in surface areas and dry weights of leaves ($p < 0.01$) among genotypes studied (Table 4.12). M18 had the greatest mean values of these characteristics, whereas M13 had the least. The growth habit of the above-ground parts of hop plants for each genotype is also presented in Table 4.12. The majority of the genotypes studied showed a cylindrical type of growth habit. The habit of the highly susceptible genotype M13 is quite conical, whereas those of the slightly susceptible genotypes M1 and M4 are rather umbrella like.

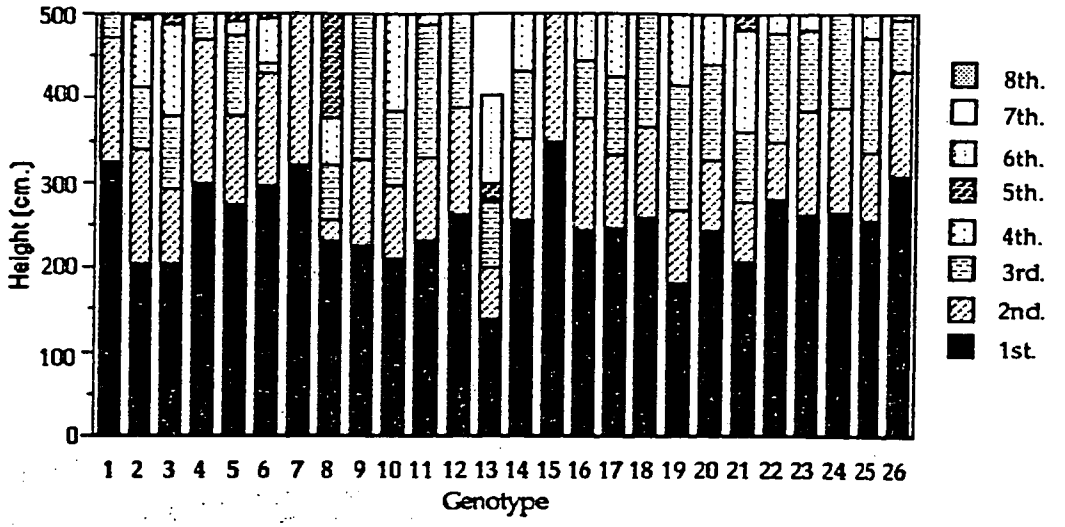
Table 4.12. Average surface areas and dry weights of hop leaves as well as the growth habit of hop plants for each genotype under field conditions.

Genotype	Leaf area (cm^2) p=0.0001** (PLSD=42.304)	Dry weight (gm.) p=0.0001** (PLSD=0.230)	Growth habit
M1	213.609 ± 20.792 ijk	1.269 ± 0.086 ghij	Umbrella+Cylindrical
M2	157.308 ± 6.252 cdef	1.038 ± 0.045 cde	Conical+Cylindrical
M3	124.668 ± 2.951 bc	0.924 ± 0.062 bcd	Conical
M4	191.951 ± 19.593 fghij	1.107 ± 0.089 efg	Umbrella+Cylindrical
M5	136.685 ± 18.174 bcde	0.825 ± 0.082 bcd	Umbrella
M6	109.783 ± 10.745 b	0.720 ± 0.061 bc	Cylindrical
M7	204.349 ± 15.051 ghijk	1.372 ± 0.051 hij	Cylindrical+Conical
M8	102.932 ± 17.560 b	0.648 ± 0.124 b	Conical+Cylindrical
M9	165.945 ± 11.532 cdefgh	1.186 ± 0.067 fghi	Cylindrical
M10	135.422 ± 15.614 bcd	0.943 ± 0.079 cde	Conical+Cylindrical
M11	187.171 ± 24.877 fghij	1.426 ± 0.137 j	Cylindrical+Conical
M12	174.006 ± 14.792 defghi	1.148 ± 0.062 efgh	Cylindrical+Umbrella
M13	55.686 ± 3.495 a	0.377 ± 0.015 a	Conical
M14	208.229 ± 24.777 hijk	1.479 ± 0.122 j	Conical+Cylindrical
M15	225.580 ± 9.772 jk	1.450 ± 0.057 j	Cylindrical+Umbrella
M16	178.748 ± 12.469 efgh	1.187 ± 0.066 fghi	Cylindrical+Umbrella
M17	200.896 ± 17.349 ghij	1.406 ± 0.101 ij	Conical+Cylindrical
M18	244.322 ± 21.897 k	1.928 ± 0.119 k	Cylindrical
M19	188.418 ± 6.354 fghij	1.340 ± 0.084 hij	Conical+Cylindrical
M20	183.797 ± 10.818 fghij	1.311 ± 0.025 ghij	Cylindrical
M21	127.570 ± 12.166 bc	0.771 ± 0.054 bc	Umbrella
M22	193.392 ± 4.803 fghij	1.283 ± 0.059 ghij	Cylindrical+Conical
M23	170.368 ± 15.737 defgh	1.258 ± 0.077 fghij	Umbrella+Cylindrical
M24	165.271 ± 22.562 cdefg	1.095 ± 0.146 efg	Cylindrical
M25	201.818 ± 10.627 ghij	1.384 ± 0.017 ij	Cylindrical+Umbrella
M26	154.676 ± 8.386 cdef	1.181 ± 0.073 fghi	Cylindrical

Means with the same letter in a column are not significantly different (P>0.05) using Fisher PLSD.

In addition, the growth rate of hop plants measured as changes in height from one observation to the next is showed in Fig. 4.15. It was apparent that M15 had the highest growth rate compared with other genotypes, whereas M13 had the lowest.

Fig. 4.15. Average plant height of 26 hop genotypes grown in the field on each occasion of sampling during the 1991/92 season.



4.3.4. Cone production

Numbers of cones per vine, dry weights of cones per vine and dry weight per cone for each genotypes tested at the Horticultural Research Centre during 1991/92 season are presented in Table 4.13. There were highly significant differences in these parameters among genotypes ($p < 0.01$). The highest number of cones per vine, dry weignt of cones per vine and dry weight per cone were found on M11, M15 and M25, respectively. It was also found that M4 and M14 did not produce any hop cones during their first year.

During 1992/93 season, highly significant differences ($p < 0.01$) in numbers of cones per vine, dry weights of cones per vine, and dry weight per cone among genotypes were also detected (Table 4.14). The highest number of cones per vine, dry weignt of cones per vine and dry weight per cone were found on M15, M18 and M10, respectively. However, there were no significant differences in these parameters between the highly susceptible genotype M26 and the slightly susceptible genotype M4 ($p \geq 0.05$).

Table 4.13. Cone production for each genotype grown at the Horticultural Research Centre during 1991/92 season.

Genotype	Number of cones per vine	Dry weight of cones per vine (gm.)	Dry weight per cone (gm.)
M2	102.00 ± 32.89	13.70 ± 4.69	0.093 ± 0.033
M4	0.00 ± 0.00	0.00 ± 0.00	0.000 ± 0.000
M9	35.00 ± 35.00	8.02 ± 8.02	0.038 ± 0.038
M10	12.17 ± 7.88	2.10 ± 1.36	0.058 ± 0.036
M11	663.67 ± 357.75	65.15 ± 37.05	0.089 ± 0.022
M14	0.00 ± 0.00	0.00 ± 0.00	0.000 ± 0.000
M15	398.17 ± 110.42	65.47 ± 19.48	0.179 ± 0.019
M18	137.83 ± 63.39	26.08 ± 11.76	0.165 ± 0.042
M21	20.50 ± 20.50	2.38 ± 2.38	0.019 ± 0.019
M23	42.00 ± 27.01	8.92 ± 5.65	0.072 ± 0.046
M25	203.00 ± 104.21	29.95 ± 13.42	0.136 ± 0.030
M26	74.33 ± 34.21	14.02 ± 6.43	0.094 ± 0.042
p-value	0.003**	0.0037**	0.0005**
PLSD	326.42	38.633	0.088

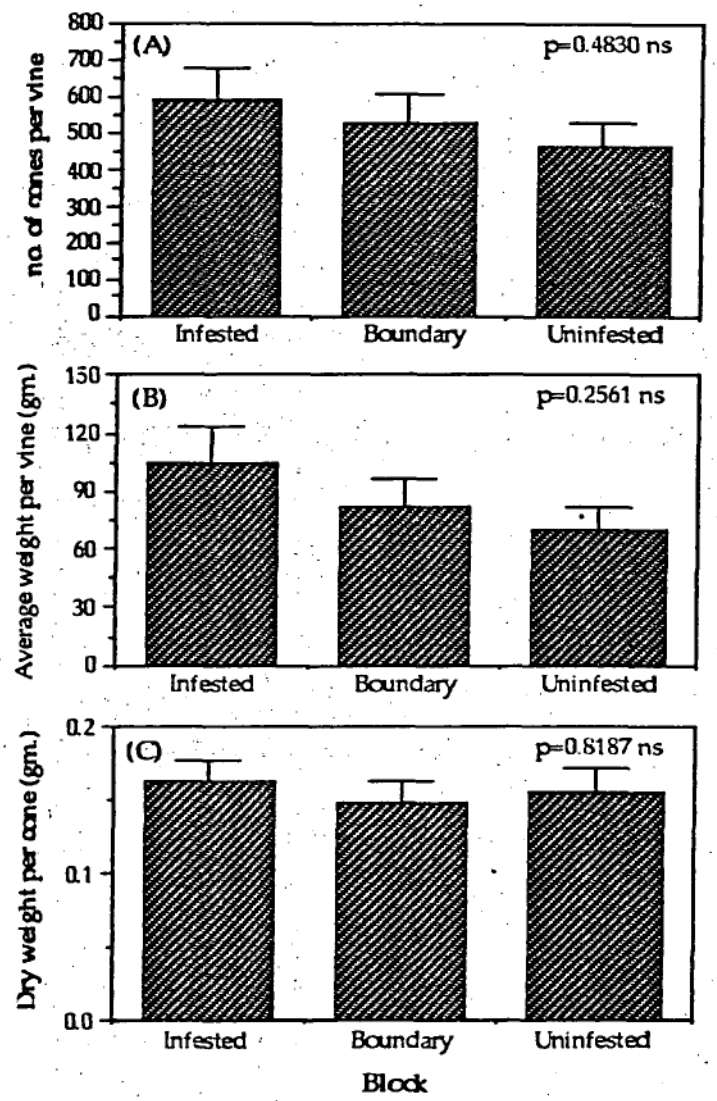
Table 4.14. Cone production for each genotype grown at the Horticultural Research Centre during 1992/93 season.

Genotype	Number of cones per vine	Dry weight of cones per vine (gm.)	Dry weight per cone (gm.)
M2	515.21 ± 42.85	58.62 ± 14.03	0.113 ± 0.028
M4	472.53 ± 81.94	62.10 ± 13.78	0.127 ± 0.009
M9	418.76 ± 81.45	42.58 ± 9.68	0.099 ± 0.007
M10	400.22 ± 58.44	112.01 ± 15.37	0.285 ± 0.023
M11	377.94 ± 55.96	32.89 ± 9.70	0.081 ± 0.017
M14	227.91 ± 75.45	40.19 ± 14.83	0.168 ± 0.008
M15	1052.96 ± 239.28	176.05 ± 48.58	0.158 ± 0.017
M18	1021.24 ± 238.05	188.86 ± 39.84	0.203 ± 0.027
M21	252.20 ± 64.71	17.23 ± 5.49	0.065 ± 0.006
M23	561.45 ± 74.53	120.17 ± 13.13	0.226 ± 0.028
M25	696.60 ± 127.12	114.65 ± 19.70	0.169 ± 0.019
M26	340.75 ± 59.20	63.16 ± 16.56	0.174 ± 0.018
p-value	0.0001**	0.0001**	0.0001**
PLSD	337.47	62.43	0.054

In addition, there were no significant differences ($p \geq 0.05$) in cone production among blocks (Fig. 4.16). The mean values varied from 592.75 to 461.29 for numbers of cones per vine (Fig. 4.16A), 104.70 to 69.97 for dry

weights of cones per vine (Fig. 4.16B) and 0.163 to 0.156 for dry weights per cone (Fig. 4.16C).

Fig. 4.16. Cone production in each block at the Horticultural Research Centre: no. of cones per vine (A), average weight of cones per vine (B) and dry weight per cone (C).



4.4. DISCUSSION

4.4.1. Fluctuations of mite populations among hop genotypes

The results from this study support those presented by others and strongly suggest the existence of a genetic component that determines the suitability of the hop plant for mite population build-up. The study by Regev and Cone (1975) indicated significant differences in mite densities between the hop varieties with European parentage and the American clusters. Similar results have been reported by Peters and Berry (1980a). In the present study, an American cultivar M25 (Aquila) proved to be less susceptible to infestation by TSSM than the German cultivar M26 (Huller Bitterer) under both field and glasshouse conditions.

It was notable that M26 was particularly susceptible to TSSM. Under glasshouse conditions, the results of both artificial and natural infestations showed that M26 was significantly more susceptible than any other genotype tested ($p < 0.05$), indicating that M26 could be useful as a susceptible standard in future screening involving TSSM.

Comparison of mite population levels between different genotypes under glasshouse conditions shows that M26 had consistently more mites on all sampling dates whereas M4 had consistently fewer mites. This indicates a large difference in susceptibility to TSSM among these genotypes.

The results also indicated that M4 (EG-86-23) displayed a low degree of susceptibility in both glasshouse and field studies. Since the response of mites to this genotype was not consistent from test to test, it requires further evaluation before definite conclusions can be drawn concerning its levels of susceptibility.

Among genotypes grown in hop yard No.1 at Bushy Park, M13, M12, and M2, which were the most susceptible genotypes based on

average mite densities at the 2 foliage strata in late season, were also among the most susceptible genotypes in mite densities on leaves of the same age in early season. This indicates that field evaluation is capable of providing consistent results in many, albeit not all, cases. In addition, it is desirable to assess the susceptibility of hop genotypes at several different stages of growth, because tests at one stage may give results that do not apply to others.

Even though differences in susceptibility of hop genotypes studied were fairly consistent, plant growth stage, plant physiology, or environment might influence susceptibility to mite infestations at various times during the growing season and therefore need to be investigated further. In addition, a feeding preference test, which indicated the possibility that resistance is present in a nonpreferred plant, does not provide a final judgement of the susceptibility in the plant (Al-Abbasi et al., 1987). Other tests should be performed to prove the fact that a particular plant is resistant (Painter, 1951).

4.4.2. Feeding damage

Feeding damage rating is one of the most common tests conducted by plant breeders to measure susceptible levels to a pest (Russell, 1978). The test reveals tolerance of a plant to feeding damage. For this reason, it was not surprising that the ranking among the genotypes for damage ratings varied somewhat from those for feeding preference. M9, which had a relatively low score in the mite damage test under glasshouse conditions, was among the genotypes that were highly preferred in the test using seasonal accumulations of mite-days to evaluate the feeding damage under field conditions. However, uncontrollable adverse environmental factors often seriously decrease the effectiveness of screening tests under natural conditions in the field, and these are absent in the controlled experiments in the glasshouse. Additionally, the

seasonal accumulation of mite-days may be affected by miticide application in some growing seasons.

There are some reports of hop cultivar screening under field conditions. For example, Kremheller (1988) in Germany observed differential population levels of both aphids and TSSM on 125 hop genotypes which were collected from the wild and grown in an untreated hop yard. This author reported the genotypes observed as aphid free but none as mite free. In the present study, all the 26 hop genotypes selected were also attacked by TSSM. Nevertheless, Neve (1991) states that the wider the range of hop genotypes available for screening, the greater the chances of finding a hop with the required character.

Under glasshouse conditions, the damage ratings reported indicated that a male parent YM-81-22 could produce not only the least susceptible progeny M4 but also the highest susceptible progeny M21 when crossed with female parents YD-81-102 and 4*J78, respectively. The genotype J78 when open-pollinated and crossed with 29/70/SH, can produce intermediate progenies M2 and M10, respectively. This suggests that J78 may be the susceptible source of these genotypes and the controlling factors for susceptibility to TSSM in hop plants may be polygenic and dominant.

4.4.3. Plant characteristics

The negative relationships between damage ratings and some plant characteristics (i.e. leaf areas, leaves per plant, tillers per plant and plant heights) were detected among hop genotypes studied, although statistically not significant. The growth rate of plants can be measured by using these characteristics. The results indicate that fast-grown genotypes may be less susceptible than slow-grown genotypes due to a tendency to escape infestations.

The results of this study also showed that the slightly susceptible genotypes with the umbrella shape of the above-ground parts, such as M4, had significantly lower mite densities than the highly susceptible genotypes with the conical shape, such as M13, under field conditions. This suggests that the type of growth habit of hop plants may affect both the population build-up and the behaviour of TSSM by modifying the microclimate in hop yard. Jesiotr et al. (1979) pointed out that microclimate in the canopy of host plants might affect a mite population.

However, the characteristics of any hop genotype vary considerably from season to season and from location to location (Neve, 1991). In this study, it was apparent that the rankings of leaf areas and plant heights among genotypes for glasshouse-grown plants differed from those for field-grown plants.

4.4.4. Cone production

The experimental plot in this study was a newly planted hop area. For this reason, a small yield of so-called baby hops (Brooks, 1962) or virgin hops (Rybacek, 1991) was obtained for each genotype. Brooks (1962) found that the length of time required for Fuggle hops to reach maximum production was the fourth season after planting, or the third year of production.

The results from this study indicated that there were significant differences in cone production among genotypes tested ($p < 0.05$) and the least susceptible genotype M4 had relatively low yields, indicating an undesirable character for this genotype.

In addition, it was also found that slight infestions of TSSM either had no effect or even increased the cone production of hop plants. This suggests that hop plants can tolerate and compensate for feeding damage of TSSM. Working under field conditions with TSSM, Bailey (1979) showed that a healthy peach tree was able to compensate for moderate

mite feeding. Sances et al. (1981), working with TSSM on strawberry, reported that the number of fruit produced was significantly increased from plants experiencing low level stress from mite populations. Thus, low levels of mite populations may be kept within hop yards for supporting populations of natural enemies.

CHAPTER 5 DEMOGRAPHIC ANALYSIS OF HOP SUSCEPTIBILITY TO TSSM INFESTATIONS

5.1. INTRODUCTION

Using resistant genotypes of many crops has been found to be an effective method of controlling TSSM, particularly in cassava, cotton, cucumber, strawberry (De Ponti, 1985)), and tomato (Stoner and Stringfellow, 1967; Aina et al., 1972). However, the improvement of hop genotypes for mite resistance remains obscure. Regev and Cone (1975) suggested that the hop genotypes evaluated so far were not resistant to spider mites but differed in their susceptibility to the pest. The previous Chapter indicated differences in TSSM population increase on different hop genotypes grown both in the field and in the glasshouse. The explanation for this phenomenon is still under investigation.

According to Huffaker et al. (1969), the condition of the host plant was recognised as an important factor affecting the abundance of spider mites. It is generally considered that this factor has an influence on the reproductive parameters, such as fecundity, hatchability, oviposition period, longevity, developmental rate, survivorship, and sex ratio, as well as the magnitude of the intrinsic rate of increase (Wrensch, 1985). These parameters have been suggested to be more appropriate measures of the impact of a resistant plant on the mite's life history (Trichilo and Leigh, 1985).

The major objective of this present investigation was to assess the effects of susceptibility of hop genotypes on the reproductive biology of TSSM under different rearing conditions. In addition, attempts were made to compare two sources of leaves used in the studies: glasshouse vs. field hop leaves.

5.2. MATERIALS AND METHODS

5.2.1. Mite Culture: Mites used in these experiments were reared on the abaxial surface of detached bean leaflets in petri dishes placed in a controlled temperature room under a photoperiod of 16:8 (L:D) at ca. 25°C and 30-40%R.H.. Adult female mites had been transferred to these leaflets and left undisturbed to oviposit for 48 hrs. Development of these eggs resulted in a cohort of evenly aged mites.

5.2.2. General Procedures: Twenty-seven genotypes of hops, grown in the glasshouse or in the field, were used in this study on antibiosis. These genotypes comprised all the genotypes mentioned in the previous chapter and an Australian cultivar "Pride of Ringwood" coded as M27.

Mite response on these genotypes was assessed by cutting 1.35-cm diameter leaf discs from mature leaves of each genotype with a test tube, the mouth of which had been sharpened by grinding and randomly placing them, abaxial side up, on filter papers surrounded by water soaked cotton pads in petri dishes. These leaf discs were examined under a binocular microscope (10X) before use and all contaminating material removed by using a fine camel's hair brush. Marked transparent plastic rings smeared with lanolin were placed around the discs to identify the positions and to prevent the escape of the mites. One mated female mite obtained from the culture was placed on each disc before oviposition took place. The design was completely random and a total of 4 females was used for each genotype. After 24 hrs, all mites were removed and the eggs were counted. No adjustment of the number of mites was taken during the development time because immature mites are too fragile to handle. The discs were observed daily to determine survival, developmental time, and sex ratio of progeny.

When the majority of the mites had reached the quiescent deutonymph stage, the number of females was adjusted to one per disc.

The leaf discs were replaced with new ones every 4 days. Female mites were observed throughout their lifetime and daily egg production recorded until the cohort became extinct. The total number of females tested on each genotype relied on the number of females alive in the quiescent deutonymph stage.

Horizontal life tables were constructed using reproductive parameters, as follows: age specific survivorship (l_x), age specific fecundity (m_x), net reproductive rate (R_o), age of mean cohort reproduction (T_c), capacity for increase (r_c), intrinsic rate of increase (r_m) according to the methods of both Birch (1948) and Wyatt and White (1977), mean generation time (T), gross reproductive rate (GRR), finite rate of increase (λ), doubling time, natality and mortality. In addition, the survival rate was also calculated: $s_x = 1 - q_x$ where s_x is the survival rate and q_x = the ratio of the number of individuals in the population that die during interval x to the number of individuals alive at the beginning of age class x (Brower et al., 1990). For the purposes of this study the sex ratio was considered as unity (after Watson, 1964)

Using these basic techniques, the following comparisons were made:

5.2.2.1. Experiment 1: The variation in mite life history due to varietal effects alone was assessed by selecting hop genotypes in the glasshouse, based on the preliminary results to represent varying levels of mite susceptibility. The following genotypes were studied: M4(slightly susceptible), M9(moderately susceptible), M26(highly susceptible), and M27(local susceptible). The experiment was conducted in a growth chamber at ca. 25°C with a 16:8 (L:D) photophase from November 21, 1991 to December 31, 1991. Illumination, ca. 700 lux at the disc level measured with a photometric sensor, (Lambda Instruments Corporation, model LI-210S, Lincoln, Nebr.), was provided inside the chamber by two fluorescent

lamps. Each petri dish was covered with a plastic lid containing a 7-cm-diameter hole for ventilation. The holes were covered by a fine nylon mesh using Kwik Grip(Selleys) contact adhesive. The relative humidity inside the dish, therefore, was higher than the outside environment.

5.2.2.2. Experiment 2: Four separate tests were conducted to determine differences in life table parameters on various hop genotypes under different conditions.

5.2.2.2.1. Test 1: All 27 genotypes were evaluated in the growth chamber from December 15, 1991 to February 14, 1992. In this test, leaf discs were arranged under the same conditions described previously. The mature hop leaves used were collected from the glasshouse.

5.2.2.2.2. Test 2: Following an unexpected electrical malfunction, the test was removed from the growth chamber to the controlled temperature room of 25°C with a 16:8 (L:D) photophase from January 14, 1992 to March 14,1992. The illumination at the level of the discs was ca. 350 lux. Leaf discs of the same twenty seven genotypes in Test 1 were cut from the field hop leaves. The remaining steps of this test were similar to those in the previous test.

5.2.2.2.3. Test 3: In this test, plastic lids were not placed on petri dishes, resulting in a more moderate humid condition, while the treatment in Tests 1 and 2 was designated as humid condition. The mites utilized in the experiment on the effect of disc area, as described below, were tested on leaf discs cut from mature field leaves. Because of chemical residues on leaf surfaces of some genotypes, all the genotypes except M25, M26, and M27 were reevaluated from January 21, 1992 to April 1, 1992. The discs were held in a transparent cage inside the controlled temperature room and the fluorescent lamps provided light at an intensity of 460 lux. The remaining steps were conducted in the same manner (described previously).

5.2.2.2.4. Test 4: The test was repeated with mites reared under identical conditions as described in Test 3 from February 16, 1992 to April 12, 1992 except that leaves were collected from hops in the glasshouse.

5.2.2.3. Experiment 3: In this study, mature hop leaves were collected from all the genotypes shown in the list except M25, M26, and M27. Three leaf discs of different surface areas (1.0, 1.35, 2.70 cm. diam.) were cut from the same leaf of field-hops with sharp mouthed test tubes. Adult female mites were held singly on each disc overnight. The following day, the mites were removed and the eggs were retained on the discs. The design was completely random and a total of 3 females was used on each genotype. As mites in the quiescent deutonymph stage appeared, one female was maintained on a disc of each surface area. The rest of the mites were adjusted to one per medium disc for use in Test 3 of Experiment 2. Additionally, the conditions and period of time were the same as that test.

The experiment was repeated during the same period as Test 4 of Experiment 2 by using the method described above except that leaves from the glasshouse were used and the test performed. In addition, leaf discs from genotypes M25, M26, and M27 were also used in this study which was conducted from February 2, 1992 to May 8, 1992.

5.2.3. Data analyses

Statistical analyses were calculated using one-factor ANOVAs with replication to detect differences in the data. Means were separated by Fisher's protected least significant differences (PLSD) test with an alpha level of 5%. Rankings of significance at $p=0.05$ were determined using the Kruskal-Wallis test. Sex ratios were compared using the Chi-square test. Linear regressions were performed using the curve fit procedure of the Cricketgraph computer program.

5.3. RESULTS

5.3.1. Experiment 1: The values of each of the life table parameters are shown separately and compared in order to investigate that parameter(s) mainly affected by any hop resistance to mites.

5.3.1.1. Hatchability: The percentage of eggs hatching on each genotype is shown in Table 1. No statistically significant differences were apparent in the hatchability of eggs among these hop genotypes ($p \geq 0.05$).

5.3.1.2. Survival of immatures: Although the percentage survival on M26 was the lowest, the survival rates of immature mites did not vary significantly among these hop genotypes (Table 5.1).

Table 5.1. Hatchability, survival of immature and sex ratio of TSSM on four genotypes of hops.

Genotype	Hatchability(%) p=0.5651ns	Survival of Immature p=0.1291ns	Sex Ratio(F./M.) p=0.7351ns
M4	83.10 ± .070	0.874 ± .044	0.817 ± 0.193
M9	96.10 ± .039	0.813 ± .098	1.096 ± 0.401
M26	94.70 ± .029	0.626 ± .062	1.800 ± 1.170
M27	88.90 ± .111	0.859 ± .072	0.933 ± 0.472

Means in columns followed by same letter are not significantly different ($p \geq 0.05$; Fisher LSD).

5.3.1.3. Sex Ratio: Differences in the sex ratio of female to male mites between these hop genotypes were not significant at the 5% level of probability (Table 5.1). However, the ratio on M26 was much higher than the ratio on the other 3 genotypes studied. According to the goodness of fit procedure, males and females were considered to occur with the same frequency in this experiment (Table 5.2).

Table 5.2. Goodness of fit procedure for male and female adults.

Ho = Males and females occurred with the same frequency (0.50:0.50).
Ha = Males and females did not occur with the same frequency.

Sex	Number of mites	Chi-Square (cal.)	Chi-Square (table)
Female	77	0.6061	3.841(∞=0.05)
Male	88	Accept Ho	

5.3.1.4. Generation mortality: In the life table, mortality (egg to adult) showed no consistent relationship with host susceptibility to attack (Table 5.3). Generation mortality varied from 36.36% on M26 to 24.19% on M9.

Table 5.3. Life table of TSSM on four genotypes of hops.

Genotype	X^a	$l_x{}^b$	$d_x{}^c$	$q_x{}^d$	$s_x{}^e$	Generation mortality (%)
M4	Egg	80	13	0.1625	0.8375	
	Immature[f]	67	8	0.1194	0.8806	
	Adult[g]	59				26.25
M9	Egg	62	1	0.0161	0.9839	
	Immature	61	14	0.2295	0.7705	
	Adult	47				24.19
M26	Egg	33	1	0.0303	0.9697	
	Immature	32	11	0.3438	0.6562	
	Adult	21				36.36
M27	Egg	51	6	0.1177	0.8823	
	Immature	45	7	0.1556	0.8444	
	Adult	38				25.49

a = Stage of life cycle.
b = Number living at beginning of stage in the x column.
c = Number dying within stage in the x column.
d = Probability of dying during x.
e = Probability of surviving interval x.
f = Larva + Protonymph + Deutonymph.
g = Female + Male.

5.3.1.5. Survival of adult stage: Since the present studies emphasized the adult stages, and since no significant differences were detected among mites on any of the hop genotypes during the juvenile stage, survivorship was considered to be 100% at the onset of adulthood and two levels of survival, namely 75% and 50% levels were selected for analysis. The period of time required for each population to reach these two levels is shown in Fig. 5.1. Survival at both the 75% and 50% levels was greatest on the local susceptible genotype M27, and decreased in turn for M4, M9 and M26. Average longevity of female mites on M27 was the longest, followed by M4, M9, and M26, but differences among genotypes were not statistically significant ($p \geq 0.05$; Fig. 5.2).

Fig. 5.1. Survivorship of TSSM on four genotypes of hops.

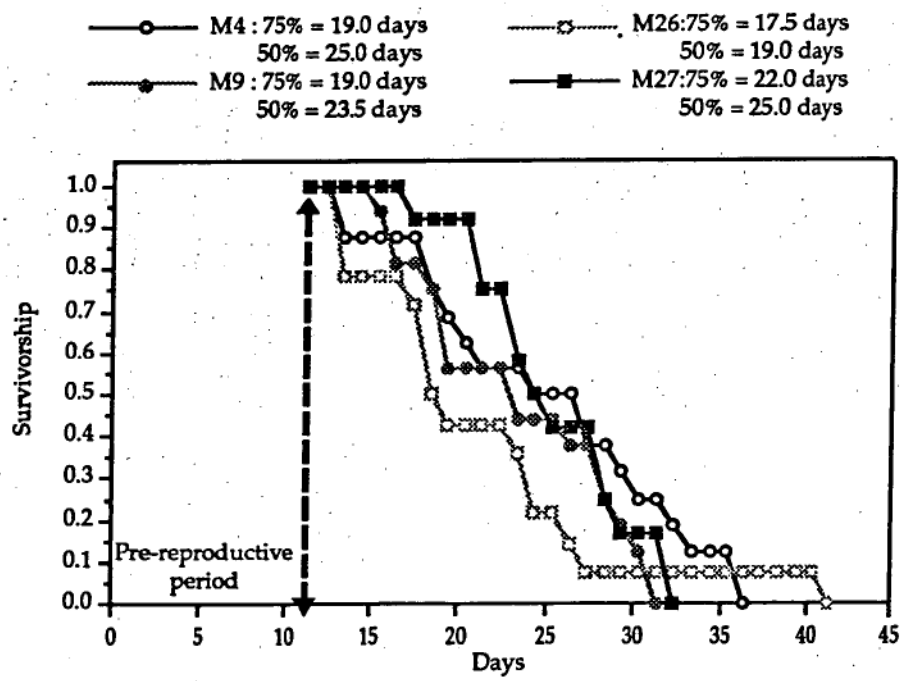
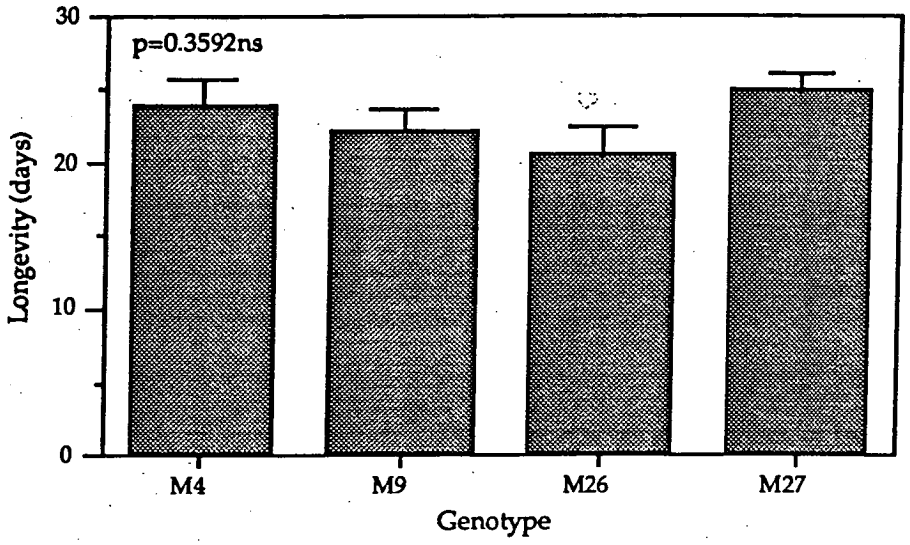


Fig. 5.2. Average longevity of TSSM on four genotypes of hops.



5.3.1.6. Fecundity: In this experiment, there were only slight differences in the average number of eggs laid per day on the four genotypes (Fig. 5.3), although the highest average peak in oviposition (ca.14.18 eggs/female/day) occurred on M27. During the first 12 days of oviposition, significant differences in the cumulative number of eggs laid by each cohort were detected between genotypes (Table 5.4). The number of eggs laid was in agreement with the degree of susceptibility. The greatest number of eggs was oviposited on M27, and the least on M4. On the 4th. day of oviposition, the highest differences in the cumulative progeny were found among the four genotypes. The mites laid more than 1/3 of the total eggs produced in an average cohort lifetime on all genotypes (>33.33%) with the exception of the slightly susceptible genotype M4 (22.13%). Statistical testing indicated that the number of eggs was significantly greater on M27 than on M4 and M9 in descending order, but was not significantly greater than on M26. In turn, the number of eggs was significantly greater on M26 than on M4, but was not significantly greater than on M9. Beyond this 12-day period, the convergence of fecundity curves resulted in very little difference in total

fecundity among these genotypes. At the end of oviposition, average total fecundity per female did not differ significantly among the hop genotypes. Genotype M27 had higher total eggs than did M4, M9 and M26. Additionally, the increased standard error associated with later-laid eggs was likely associated with an increased variation in viability of parent females during this period; that is, some females stopped laying eggs while others were still in their prime.

Fig. 5.3. Fecundity of TSSM on four genotypes of hops.

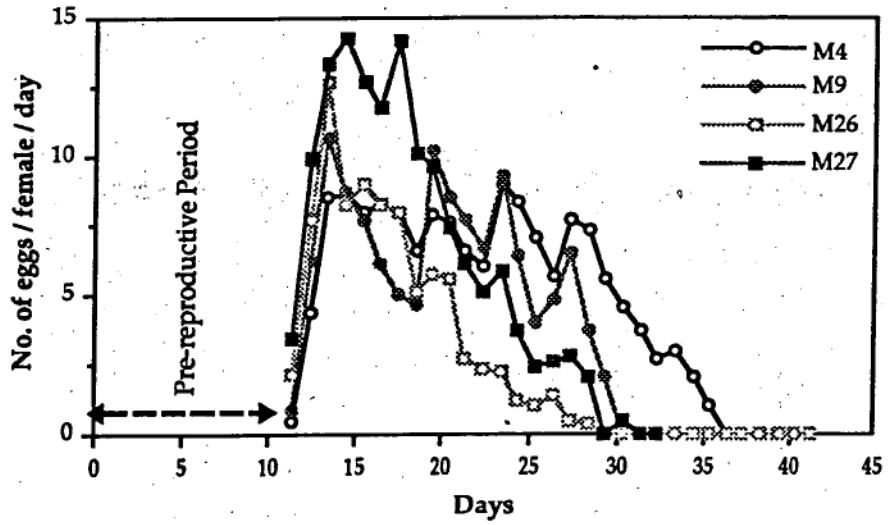


Table 5.4. Cumulative numbers of eggs laid by adult female mites on four genotypes of hops.

Time	p-value	Genotype (Means ± S.E.)			
		M4	M9	M26	M27
1	0.0220*	0.438 ± 0.203 a	0.812 ± 0.518 a	2.143 ± 0.882 ab	3.417 ± 1.145 b
2	0.0170*	4.750 ± 1.101 a	7.000 ± 1.245 a	9.786 ± 2.162 ab	13.33 ± 3.048 b
3	0.0055**	12.19 ± 1.761 a	17.63 ± 1.779 ab	22.50 ± 3.465 bc	26.67 ± 4.463 c
4	0.0030**	19.75 ± 2.756 a	26.38 ± 2.297 ab	30.71 ± 4.230 bc	40.92 ± 5.949 c
5	0.0034**	26.69 ± 4.032 a	33.56 ± 2.965 a	39.71 ± 5.569 ab	53.58 ± 7.212 b
6	0.0049**	33.88 ± 5.299 a	38.56 ± 3.601 a	48.00 ± 7.111 ab	65.33 ± 8.675 b
7	0.0038**	40.88 ± 6.492 a	42.63 ± 4.135 a	55.57 ± 8.745 ab	78.33 ± 10.38 b
8	0.0038**	45.81 ± 7.481 a	46.13 ± 4.852 a	60.64 ± 9.967 a	87.58 ± 11.49 b
9	0.0073**	51.25 ± 8.606 a	51.88 ± 5.927 a	66.43 ± 11.49 a	96.42 ± 12.69 b
10	0.0142*	56.00 ± 9.672 a	56.69 ± 6.984 a	72.00 ± 13.03 ab	103.2 ± 13.66 b
11	0.0237*	59.69 ± 10.50 a	61.00 ± 7.759 a	74.64 ± 13.90 ab	107.8 ± 14.42 b
12	0.0366*	63.06 ± 11.31a	64.75 ± 8.550 a	76.92 ± 14.76 ab	111.6 ± 14.98 b
13	0.0688ns	68.13 ± 12.52	68.81 ± 9.557	79.50 ± 15.81	115.0 ± 15.35
14	0.1069ns	72.31 ± 13.60	71.63 ± 10.28	80.50 ± 16.21	116.8 ± 15.57
15	0.1492ns	75.81 ± 14.49	73.38 ± 10.77	81.64 ± 16.72	117.8 ± 15.70
16	0.1911ns	78.63 ± 15.24	75.19 ± 11.28	82.93 ± 17.27	118.9 ± 15.82
17	0.2458ns	81.50 ± 16.07	77.63 ± 11.99	84.21 ± 17.89	120.1 ± 15.92
18	0.2798ns	84.25 ± 16.91	78.56 ± 12.24	84.21 ± 17.89	120.6 ± 15.94
19	0.3080ns	86.00 ± 17.37	78.94 ± 12.37	84.57 ± 18.08	120.6 ± 15.94
20	0.3166ns	87.13 ± 17.67	78.94 ± 12.37	84.57 ± 18.08	120.7 ± 15.94
21	0.3249ns	88.06 ± 17.92	78.94 ± 12.37	84.57 ± 18.08	120.7 ± 15.94
22	0.3289ns	88.56 ± 18.05	78.94 ± 12.37	84.57 ± 18.08	120.7 ± 15.94
23	0.3317ns	88.94 ± 18.14	78.94 ± 12.37	84.57 ± 18.08	120.7 ± 15.94
24	0.3334ns	89.19 ± 18.20	78.94 ± 12.37	84.57 ± 18.08	120.7 ± 15.94
25	0.3339ns	89.25 ± 18.21	78.94 ± 12.37	84.57 ± 18.08	120.7 ± 15.94
26	0.3339ns	89.25 ± 18.21	78.94 ± 12.37	84.57 ± 18.08	120.7 ± 15.94
27	0.3339ns	89.25 ± 18.21	78.94 ± 12.37	84.57 ± 18.08	120.7 ± 15.94
28	0.3339ns	89.25 ± 18.21	78.94 ± 12.37	84.57 ± 18.08	120.7 ± 15.94
29	0.3339ns	89.25 ± 18.21	78.94 ± 12.37	84.57 ± 18.08	120.7 ± 15.94
30	0.3339ns	89.25 ± 18.21	78.94 ± 12.37	84.57 ± 18.08	120.7 ± 15.94

* Means in rows followed by same letter are not significantly different ($p \geq 0.05$; Fisher LSD)

5.3.1.7. Other parameters: A summary of the effect of genotype on other reproductive parameters are shown in Table 5.5. Comparisons of these parameters are based on the 25% difference criterion of Southwood (1978). The intrinsic rates of increase (r_m) of calculations using Wyatt and White's formula and Birch's equation on M4 was the smallest, followed by M9, M26 and M27 in ascending order. There were no significant differences between these genotypes. However, the gross reproductive rate was significantly greater on M26 than on M9. The net reproductive rate (R_o) revealed that this ratio of the total number of female births in one generation to the number in the previous generation was

Table 5.5. Life history analysis of TSSM on four genotypes of hops.

Reproductive parameters	Genotypes			
	M4 (n=16)	M9 (n=16)	M26 (n=14)	M27 (n=12)
Intrinsic Rate of increase (Wyatt and White)	0.2435a	0.2450a	0.2710a	0.2712a
Intrinsic Rate of increase (Birch)	0.2250a	0.2322a	0.2472a	0.2697a
Gross Reproductive Rate	74.100ab	59.886a	77.599b	68.826ab
Net Reproductive Rate	44.656a	39.469a	41.964a	60.333b
Capacity for Increase	0.1969a	0.2077ab	0.2272ab	0.2471b
Mean Generation Time (days)	16.884a	15.829a	15.117a	15.202a
Cohort Generation Time (days)	19.293a	17.698a	16.444a	16.592a
Pre-reproductive Period (days)	11.800a	11.750a	11.500a	11.500a
Finite Rate of Increase	1.2520a	1.2610a	1.2800a	1.3100a
Doubling Time (days)	3.0800a	2.9840a	2.8030a	2.5700a
Natality	2.7855a	3.0277a	4.1887b	4.7897b
Mortality	2.5605a	2.7956a	3.9415b	4.5201b

Means followed by the same letter in the same row are not significantly different using the 25% difference criterion of Southwood (1978).

significantly higher on M27 than on the other genotypes. The capacity for increase (r_c) on M27 was significantly higher than M4, but no differences between M27 and M26 or M9 were found. The corresponding rm values were all slightly greater than r_c values. The r_ms', as a percentage of r_cs', were 114.27, 111.80, 108.80, and 109.15 for mites on M4, M9, M26, and M27 respectively. No significant differences were found in both generation times of the mites on these genotypes. The pre-reproductive period did not differ significantly among these genotypes. Again, the finite rate for increase was highest on M27, followed by M26, M9, and M4 in descending order. Doubling time (DT) conformed to the reverse order of r_m and there were no significant differences between genotypes in both parameters. Natality and mortality varied, with mites on M27 having the highest rates and M4 having the least.

5.3.2. Experiment 2: The influences of different factors on each reproductive parameter of TSSM were shown separately in this study.

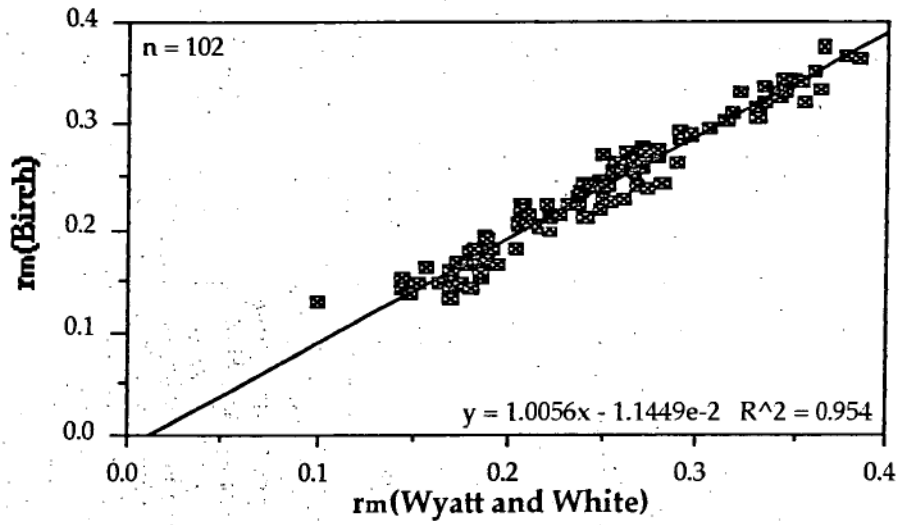
5.3.2.1. Effects of genotypes: The following comparisons of the reproductive parameters of mites on each genotype were obtained by pooling data taken from all tests in this experiment. The results are presented in Table 5.6. Pre-reproductive period, defined as days to first reproduction, was nearly identical on all 27 genotypes tested. The range was 10.5-12.8 days with an average of 12.00 days. The mites on M4 had the slowest rate of development and those on M11, M25, and M26 had the highest rates. According to the Kruskal-Wallis test, there were no significant differences in intrinsic rate of increase, net reproductive rate, mean generation time, capacity for increase, cohort generation time, finite rate of increase, doubling time and natality among the hop genotypes ($p \geq 0.05$). Nevertheless, the variation in net reproductive rate among mites on these genotypes was higher than the variation in other parameters. Results of regression analysis of the intrinsic rate of increase

Table 5.6. Pooled life table of TSSM on 27 hop genotypes under different conditions.

Genotypes (total no. of mites)	Reproductive Parameters (Means ± S.E.)								
	Pre-reproductive period p=1.000ns	rm (Birch) p=0.9997ns	Ro p=0.1356ns	T p=1.0000ns	rc p=0.9912ns	Tc p=0.9500ns	Finite rate for increase p=0.9997ns	Doubling time p=0.9980ns	Natality p=0.6952ns
M1 (n=21)	12.2 ± 1.47	.214 ± .036	39.62 ± 14.42	16.7 ± 1.70	.189 ± .025	18.6 ± 1.7	1.24 ± .045	3.53 ± .587	2.77 ± 0.67
M2 (n=22)	12.0 ± 1.48	.248 ± .027	40.93 ± 3.82	15.4 ± 1.52	.226 ± .026	16.9 ± 1.7	1.28 ± .035	2.91 ± .342	3.98 ± 0.57
M3 (n=19)	12.1 ± 1.85	.236 ± .039	33.98 ± 5.29	15.9 ± 2.16	.215 ± .032	17.1 ± 2.1	1.26 ± .050	3.22 ± .580	3.81 ± 0.60
M4 (n=19)	12.8 ± 1.44	.204 ± .024	33.93 ± 9.15	17.1 ± 1.51	.184 ± .018	18.8 ± 1.6	1.23 ± .030	3.57 ± .491	2.83 ± 0.51
M5 (n=22)	12.1 ± 1.79	.255 ± .039	66.58 ± 15.73	17.3 ± 2.59	.211 ± .026	20.6 ± 2.8	1.29 ± .050	2.93 ± .474	4.31 ± 0.85
M6 (n=19)	12.8 ± 1.68	.223 ± .028	48.95 ± 9.25	17.9 ± 1.96	.183 ± .014	21.2 ± 1.6	1.25 ± .036	3.25 ± .379	3.16 ± 0.07
M7 (n=20)	12.0 ± 1.62	.250 ± .031	60.78 ± 10.67	17.0 ± 2.53	.216 ± .022	19.6 ± 2.9	1.29 ± .039	2.90 ± .363	3.83 ± 0.45
M8 (n=20)	11.8 ± 1.91	.256 ± .036	50.10 ± 2.81	16.2 ± 2.40	.215 ± .022	18.8 ± 2.1	1.29 ± .047	2.88 ± .430	3.75 ± 0.56
M9 (n=21)	11.9 ± 1.69	.237 ± .033	37.98 ± 5.25	16.4 ± 2.93	.218 ± .030	17.9 ± 3.4	1.27 ± .041	3.14 ± .513	3.13 ± 0.25
M10(n=19)	11.7 ± 1.71	.244 ± .036	35.79 ± 5.53	15.4 ± 2.44	.225 ± .030	16.7 ± 2.7	1.28 ± .046	3.04 ± .448	3.71 ± 0.70
M11(n=15)	10.5 ± 1.28	.292 ± .038	67.78 ± 11.63	14.9 ± 2.22	.257 ± .044	17.4 ± 3.2	1.34 ± .052	2.45 ± .281	5.31 ± 1.05
M12(n=22)	11.4 ± 1.85	.221 ± .055	32.33 ± 10.86	15.2 ± 2.63	.196 ± .045	16.9 ± 3.2	1.25 ± .071	3.72 ± .815	3.76 ± 1.09
M13(n=20)	12.1 ± 2.00	.247 ± .036	53.47 ± 6.81	17.3 ± 2.95	.213 ± .029	19.8 ± 3.1	1.28 ± .047	3.02 ± .483	3.62 ± 0.60
M14(n=16)	11.9 ± 1.45	.260 ± .035	60.13 ± 18.34	16.1 ± 2.11	.224 ± .027	18.6 ± 2.4	1.30 ± .045	2.85 ± .470	4.44 ± 0.79
M15(n=18)	12.0 ± 1.51	.236 ± .037	40.89 ± 12.10	15.7 ± 2.11	.209 ± .027	17.5 ± 2.3	1.27 ± .047	3.18 ± .509	3.65 ± 0.56
M16(n=16)	11.9 ± 1.67	.260 ± .036	54.67 ± 6.47	16.2 ± 2.38	.231 ± .029	18.1 ± 2.5	1.30 ± .048	2.82 ± .397	4.45 ± 0.52
M17(n=31)	12.6 ± 1.73	.219 ± .032	39.73 ± 4.81	17.7 ± 2.22	.189 ± .024	20.2 ± 2.3	1.25 ± .040	3.41 ± .557	2.87 ± 0.49
M18(n=12)	12.2 ± 1.73	.257 ± .034	53.21 ± 4.40	16.4 ± 2.55	.232 ± .029	18.2 ± 2.9	1.30 ± .044	2.87 ± .442	4.28 ± 0.60
M19(n=16)	12.3 ± 1.64	.231 ± .043	44.84 ± 16.70	16.2 ± 1.87	.199 ± .030	18.5 ± 2.0	1.26 ± .054	3.37 ± .695	3.17 ± 0.62
M20(n=12)	12.2 ± 2.07	.238 ± .043	39.56 ± 7.61	16.3 ± 3.02	.221 ± .036	17.3 ± 2.9	1.27 ± .056	3.09 ± .495	3.14 ± 0.40
M21(n=16)	12.5 ± 1.44	.196 ± .035	25.44 ± 9.57	15.6 ± 1.45	.181 ± .027	16.6 ± 1.4	1.22 ± .043	3.89 ± .660	2.77 ± 0.61
M22(n=15)	12.7 ± 1.47	.226 ± .026	53.96 ± 9.36	18.1 ± 2.01	.184 ± .018	21.9 ± 1.8	1.25 ± .032	3.21 ± .418	3.74 ± 0.36
M23(n=18)	11.9 ± 1.82	.244 ± .038	39.38 ± 9.49	15.4 ± 1.65	.223 ± .027	16.5 ± 1.2	1.28 ± .049	3.09 ± .543	3.73 ± 0.60
M24(n=16)	12.1 ± 2.00	.254 ± .049	46.48 ± 10.05	16.2 ± 2.40	.220 ± .032	18.0 ± 2.1	1.29 ± .064	3.08 ± .624	4.14 ± 1.12
M25(n= 7)	11.4 ± 1.58	.229 ± .008	66.89 ± 29.61	17.9 ± 2.67	.180 ± .003	22.8 ± 3.1	1.26 ± .010	3.02 ± .101	3.07 ± 0.49
M26(n=12)	11.5 ± 1.50	.241 ± .036	84.05 ± 31.45	18.7 ± 4.40	.186 ± .030	24.4 ± 6.1	1.27 ± .045	2.94 ± .435	3.42 ± 0.75
M27(n=19)	11.3 ± 1.25	.256 ± .045	64.60 ± 6.10	17.1 ± 2.27	.200 ± .033	21.7 ± 2.8	1.29 ± .059	2.86 ± .430	3.98 ± 0.43

among hop genotypes studied indicated that a positive linear relationship existed between calculations using Wyatt and White' formula and Birch's equation (Fig. 5.4).

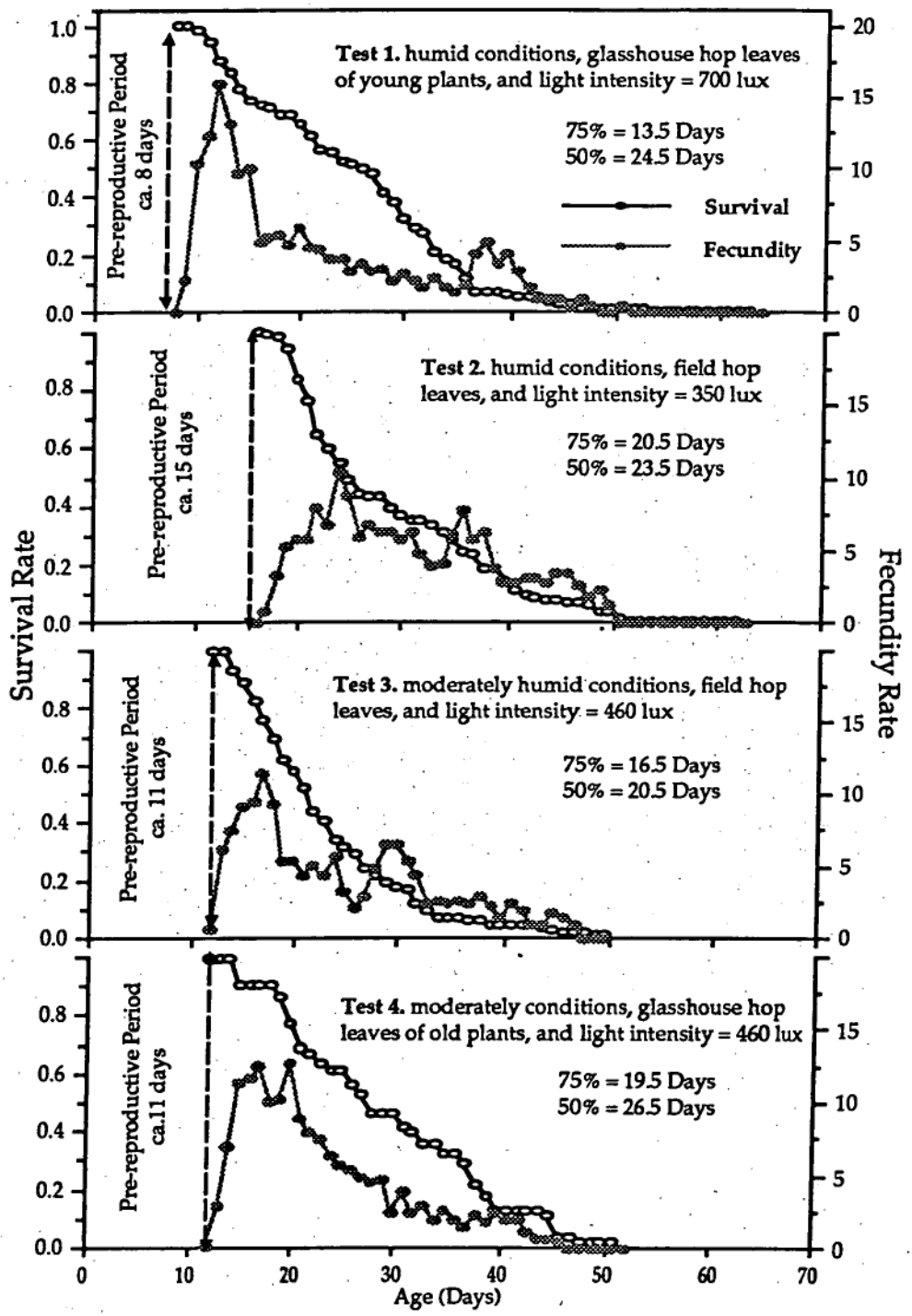
Fig. 5.4. Relationship between rm(Birch) and rm(Wyatt and White) of TSSM.



5.3.2.2. Effects of experimental conditions: Since there was no significant difference in the intrinsic rate of increase among the genotypes used (Table 5.6), it is likely that, in general, mite responses are the same on these genotypes. Consequently, data were grouped according to rearing conditions, and comparisons of the data were repeated.

When survival of female adult mites on leaf discs of various hop genotypes were compared under different environmental conditions, similar survival curves of the adults were observed. The time required for population survival to decline to the 75 and 50 per cent levels in all the tests employed for this comparison are graphically depicted in Fig. 5.5. Survival was greater on field hop leaf discs under humid conditions than under any other rearing conditions at the 75 per cent survival level. However, greatest survival was on glasshouse hop discs under moderately humid conditions at the 50 per cent survival level. As indicated in Table 5.7, rearing conditions significantly affected the

Fig 5.5. Survivorship and average number of eggs laid per day per female on various hop genotypes under different conditions.



longevity of reproducing females. The average lifetime of adult females was significantly longer on field hop leaf discs under humid conditions in Test 1 than when kept at the environmental regimes in the other three tests. It was notable that the mites on both glasshouse and field leaf discs were able to survive longer under high humid conditions than under moderately humid conditions.

Table 5.7. Average total number of eggs and longevity of TSSM under different environmental conditions.

Source of leaves	Conditions	Average life time/female (days) p=0.0001**	Average no.eggs/female p=0.0001**
Glasshouse	Humid	22.919 ± 1.26 bc	103.28 ± 4.52 b
Field	Humid	28.718 ± 1.13 d	75.773 ± 7.07 a
Field	Moderately Humid	21.261 ± 0.72 ab	66.036 ± 6.00 a
Glasshouse	Moderately Humid	17.709 ± 1.99 a	121.38 ± 10.3 b

Means in columns followed by same letter are not significantly different ($p \geq 0.05$; Fisher LSD).

The egg-to-egg developmental period of female mites in each environmental regime is presented in Fig. 5.5. It was found that this total developmental period of mites took longer on field hop leaf discs at the lowest light intensity (350 lux) under humid conditions than in the other environmental regimes, whilst the mites reared on glasshouse hop leaf discs at the highest light intensity (700 lux) under humid conditions had the shortest period. The total numbers of eggs for leaf type under different rearing conditions are given in Table 5.7. Highly significant differences in average total number of eggs were apparent among these environmental conditions. Mites laid significantly more eggs on

glasshouse hop leaf discs than on field hop leaf discs. The daily egg-laying curves of the mites under different conditions are shown in Fig. 5.5. Each point on the curves represents the mean number of eggs per day. The first peak of each curve varies according to different rearing conditions. Under humid conditions, the maximum daily egg production on glasshouse hop leaf discs was reached on the 12th. day after the first deposition of the eggs, while the mites on field hop leaf discs were still immature and the mites under moderately humid conditions had just entered the reproductive stages. The mites reared under moderately humid conditons had stopped producing eggs after a total of 58 days and 41 days of oviposition on field and glasshouse hop leaf discs, respectively. The highest average peak oviposition for mites on glasshouse hop leaf discs under humid conditions, field hop leaf discs under humid conditions, field hop leaf discs under moderately humid conditions and glasshouse hop leaf discs under moderately humid conditions were 15.87, 10.39, 10.79 and 12.34 eggs/female/day, respectively. This indicated that the daily fecundity of mites reared under both humid conditions and moderately humid conditions was lower on field hop leaf discs than on glasshouse hop leaf discs, especially on the glasshouse hop leaves of young plants.

Data presented earlier shows the effects of rearing conditions upon survival and fecundity rates. These two reproductive parameters can be used to estimate other more meaningful parameters (Table 5.8). According to the analysis of variance, highly significant differences were found in all of the parameters of this life table ($p < 0.01$). The intrinsic rate of increase for the mites reared on the discs from glasshouse hop leaves was higher than that from field hop leaves under both humid conditions and moderately humid conditions. Values for the gross reproductive rate calculated for each condition indicated that this

Table 5.8. Life history analysis of TSSM under different rearing conditions.

Reproductive Parameters	Source of Leaves and Conditions (Means ± S.E.)			
	Glasshouse and Humid	Field and Humid	Field and Moderately Humid	Glasshouse and Moderately Humid
Intrinsic Rate of Increase (Wyatt and White) p=0.0001**	0.330 ± .007d	0.177 ± .003a	0.229 ± .007b	0.257 ± .008c
Intrinsic Rate of Increase (Birch) p=0.0001**	0.322 ± .007d	0.158 ± .003a	0.220 ± .006b	0.253 ± .007c
Gross Reproductive Rate p=0.0099**	71.91 ± 3.18b	68.76 ± 5.20b	51.75 ± 5.07a	70.84 ± 5.34b
Net Reproductive Rate p=0.0001**	51.63 ± 2.26b	37.89 ± 3.54a	32.85 ± 2.99a	60.69 ± 5.14b
Capacity for Increase p=0.0001**	0.268 ± .007d	0.145 ± .003a	0.201 ± .005b	0.225 ± .007c
Mean Generation Time (days) p=0.0001**	12.29 ± .295a	22.38 ± .337c	15.30 ± .207b	15.74 ± .361b
Cohort Generation Time (days) p=0.0001**	14.93 ± .504a	24.44 ± .517c	16.73 ± .408b	17.81 ± .595b
Pre-reproductive Period (days) p=0.0001**	8.726 ± .165a	16.68 ± .105d	11.79 ± .098c	11.28 ± .125b
Finite Rate of Increase p=0.0001**	1.381 ± .009d	1.171 ± .004a	1.246 ± .007b	1.288 ± .009c
Doubling Time (days) p=0.0001**	2.171 ± .048a	4.430 ± .090d	3.217 ± .104c	2.821 ± .130b
Natality p=0.0001**	4.536 ± .252c	2.596 ± .114a	3.201 ± .185b	4.328 ± .237c
Mortality p=0.0001**	4.214 ± .247b	2.438 ± .112a	2.981 ± .180a	4.075 ± .231b

Means in the same row followed by the same letter are not significantly different ($p \geq 0.05$; Fisher PLSD)

summation of fecundity was significantly less on field hop leaf discs under moderately humid conditions than under the other conditions and there were no statistically significant differences among them. Under different conditions, the net reproductive rates of mites on the discs cut from glasshouse hop leaves were significantly higher than those from field hop leaves. Significant differences of mites reared on different sources of leaves were also found in the capacity for increase. Similarly, significant differences in both mean generation time and cohort generation time for mites reared under different conditions were detected. The longest times were found in the mites on discs from field leaves under humid conditions and shortest on glasshouse hop leaf discs under the same conditions. The variation in pre-reproductive periods among these environmental regimes were highly significant ($p < 0.01$). The finite rate of increase on field hop leaf discs under humid conditions was the smallest, followed by field hop leaf discs under moderately humid conditions, on glasshouse hop leaf discs under moderately humid conditions and on glasshouse hop leaf discs under humid conditions in ascending order. On the other hand, doubling time (DT) was the reverse. The mites reared on field hop leaves under humid conditions had lower natality and mortality rates than under other conditions.

5.3.3. Experiment 3: The survival and fecundity of mites reared on 3 different surface areas of leaf discs cut from 24 genotypes grown in the glasshouse and the field are shown in Fig. 5.6 and 5.7. It was apparent that the longevity and oviposition of mites reared on leaf discs cut from field leaves were greater than those on leaf discs from glasshouse. The results also showed that survival and age-specific fecundity rates of the female mites tended to be proportional to the surface area of the leaf disc used, i.e., the longest periods of both survivorship and oviposition were obtained on the largest surface area.

Fig. 5.6. Survivorship of TSSM on different sizes and source of leaves.

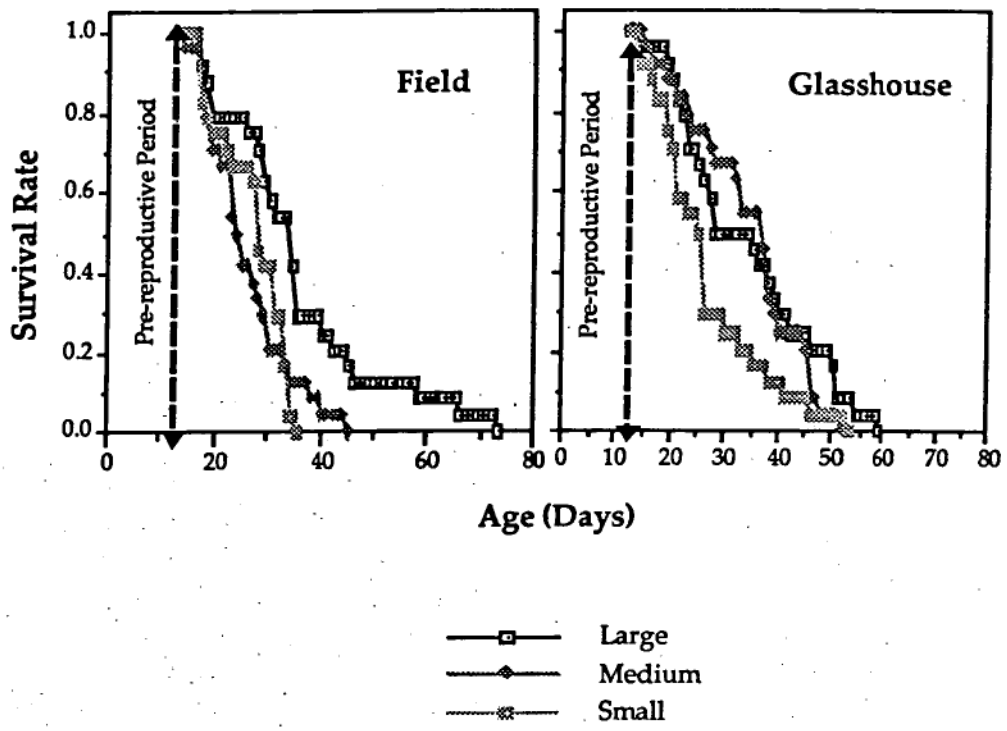
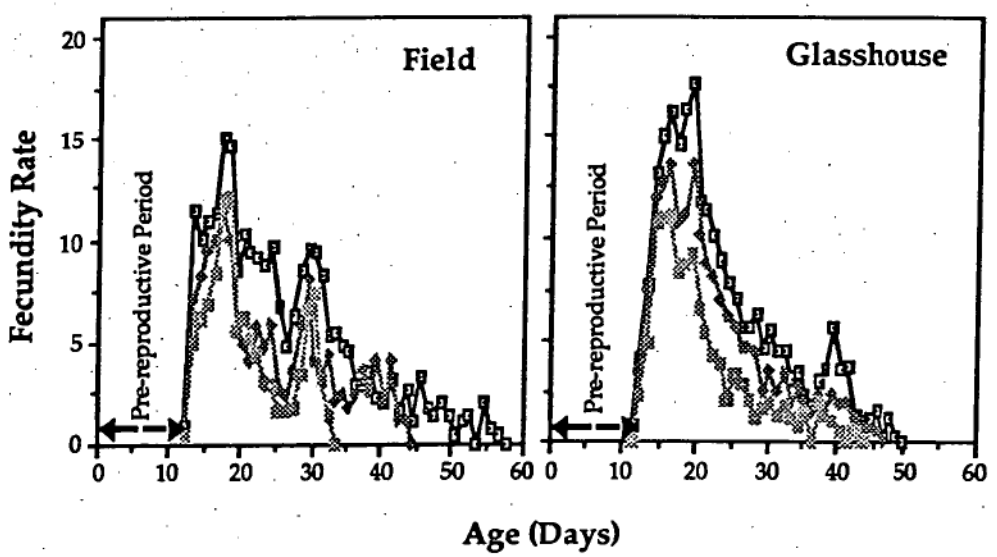


Fig. 5.7. Average number of eggs laid per day per living female TSSM on different sizes and sources of leaves.



Throughout this experiment, no significant differences ($p \geq 0.05$) in average number of progeny per female mite were found between different surface areas of leaf discs (Fig. 5.8 and 5.9). However, average total number of progeny per female was significantly lower on small than on large surface areas. There were no significant differences in the longevity of mites among these surface areas of leaf discs ($p \geq 0.05$). For other reproductive parameters of the mites except gross reproductive rate, natality and mortality, no significant differences ($p \geq 0.05$) among these surface areas of leaf discs were found (Table 5.9).

Fig. 5.8. Average total number of eggs of TSSM on different surface areas of leaf discs.

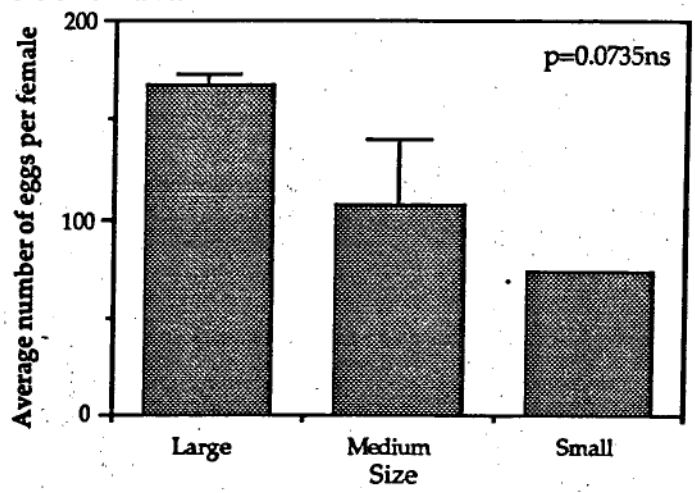


Fig. 5.9. Average longevity of TSSM on different surface areas of leaf discs.

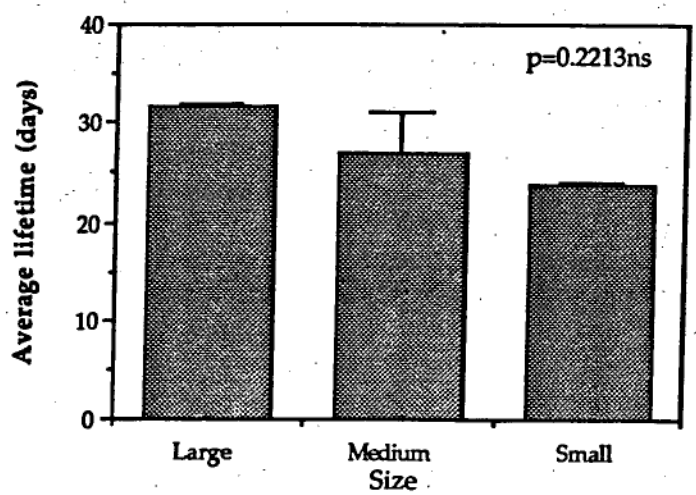


Table 5.9. Life history analysis of TSSM on different surface areas of leaf discs.

Reproductive Parameters	Areas (Means ± S.E.)		
	Large (2.70 cm. diam.)	Medium (1.35 cm. diam.)	Small (1.00 cm. diam.)
Intrinsic Rate of Increase (Wyatt) p=0.4590ns	0.286 ± .015	0.265 ± .020	0.253 ± .013
Intrinsic Rate of Increase (Birch) p=0.1620ns	0.268 ± .007	0.247 ± .015	0.230 ± .007
Gross Reproductive Rate p=0.0048**	119.3 ± 1.40c	80.90 ± 7.45b	54.30 ± 2.25a
Net Reproductive Rate p=0.0735ns	83.42 ± 2.61	53.91 ± 15.2	36.61 ± .050
Capacity for Increase p=0.6022ns	0.220 ± .009	0.213 ± .008	0.208 ± .007
Mean Generation Time (days) p=0.3767ns	16.52 ± .346	15.98 ± .234	15.70 ± .453
Cohort Generation Time (days) p=0.1234ns	20.14 ± .690	18.51 ± .688	17.36 ± .578
Pre-reproductive Period (days) p=0.8304ns	11.32 ± .315	11.38 ± .290	11.55 ± .200
Finite Rate of Increase p=0.1672ns	1.307 ± .010	1.280 ± .019	1.258 ± .008
Doubling Time (days) p=0.1653ns	2.589 ± .073	2.818 ± .166	3.022 ± .088
Natality p=0.0048**	4.134 ± .158c	3.208 ± .097b	2.597 ± .026a
Mortality p=0.0052**	3.866 ± .165c	2.961 ± .083b	2.367 ± .033a

Means followed by the same letter in the same row are not significantly different using Fisher PLSD of Statview ($p \geq 0.05$).

5.4. DISCUSSION

5.4.1. Genotypic effects.

It is generally accepted that the susceptibility of the host plant is reflected in the life history of the mite, i.e. greater susceptibility should proportionately increase mite reproductive fitness (Trichilo and Leigh, 1985). The results reported here appear to support this hypothesis as there were differences in life history statistics among the genotypes studied, although they were not significant ($p \geq 0.05$). It was found that the highly susceptible genotype M26 resulted in a faster growth rate of the mite population than did the slightly susceptible genotype M4. This may be due to slight differences in various interrelated life history parameters, which led to somewhat lower or higher intrinsic rates of increase (r_m) of mites on these genotypes.

Reproduction of organisms with a high r_m such as spider mites, seems highly dependent on the variation in developmental rates (Caswell, 1982; Lewontin, 1965; Snell, 1978), whilst fecundity becomes more important in changing population growth rate of organisms with low rm (Romanow et al., 1991). For this reason, it was likely that slight differences in the value of rm among all genotypes studied, may be due to the influence of developmental rates of mites. Similar observations were made by Peters and Berry (1980a), who indicated that there were highly significant differences in developmental rates of TSSM between hop genotypes.

Even though the results from this study indicated that pre-reproductive periods of TSSM on the slightly susceptible genotype were longer than those on the highly susceptible genotype, none of these differences was significant ($p \geq 0.05$). Nevertheless, the effect of different hop genotypes on mite development was apparent during the first 12 days of the reproductive period and the highest differences in the

cumulative number of eggs were found on the fourth day of oviposition. The rankings of the number of eggs laid for each genotype were in agreement with those of the degree of susceptibility and the pre-reproductive periods. This indicates that adult females on highly susceptible genotypes may be older than those on slighly susceptible ones. Li and Harmsen (1993), working in the laboratory with TSSM on leaf discs of lima beans, found that the maternal age of TSSM had significant effects on fecundity. In addition, Wrensch and Young (1975), working with TSSM on kidney beans, indicated that the cumulative egg laying for 18 days may have been used as a predictor of total egg production.

Peters and Berry (1980a) reported that the variation in mean number of eggs laid on leaf discs of four hop varieties by unmated TSSM females during five days was not significant. This does not appear to be in agreement with the present studies, which indicated that highly significant differences in the number of eggs were apparent on the 4th. day of oviposition. However, these authors' data represented mainly the average fecundity rate over the five-day period, while the data of the present studies represent the cumulative rate for a one-day period. Other reasons, such as the hop genotypes employed, also may have been responsible for the discrepancies between these two results.

Although the oviposition of mites described above seem to be a useful parameter, the age-specific fecundity was a variable criterion due to differences in ranking for these genotypes between the earlier and later reproductive periods. In this study, the average numbers of eggs laid on the 4th. day on M4, M9, M26 and M27 were 19.75, 26.38, 30.71 and 40.92, respectively, while those on the final date of oviposition test were 89.25, 78.94, 84.57, and 120.7 for M4, M9, M26 and M27, respectively (Table 4).

Several investigators (Arcanin, 1958; Bohm, 1961; Gasser, 1951; Williams, 1954; Lehr and Smith, 1957; Rambier, 1958; Shih et al., 1976)

showed egg production per female in the range 30-312 eggs at a rate of 2-12 per day. An average number of 70 eggs per female over a biweekly period can be suggested as typical of the species. Unwin (1971) stated that the reproduction of the mite population may be affected by host genotype. For example, the population potential on Queensland apples was observed to be greatest on Delicious and least on Gravenstein (Bengston, 1970).

In addition, the results from this study show that the survival trends of female adults were fairly similar on all genotypes tested. Using the 25% difference criterion of Southwood (1978), significant differences were found in values of gross reproductive rate, net reproductive rate, capacity for increase, natality and mortality between some genotypes, indicating variation in mite survival and reproduction on different hop genotypes. It was also apparent that the higher mortality associated with higher intrinsic rate of increase may be due to reproductive exhaustion.

Birch (1948) defined the intrinsic rate of increase (r_m) as the constant 'r' in the differential equation for population increase in an unlimited environment. The equation combines several biological components and has immense value in the biological components and ecological understanding of tetranychid mites. In the present study, the equation of Wyatt and White (1977) proved to be more convenient method of assessing the intrinsic rate of increase obtained from the equation of Birch (1948). Birch's equation resulted in part from survival data, which were not required for the intrinsic rate equation of Wyatt and White.

5.4.2. Environmental effects

In addition to genotypic effects, several environmental factors affected mite population growth rate in these studies, for example humidity, light intensity, plant age, source of leaves and leaf surface

areas. Changes in these factors may contribute to the variation in mite population build-up on the plant.

The environmental factors may have a profound effect on the expression of resistance. It is known that the environment may have a controlling effect on the expression of many genetic characters, thus it might be expected that a plant could display a varying degree of resistance or susceptibility under different environmental conditions. This has been pointed out by Painter (1954), who cited several examples of this phenomenon.

At the optimum level, humidity and light intensity may in some way affect TSSM directly so that the mites are better able to survive and reproduce on the plants. On the other hand, both factors may affect certain physiological or other processes of the plant itself so that it becomes more favorable for mite feeding and survival.

The results obtained from Tests 2 and 3 show that humidity may have been responsible for the differences in mite survival and reproduction between humid and moderately humid conditions. Using the mature leaves of field hop plants, humid conditions resulted in greater longevity and lower fecundity than moderately humid conditions. This is in accordance with the data presented by Boudreaux (1958) who found that mites oviposited at a higher rate in a dry atmosphere than in a wet atmosphere and attributed this to their ability to ingest and utilize larger amounts of food in a dry atmosphere through the elimination of body moisture by evaporation from the cuticle. However, Boudreaux's findings that mites also lived longer under dry conditions were not supported by the above longevity data. It is well known that humidity is a critical factor which strongly affects the value of r_m in mite life history studies (Carey, 1982a). In addition, Tulisalo (1974), who studied the effect of relative humidity on survival and reproduction

of TSSM under laboratory conditions, showed that conditions of constant high relative humidity resulted in the production of fewer eggs, and shorter longevity for egg-laying females than at a constant low relative humidity.

For light intensity, an acceleration of mite growth rate was due to a decrease in the pre-reproductive period, which may in turn result from high light intensity. This indicated that greater levels of susceptibility to TSSM in plants as light intensity increased. This is in accordance with the results of numerous studies of the influence of light intensity on arthropod performance which have shown loss of resistance of plants with decreasing light intensity (Tingey and Singh, 1980).

The results from the present study also indicated that the fecundity of mites reared on glasshouse hop leaves was higher than those on field hop leaves. This may have been due to differences in nutrient content and leaf texture and hardness between these hop leaves. Campbell et al. (1990) working with apple and peach leaves, showed similar results; that is, greenhouse-grown leaves are more susceptible to mite feeding than field-grown leaves.

With regard to plant age, the results obtained from Tests 1 and 4 show significant differences in growth rates of mites between glasshouse hop leaves of young plants and those of old plants. The growth rate of mites was greater on leaf discs of the young plant than on those of the old plant. This indicated that the growth rate of TSSM decreased with the chronological age of the host plant. Watson (1964), working with TSSM on bean plants, reported that fecundity was reduced on older plants but survival was not affected. The growth rates of tetranychids depend not only on the age of the host plant but also on the phase of the plant nitrogen cycle (Yaninek et al., 1989). In general, the ratios of carbon to nitrogen in hop plants vary at different times in the annual cycle

(Rybacek, 1991). Howeler and Cadavid (1983), working with cassava, stated that aging leaves have reduced leaf nitrogen. A subsequent investigation by Wermelinger et al. (1985) showed that the reduction of leaf nitrogen influenced development rates and fecundity in TSSM.

In the feeding surface area study, there were significant differences in gross reproductive rates, natality and mortality of mite populations among the three feeding surface areas studied. Although no significant differences were recorded in the other parameters at the 0.05 level, the trend in survivorship indicated that the mortality rate for mites confined on the smallest area was significantly affected during the initial period when mite numbers were high. This would indicate density related competitive effects on mite activity. Mitchell (1973) found that the available area of TSSM feeding was approximately 9.4 ± 0.97 mm^2 although Li and Harmsen (1993) found that female density was not an important factor in determining fecundity.

CHAPTER 6 INFLUENCE OF ENVIRONMENTAL FACTORS ON POPULATION INCREASE OF TSSM

6.1. INTRODUCTION

In general, environmental factors which permit economic pests to increase to destructive numbers are of particular interest in agricultural entomology. These factors include temperature, humidity, plant variables and light intensity. For TSSM, the effects of temperature, relative humidity and plant variables on the ability to increase have been explored most extensively by several workers (Nickel, 1960; Watson, 1964; Herbert, 1981; Carey and Bradley, 1982), whereas those of light intensity have not been investigated.

As the results in the previous chapter demonstrated the influence of rearing conditions on reproductive parameters of TSSM, the present study was designed to characterize the effects of the environmental factors on TSSM population increase and to determine whether the degree of hop susceptibility to TSSM was related to the environmental factors.

6.2. MATERIALS AND METHODS

6.2.1. Plant and spider mite culture: The two genotypes of hops used, M4 and M27, were grown under both field and glasshouse conditions. Cultures of TSSM were maintained on dwarf bean leaves in a controlled temperature room under a photoperiod of 16:8 (L:D) at ca. 25°C and 30-40%R.H.

6.2.2. Experimental procedures: Procedures employed in these studies were the same as those described in Chapter 5 except for the modifications necessary to maintain controlled temperatures, humidities and light intensities. All experiments were conducted in a Contherm

CAT 150 MCP cooled incubator (Contherm Scientific Limited, New Zealand) in which photoperiod and temperature could be controlled. The incubator was programmed to a photoperiod of 16:8 (L:D) throughout the study period. Several series of experiments were performed at 20°, 25°, and 30°C (Table 6.1), which are described below.

Table 6.1. Environmental conditions proceeding within a series of experiments to investigate their effect on TSSM increase.

Temperature	Container	Relative humidity	Light intensity	Plant variable
20°C	Closed	Glucose (55%)	43.0 lux	1. Leaves at the fourth and the eighth node of the plant 2. Fully expanded leaves of M4 and M27
		NaCl (76%)	43.0 lux 171.0 lux	
		KCl (85%)	43.0 lux	
		Water (100%)	43.0 lux 171.0 lux	
25°C	Open	Ambient RH (40%)	61.5 lux 150.0 lux 360.0 lux	Distal and basal regions of fully expanded leaves
	Closed	Glucose (55%)	43.0 lux	Fully expanded leaves of M4 and M27
		NaCl (75.5%)	43.0 lux 171.0 lux	
		KCl (85%)	43.0 lux	
		Water (100%)	43.0 lux 171.0 lux	
30°C	Closed	Glucose (55%)	43.0 lux	Fully expanded leaves of M4 and M27
		NaCl (75.5%)	43.0 lux 171.0 lux	
		KCl (84.5%)	43.0 lux	
		Water (100%)	43.0 lux 171.0 lux	

6.2.2.1. Experiments at 20°C: Laboratory experiments were initiated by placing individual adult females onto 1.35 cm diameter leaf discs for 24

h to allow oviposition. The females were then removed and eggs were either added, removed, or transferred to bring the total number to five eggs per leaf disc. A rearing unit consisted of leaf discs placed in a petri dish ranging from 2 to 13 discs depending on the number of eggs laid. The leaf discs were cut from fully expanded mature leaves of hop plants under field conditions. In addition, leaves at the fourth node and the eighth node of the hop plant under glasshouse conditions were also employed for studying the effect of leaf age on the mite populations. The rearing units rested on hardware platforms in plastic food containers, 28 x 21 x 7 cm, with tight fitting lids. Humidity was controlled by the use of various saturated solutions in the bottom of the container (Winston and Bates, 1960). The four main relative humidity levels used were low (55.0 percent), moderate (76.0 percent), high (85.0 percent) and very high (100 percent). The solutions used in maintaining these levels were: low-glucose, moderate-sodium chloride, high-potassium chloride, and very high-water. At each humidity level, the rearing units were illuminated by fluorescent lamps at a light intensity on the rearing unit of about 43 lux. Furthermore, another intensity of illumination at approximately 171 lux was provided for rearing units at both moderate and very high humidities by covering the container with glass held in place with petroleum jelly.

6.2.2.2. Experiments at 25°C: Two types of containers were used in this series of experiments. The first type used was open containers in which relative humidity was similar to that of the ambient air in the incubator (ca. 40% RH). The container consisted of a petri dish covered with a plastic lid containing a hole for ventilation. Four leaf discs cut from distal and basal regions of the fully expanded leaves of M4 and M27 (i.e., one from the distal and one from the basal for each genotype) were placed in each petri dish and three eggs of TSSM were allowed to remain

on a leaf disc. Three intensities of illumination employed at the level of the leaf disc included 61.5, 150, and 360 lux. A total of 36 eggs was tested at each light intensity.

The other type of container used was those previously described in the series of experiments at 20°C. Only the full expanded leaves of M4 and M27 were employed for cutting leaf discs in this container. The remaining steps of this procedure were similar to those in the previous experiment.

6.2.2.3. Experiments at 30°C: All experiments for closed containers were performed as at 25°C. Open container experiments were omitted.

6.2.3. Data analyses

Three life-history traits of TSSM on different genotypes of hops were examined. They were the length of egg and egg to adult development time, and age at first oviposition. In addition, the intrinsic rate of natural increase (r_m) of a culture was calculated from the equation (Wyatt and White, 1977), as follows:

$$r_m = 0.74 (\log_e M_d)/d$$

where d is minimum pre-reproductive time (birth to first reproduction) and M_d is the number of progeny produced in an equal time of the pre-reproductive time.

Also calculated were the mean generation time (T) as given by the following formula (Wyatt and White, 1977):

$$T = 4d/3.$$

Data from the experiments were analyzed separately as completely randomized designs with unpaired t-test for two group tests and analysis of variance (ANOVA) for 3 or more group tests. Means were compared using least significant difference analysis with an alpha level of 5%. Linear regressions were performed using the curve fit procedure of the Cricketgraph computer program.

6.3. Results

6.3.1. Temperature

6.3.1.1. The first series of experiments: Table 6.2 presents the number of TSSM individuals alive at each age interval when reared on two genotypes of hops at 76%RH, a light intensity of 171 lux and three temperatures. As can be seen from the table, generation mortality (egg to adult) varied from 30% on M4 to 10% on M27 at 20°C, 0% to 16% at 25°C and 27.69% to 36.92% at 30°C. At all temperatures, the mortality rate of the immature stage was higher than that of the egg stage. For both stages, the mites reared at 30°C suffered the highest mortality.

Table 6.2. Life table of TSSM on two hop genotypes at 76%RH under constant illumination (16L:8D; 171 lux) and at three temperatures.

Temperature	Genotype	X[a]	l_x[b]	d_x[c]	q_x[d]	s_x[e]	Generation mortality (%)
20°C	M4	Egg	20	2	0.100	0.900	
		Immature[f]	18	4	0.222	0.778	
		Adult[g]	14				30.00%
	M27	Egg	20	0	0.000	1.000	
		Immature	20	2	0.100	0.900	
		Adult	18				10.00%
25°C	M4	Egg	25	0	0.000	1.000	
		Immature	25	0	0.000	1.000	
		Adult	25				0.00%
	M27	Egg	25	0	0.000	1.000	
		Immature	25	4	0.160	0.840	
		Adult	21				16.00%
30°C	M4	Egg	65	5	0.077	0.923	
		Immature	60	13	0.217	0.783	
		Adult	47				27.69%
	M27	Egg	65	11	0.169	0.831	
		Immature	54	13	0.241	0.759	
		Adult	41				36.92%

a = Stage of life cycle.
b = Number living at beginning of stage in the x column.
c = Number dying within stage in the x column.
d = Probability of dying during x.
e = Probability of surviving interval x.
f = Larva + Protonymph + Deutonymph.
g = Female + Male.

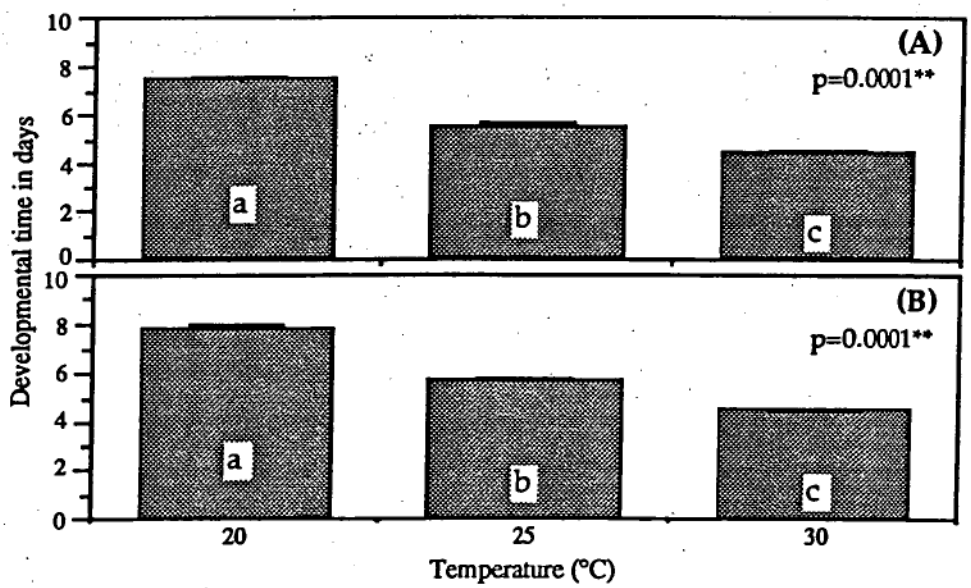
When the mites reached adulthood, sex ratios were observed to favour females for all 3 temperature regimes (Table 6.3). Nevertheless, sex ratio determinations indicated a shift towards a smaller female:male ratio with an increase in temperature.

Table 6.3. Sex ratio of TSSM at 76%RH, constant illumination (16L:8D; 171 lux) and three temperatures.

Temperature	Adult females	Adult males
20°C	23	9
25°C	33	13
30°C	57	31

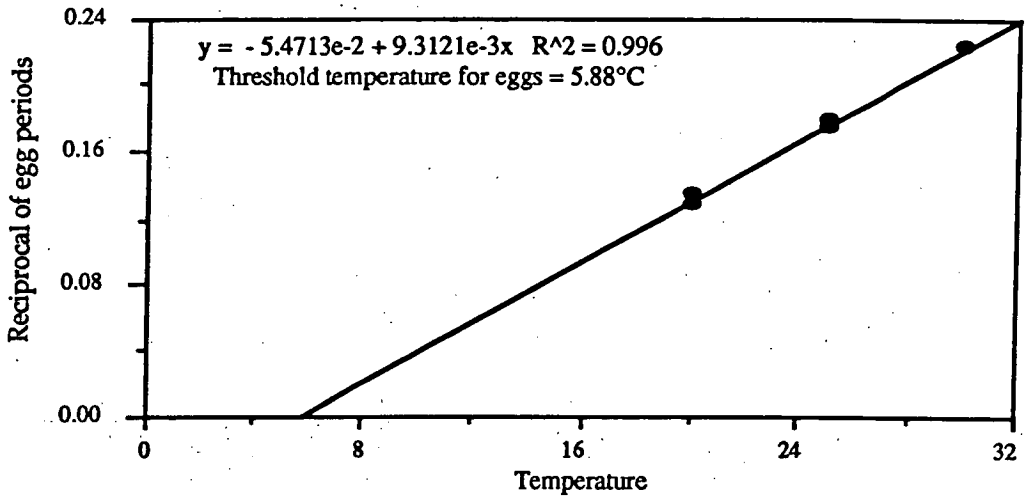
The developmental time in days for eggs of TSSM on both M4 and M27 varied significantly ($p < 0.01$) for the three rearing temperatures (Fig. 6.1). The length of egg development was longest at 20°C and shortest at 30°C.

Fig. 6.1. Developmental period for eggs of TSSM on M4(A) and M27(B) at 76% RH and 171 lux. Columns with the same letter are not significantly different ($p \geq 0.05$; PLSD).



From the regression of the reciprocal of the development time on temperature the threshold of development where x = -a/b was calculated. The rate of development through the egg stage was expressed by $y = 9.3121e^{-3}x - 5.4713e^{-2}$ ($r^2 = 0.996$) with a threshold temperatue of 5.88°C (Fig. 6.2).

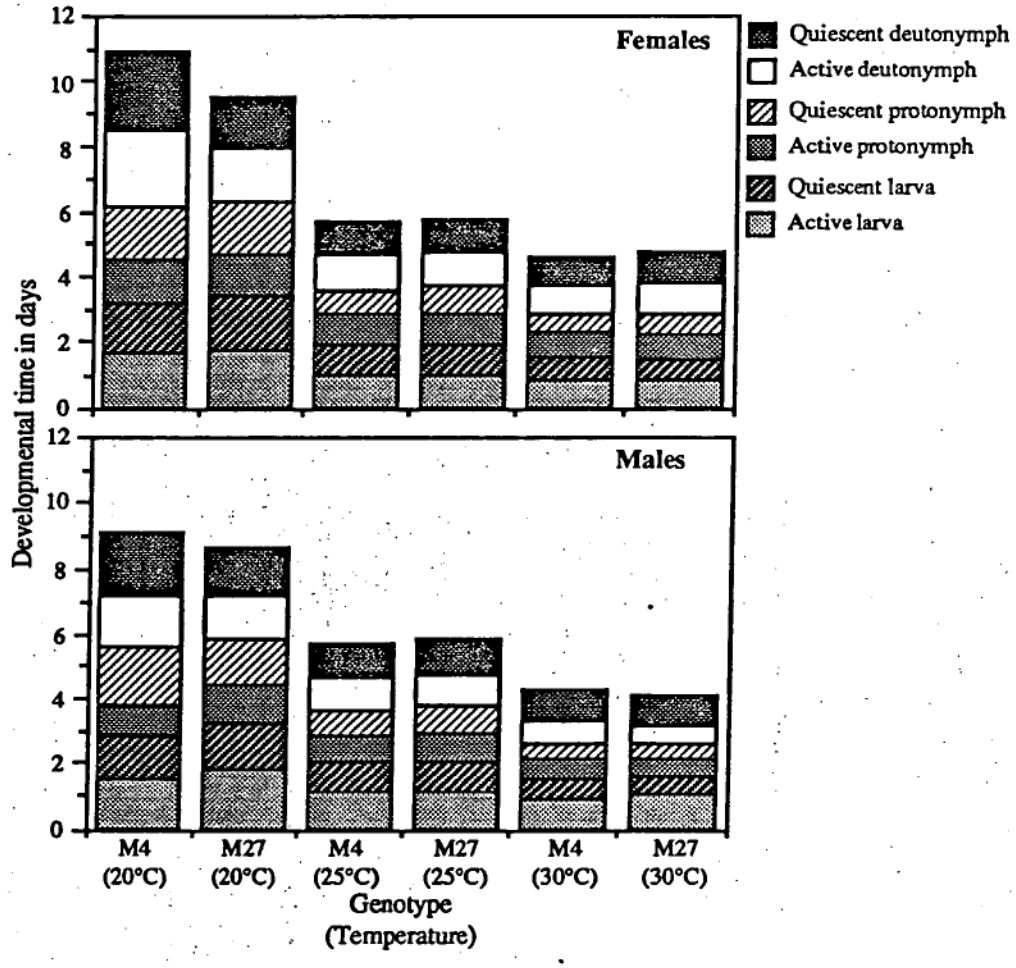
Fig. 6.2. The regression of the reciprocal of the developmental period for eggs in days (y) on temperature (x).



For females and males, the developmental periods of the active and quiescent periods for larva, protonymph and deutonymph reared on M4 and M27 within each of the temperature ranges are presented in Fig. 6.3A and B, respectively. Comparisons of the three rearing temperatures show that the length of the developmental periods for females and males on both genotypes decreased with increasing temperature levels. At 20°C, the developmental period from active larva to quiescent deutonymph of the female on both genotypes was longer than that of the male. However, the developmental periods were nearly identical for both female and male at 25° and 30°C. A comparison between the hop genotypes also shows that the developmental periods for females and

males on M4 were longer than those on M27 at 20°C, but the developmental periods of the mites at 25° and 30°C were nearly identical for both genotypes.

Fig. 6.3. Developmental period from active larva to quiescent deutonymph of TSSM on M4 and M27 at 76% RH and 171 lux.



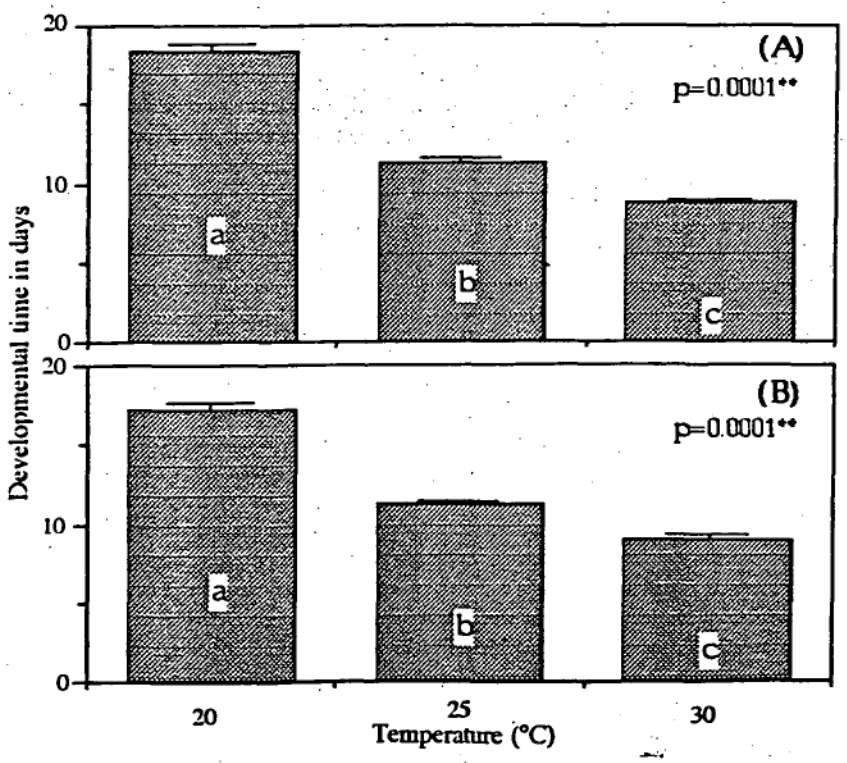
The threshold temperature of development (x at y = 0) varied from 8.13° to 15.16°C and 5.68° to 15.68°C for active and quiescent immature stages of female and male TSSM, respectively (Table 6.4). When the data for the postembryonic stages were pooled the temperatures for threshold of development for females and males were 10.99° and 11.33°C, respectively.

Table 6.4. Determination of the developmental threshold temperature(°C) for TSSM at 76%RH and 171Lux.

Stage	Threshold temperature (°C) (X(Y=0))	
	Female	Male
Active larva	8.41	5.68
Quiescent larva	12.36	12.32
Active protonymph	8.13	10.71
Quiescent protonymph	15.16	15.68
Active deutonymph	10.15	12.16
Quiescent deutonymph	10.59	7.51
Postembryonic stages	**10.99**	**11.33**

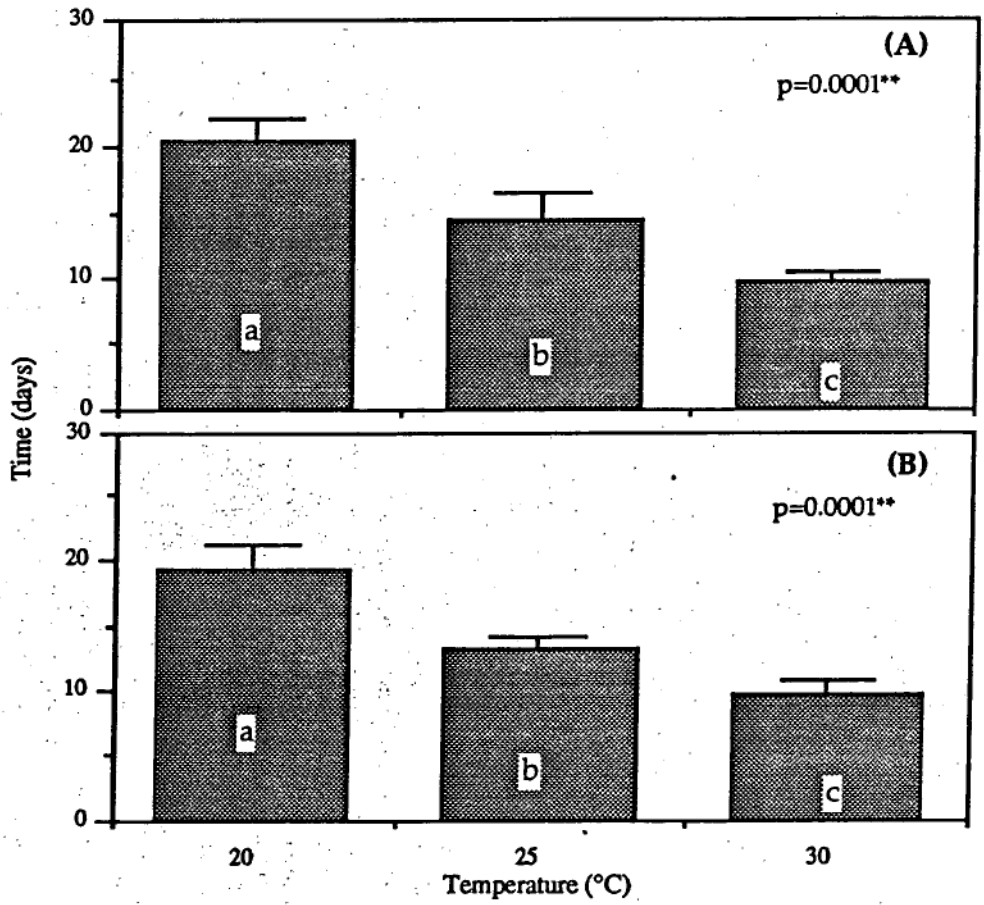
For both M4 and M27, there were highly significant differences ($p < 0.01$) in the developmental period from eggs to adults of TSSM females among the three temperatures selected (Fig. 6.4). The shortest periods of the total pre-adult development occurred at 30°C and the longest at 20°C.

Fig. 6.4. Developmental period from eggs to adults of TSSM females on M4(A) and M27(B) at 76%RH and 171 lux.



In addition, temperature had a significant influence on the pre-reproductive period (egg-to-egg developmental period) of TSSM on M4 and M27 (Fig. 6.5A and B). The longest and shortest periods were found to occur at 20° and 30°C, respectively.

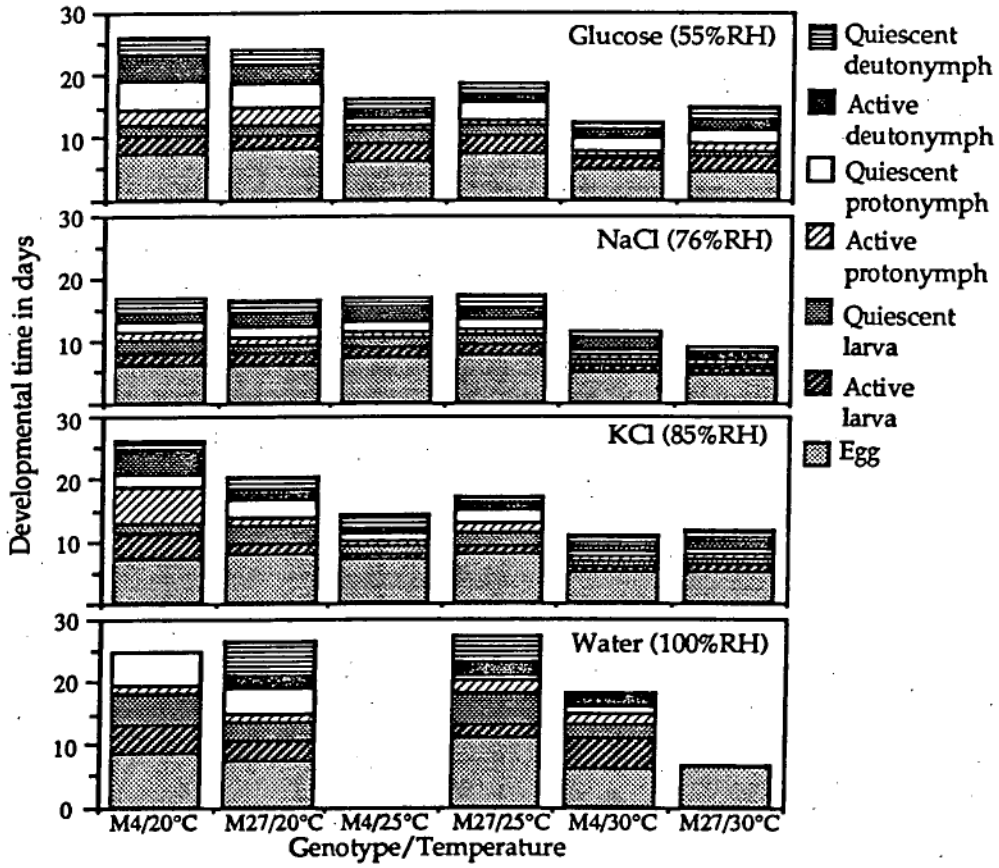
Fig. 6.5. Pre-reproductive periods of TSSM on M4(A) and M27(B) at 76%RH and 171 lux. Columns with the same letter are not significantly different ($p \geq 0.05$; PLSD).



6.3.1.2. The second series of experiments To determine whether the effects of temperature on the duration of immature stages under various conditions would give different results from each other, a series of observations for the three rearing temperatures as mentioned previously were conducted at a light intensity of 43 lux under low

(55%RH), moderate (76%RH), high (85%RH) and very high (100%RH) humidity conditions. The results of these observations are illustrated in Fig. 6.6. Although developmental periods of the immature stages were shortest at 30°C, the duration within each immature stage does not show a consistent trend at the three temperatures under these conditions. At each temperature, most of the mites could not reach adulthood under very high humidity (100%RH).

Fig. 6.6. Developmental time of TSSM on M4 and M27 at a light intensity of 43 lux.



The time spent in development represents approximately 39.20, 20.60, 19.37 and 20.83% of the juvenile stage for eggs, larvae, protonymph and deutonymph, respectively (Table 6.5). The longest time was spent in the egg stage. It was also found that the proportion of the egg period

increased with an increase in temperature from 20° to 25°C and began to level off between 25° and 30°C.

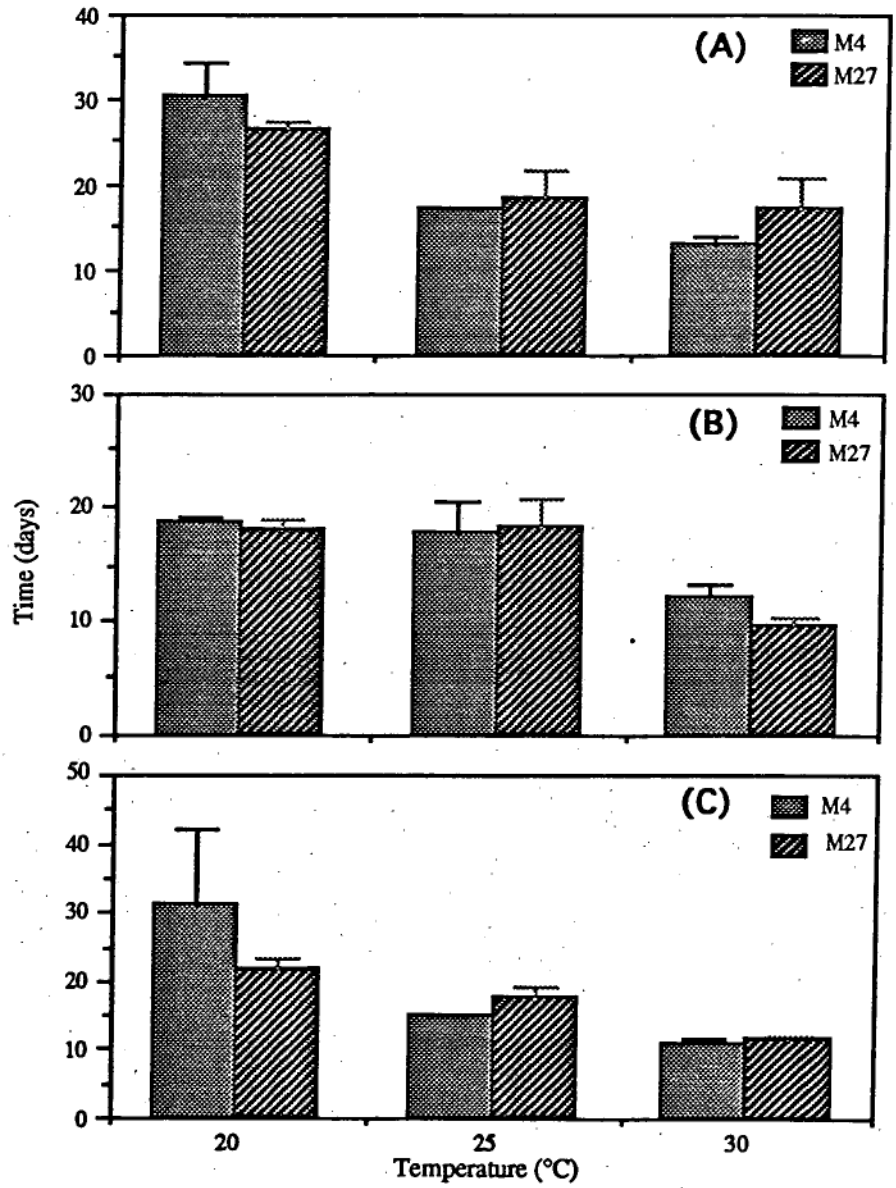
Table 6.5. Percentages representative of developmental periods for all immature stages of TSSM under various conditions.

Temperature	Genotype	Humidity	Stages			
			Egg	Larva	Protonymph	Deutonymph
20°C	M4	55%RH	27.83	18.55	26.67	26.95
		76%RH	36.04	24.02	18.62	21.32
		85%RH	26.82	22.99	28.35	21.84
		100%RH	-	-	-	-
	M27	55%RH	33.61	15.96	27.74	22.69
		76%RH	36.50	19.46	19.46	24.58
		85%RH	38.54	23.02	21.53	16.92
		100%RH	28.85	23.08	21.16	26.92
25°C	M4	55%RH	37.50	31.25	12.50	18.75
		76%RH	43.25	10.66	17.17	21.80
		85%RH	50.00	14.00	14.00	22.00
		100%RH	-	-	-	-
	M27	55%RH	39.74	23.95	21.77	14.53
		76%RH	46.36	16.43	17.02	20.19
		85%RH	46.68	16.92	23.34	13.07
		100%RH	40.74	25.93	11.11	22.23
30°C	M4	55%RH	39.31	18.84	21.29	20.56
		76%RH	43.36	15.93	17.71	23.01
		85%RH	48.34	12.33	18.96	20.38
		100%RH	33.33	38.89	16.67	11.12
	M27	55%RH	31.08	22.30	20.95	25.67
		76%RH	50.61	14.30	14.30	20.79
		85%RH	44.62	16.61	16.61	22.13
		100%RH	-	-	-	-
Average			**39.20**	**20.60**	**19.37**	**20.83**

The duration of the pre-reproductive period of TSSM females on different hop genotypes in various environments is presented in Fig. 6.7. It was apparent that the average time of egg-to-egg developmental periods decreased with increasing temperature levels. The pre-reproductive

periods for the 3 constant temperature regimes fluctuated between 10.90 and 31.00 days.

Fig. 6.7. Pre-reproductive period of TSSM on two hop genotypes between different temperatures at 55%RH(A), 76%RH(B), and 85%RH(C) at a light intensity of 43 lux.



Values of the intrinsic rate of natural increase (r_m) calculated for cohorts of TSSM females at each temperature level within any given conditions are presented in Fig. 6.8. The value of r_m was lowest on M4 at

20°C and highest on M27 at 30°C. This larger r_m was related to shorter generation times (Fig. 6.9 A, B, and C). It can be seen from the figures that the mean length of generations decreased as constant temperatures increased. These estimates of reproductive indices indicate that of the temperatures tested, the most favourable temperature for population increase is 30°C.

Fig. 6.8. Intrinsic rates of increases of TSSM on different hop genotypes at 55%RH(A), 76%RH(B) and 85%RH(C) at a light intensity of 43 lux and three temperatures.

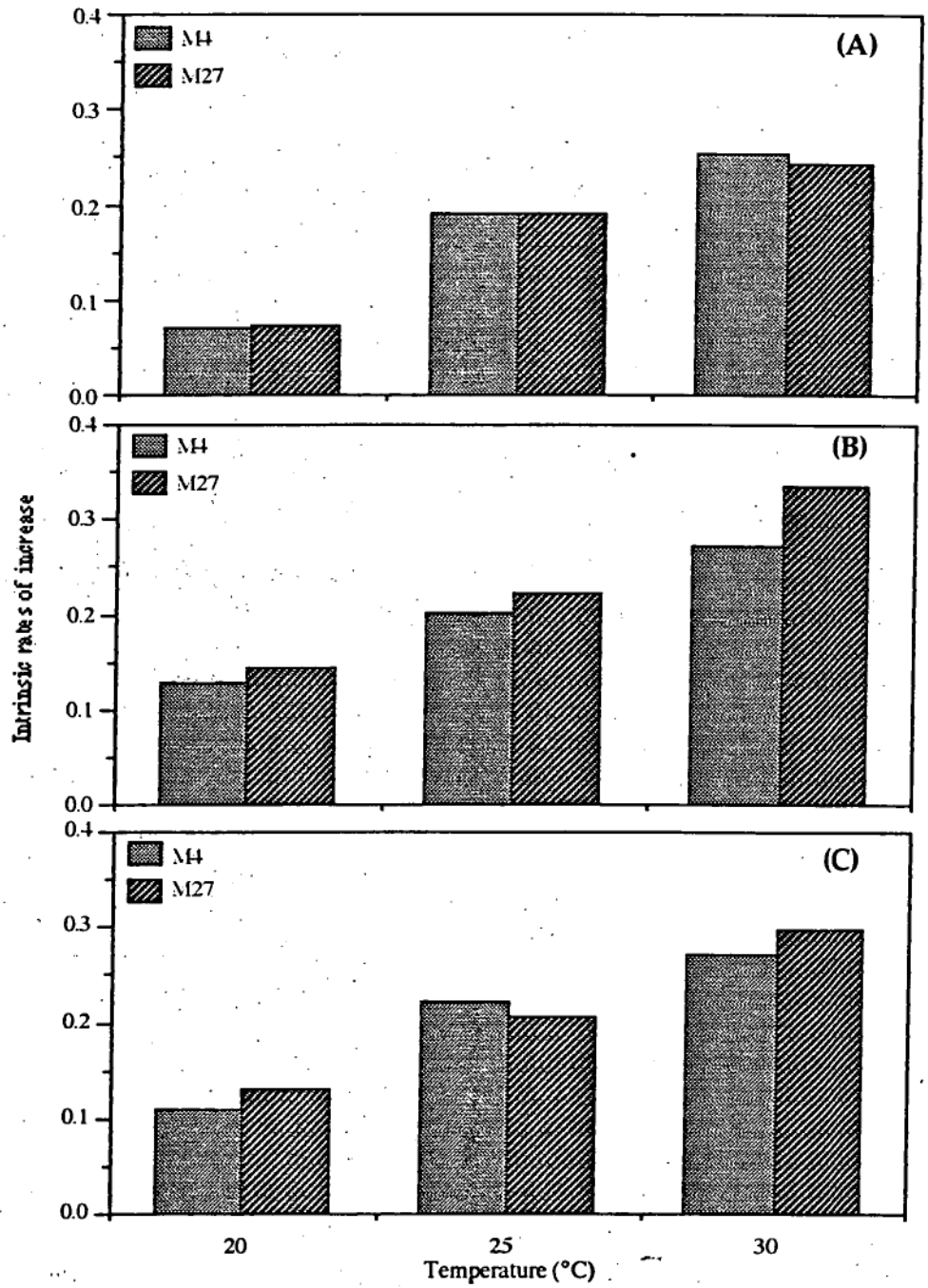
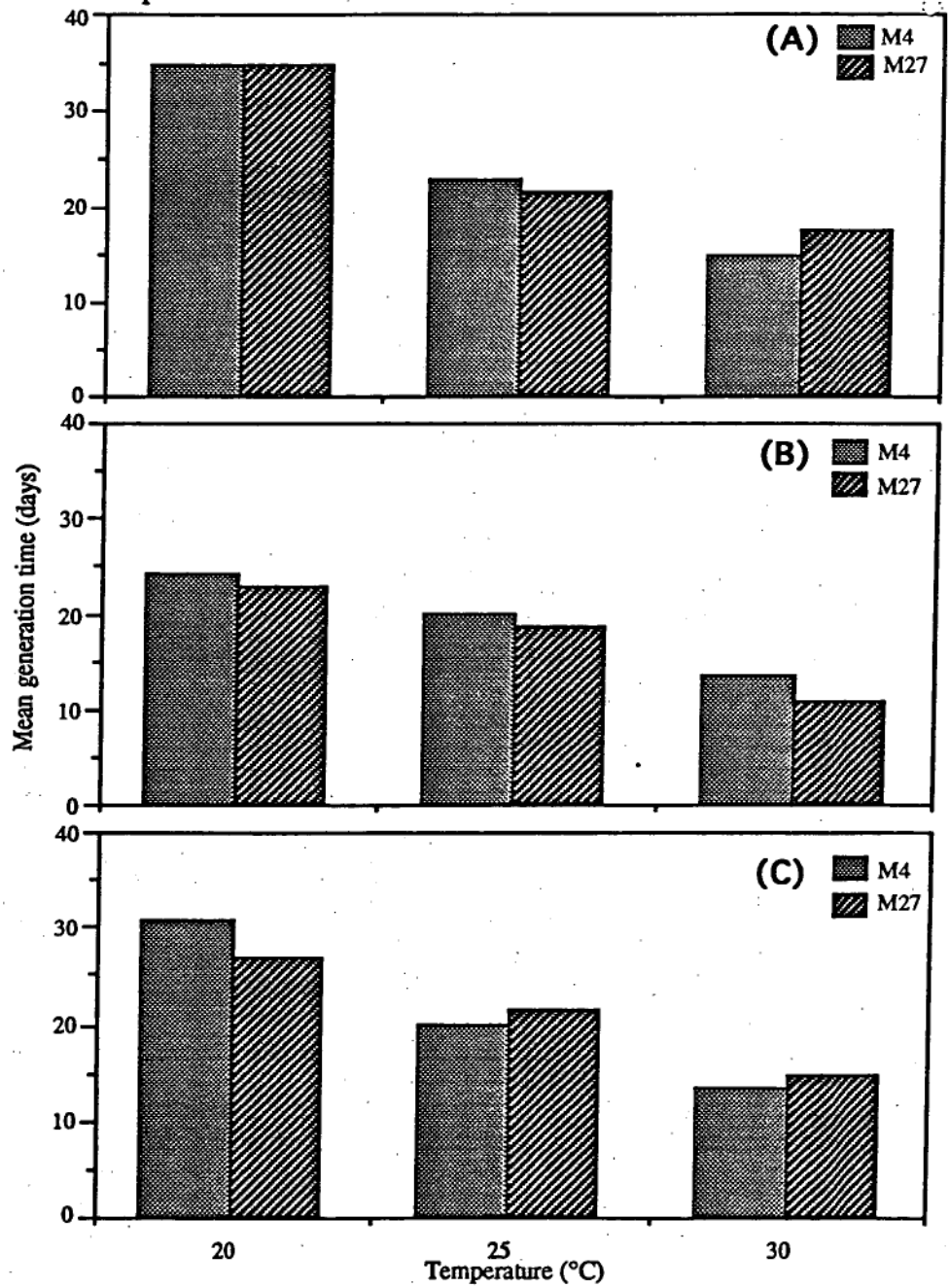


Fig. 6.9. Mean generation times of TSSM on different hop genotypes at 55%RH(A), 76%RH(B) and 85%RH(C) at a light intensity of 43 lux and three temperatures.



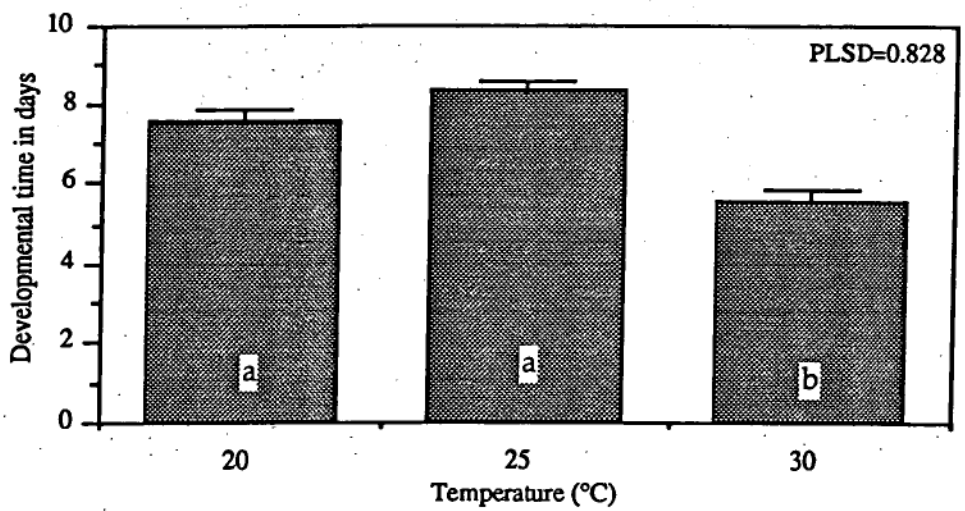
Using the average values of the developmental periods for eggs under various conditions as mentioned previously, a two-way analysis of variance was performed (Table 6.6). Highly significant differences in egg

periods were detected among different temperatures ($p < 0.01$). However, there were no significant differences in these periods among different genotypes and no significant interaction between genotypes and temperatures was found ($p \geq 0.05$). According to Fisher's protected least significant differences test, the duration of egg periods at 30°C was significantly shorter than that at 20° and 25°C (Fig. 6.10).

Table 6.6. Analysis of variance of the developmental periods for eggs of TSSM on two hop genotypes at 43 lux.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Temperature (A)	2	29.097	14.549	22.409	.0001
Genotype (B)	1	0.363	0.363	0.559	.4650
AB	2	0.415	0.207	0.320	.7307
Error	17	11.037	0.649		

Fig. 6.10. Developmental periods for eggs of TSSM at 20°, 25°, and 30°C.



Because of the high mortality in rearing the mites within very high humidity conditions (100%RH), information other than that

regarding duration of the egg stage is incomplete. The other three conditions (55%, 76% and 85%RH) were tested for the developmental period from eggs to adult, the pre-reproductive period, the intrinsic rate of increase and the mean generation time.

Analysis of variance of the developmental period showed highly significant differences between temperature levels (Table 6.7). Immature mites developed faster at 30°C than at 20° and 25°C in this series of experiments (Fig. 6.11). The developmental period of mites reared on different genotypes did not vary significantly (Table 6.7). Furthermore, there was no significant interaction between temperatures and genotypes.

Table 6.7. Analysis of variance of the developmental periods from eggs to adults of TSSM on two hop genotypes at 43 lux.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Temperature (A)	2	334.359	167.179	9.982	.0018
Genotype (B)	1	1.084	1.084	0.065	.8026
AB	2	38.688	19.344	1.155	.3415
Error	15	251.210	16.747		

Fig. 6.11. Developmental periods from eggs to adults of TSSM at 20°, 25°, and 30°C

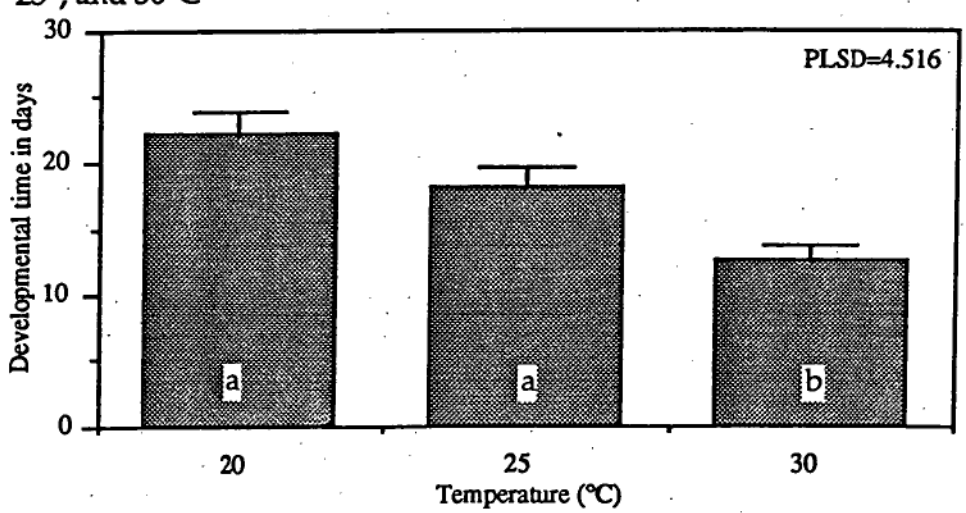
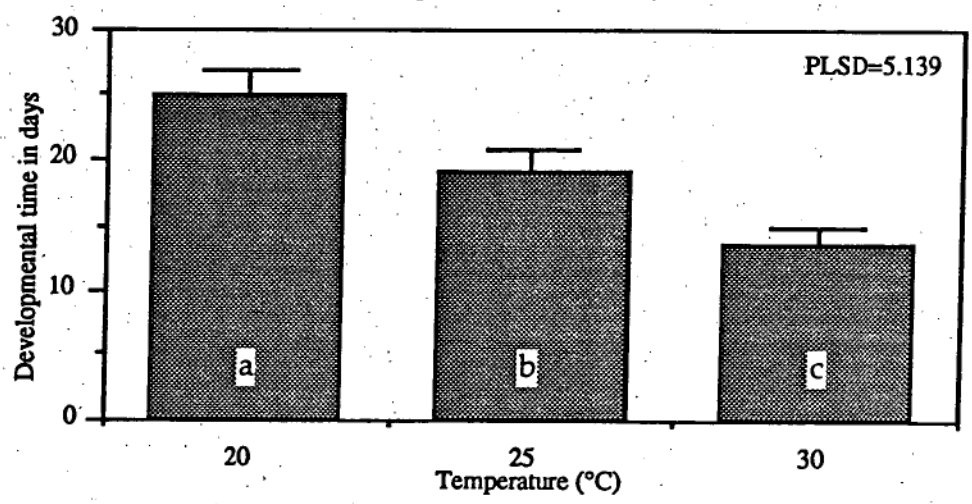


Table 6.8 shows that the pre-reproductive period of female mites under various conditions varied significantly among temperature regimes, whereas no significant differences between genotypes as well as no significant interaction between temperatures and genotypes were detected ($p \geq 0.05$). It was apparent that the mites at 30°C had the shortest period and the mites at 20°C had the longest period (Fig. 6.12).

Table 6.8. Analysis of variance of the pre-reproductive periods of TSSM on two hop genotypes at 43 lux.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Temperature (A)	2	468.723	234.361	10.753	.0013
Genotype (B)	1	0.016	0.016	0.001	.9790
AB	2	49.984	24.992	1.147	.3440
Error	15	326.917	21.794		

Fig. 6.12. Pre-reproductive periods of TSSM at 20°, 25°, and 30°C.



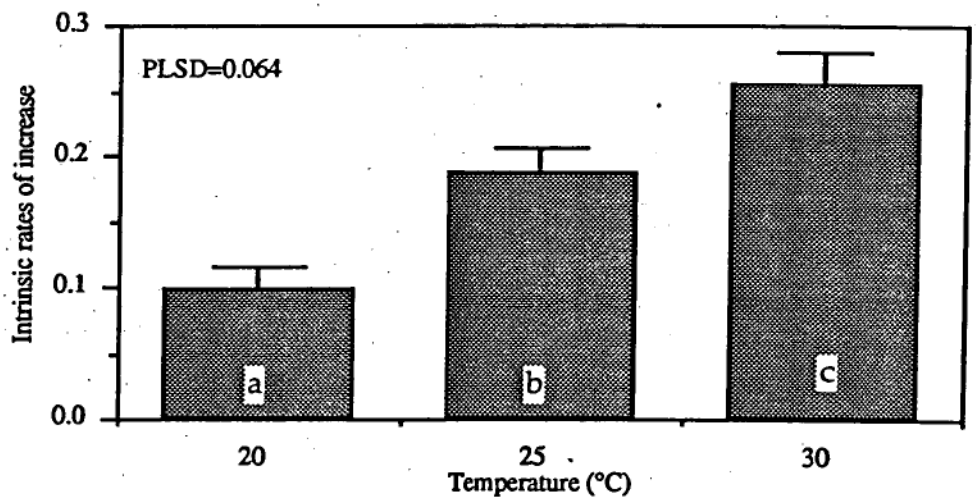
According to analysis of variance, intrinsic rates of increase of mites reared at different temperatures varied significantly whilst variation among genotypes was not significant (Table 6.9). There was no

significant interaction of this value between temperatures and genotypes. The highest value was found at 30°C and the lowest value was found at 20°C (Fig. 6.13).

Table 6.9. Analysis of variance of the intrinsic rates of increase of TSSM on two hop genotypes at 43 lux.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Temperature (A)	2	0.089	0.045	13.727	.0004
Genotype (B)	1	3.442E-4	3.442E-4	0.106	.7496
AB	2	0.009	0.005	1.395	.2781
Error	15	0.049	0.003		

Fig. 6.13. Intrinsic rates of increase of TSSM at 20°, 25°, and 30°C.



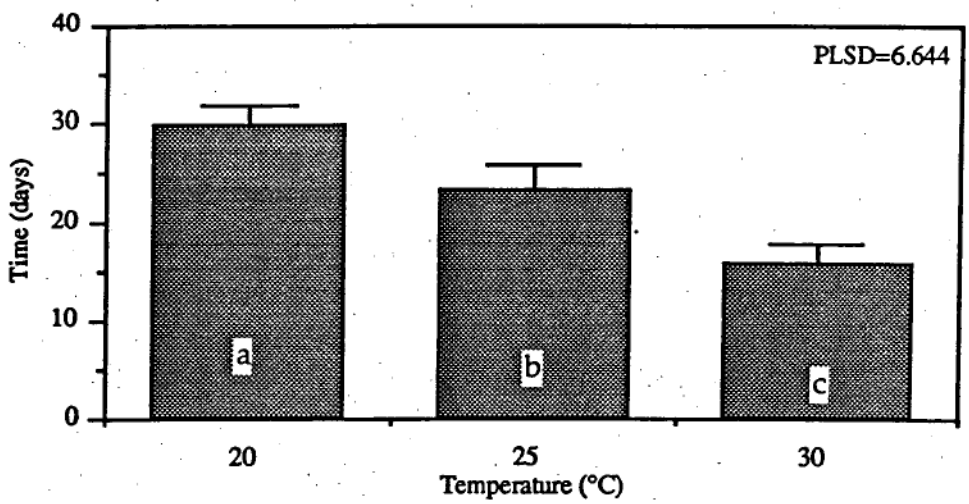
For mean generation times, analysis of variance showed significant differences among the given temperatures (Table 6.10). In addition, it can be seen from the table that there were no significant differences in the mean generation time between genotypes selected and no significant interaction between genotypes and temperatures was found. Populations

of TSSM at 30°C had the shortest mean generation time, whereas those at 20°C had the longest. The mean generation was greatest at 20°C and least at 30°C (Fig. 6.14).

Table 6.10. Analysis of variance of the mean generation times of TSSM on two hop genotypes at 43 lux.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Temperature (A)	2	699.279	349.640	8.924	.0028
Genotype (B)	1	1.383	1.383	0.035	.8535
AB	2	40.876	20.438	0.522	.6039
Error	15	587.720	39.181		

Fig. 6.14. Mean generation time of TSSM at 20°, 25°, and 30°C.



6.3.2. Humidity

6.3.2.1. The first series of experiments: Comparison of the juvenile survival between mites reared under conditions of controlled relative humidity with the NaCl solution (76%RH) and those reared at a humidity near saturation without the salt (100%RH) at 20°-30°C and a light intensity of 171 lux shows that the percentage of immatures reaching adulthood on both M4 and M27 was higher at 76%RH than at 100%RH (Table 6.11). Generation mortality varied from 30.91% on M4 to

27.27% on M27 at 76%RH and 78.13% to 44.74% at 100%RH. Sex ratios of immatures becoming adults were observed to favour females for both humidity regimes (Table 6.12). This favourability was most evident at 100%RH which averaged about four females to one male. At 76%RH, sex ratio determinations indicated a shift towards a smaller female:male ratio.

Table 6.11. Life table of TSSM on two hop genotypes at 20-30°C under constant illumination (16L:8D; 171 lux) and at two humidities.

Humidity	Genotype	X[a]	l_x[b]	d_x[c]	q_x[d]	s_x[e]	Generation mortality (%)
75%RH	M4	Egg	110	7	0.0636	0.9364	
		Immature[f]	103	17	0.1650	0.8350	
		Adult[g]	86				30.91%
	M27	Egg	110	11	0.1000	0.9000	
		Immature	99	19	0.1919	0.8081	
		Adult	80				27.27%
100%RH	M4	Egg	64	17	0.2656	0.7344	
		Immature	47	33	0.7021	0.2979	
		Adult	14				78.13%
	M27	Egg	76	6	0.0790	0.9210	
		Immature	70	28	0.4000	0.6000	
		Adult	42				44.74%

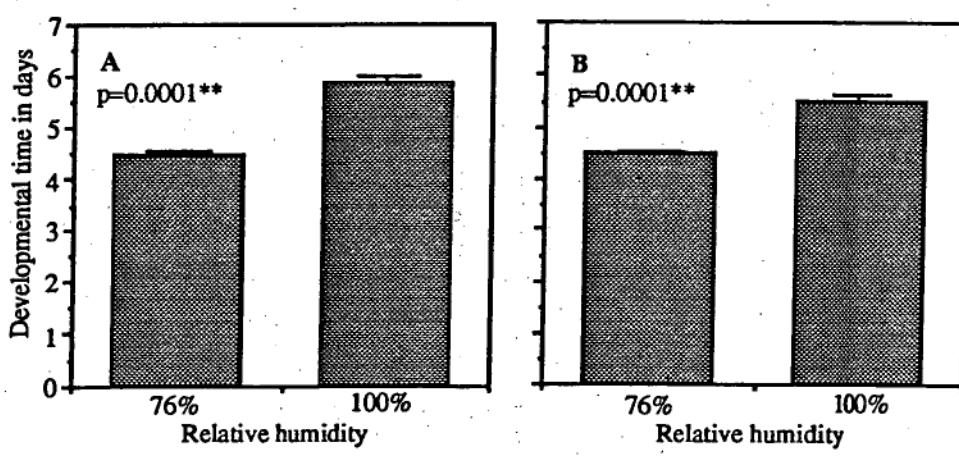
a = Stage of life cycle.
b = Number living at beginning of stage in the x column.
c = Number dying within stage in the x column.
d = Probability of dying during x.
e = Probability of surviving interval x.
f = Larva + Protonymph + Deutonymph.
g = Female + Male.

Table 6.12. Sex ratio of adult TSSM at 20-30°C under constant illumination (16L:8D; 171 lux) and at two humidities.

Relative humidity	Adult females	Adult males
75%	113	53
100%	46	10

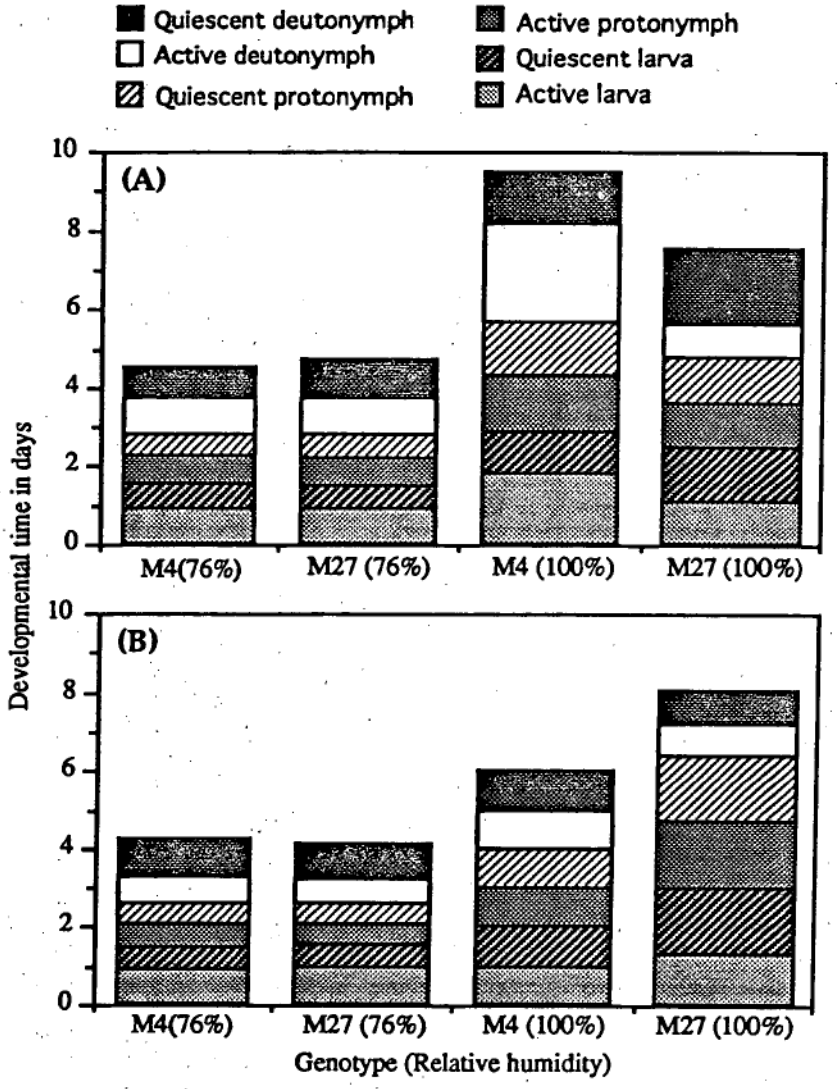
Because of the high mortality of mites reared at 20° and 25°C under very high humidity conditions, all the following results in this section are based on the data collected on mites reared at 30°C and a light intensity of 171 lux under moderately and very high humidity conditions. According to an unpaired t-test, there were highly significant differences ($p < 0.01$) in developmental period for eggs between these two humidity conditions (Fig. 6.15). The duration of egg stage varied from 4.45 at 76%RH to 5.84 days at 100%RH and 4.46 at 76%RH to 5.44 days at 100%RH for the mites on M4 and M27, respectively.

Fig. 6.15. Developmental period for eggs of TSSM on M4(A) and M27(B) at 30°C and 171 lux.



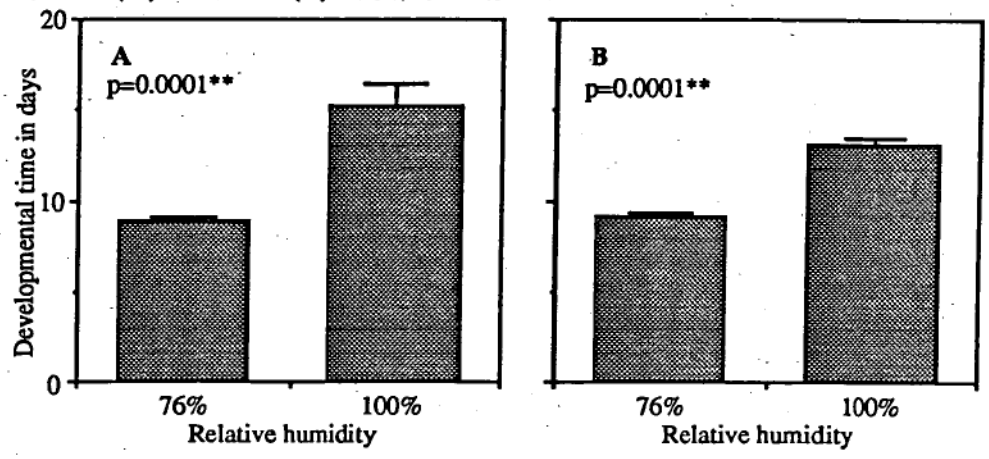
The developmental times for each postembryonic stage of both female and male immatures on M4 and M27 at 76% and 100%RH are illustrated in Fig. 6.16A and B. On both genotypes, the mites reared at 76%RH developed faster than those reared at 100%RH. At each stage the mites at 100%RH took longer to develop than those at 76%RH.

Fig. 6.16. Developmental period from active larva to quiescent deutonymph of females (A) and males(B) on M4 and M27 at 30°C and 171 lux.



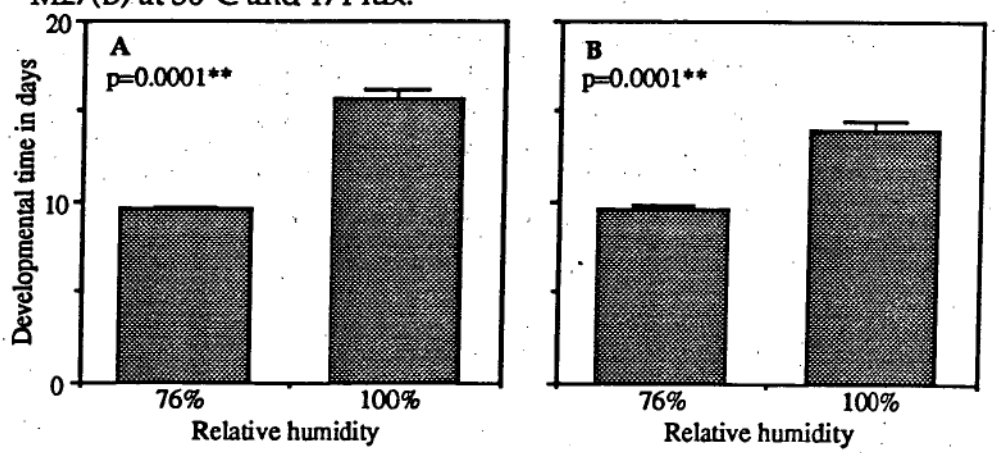
Developmental periods from eggs to adults of TSSM females on M4 and M27 at the different relative humidity were presented in Fig. 6.17A and B, respectively. Highly significant decreases in the total developmental time of juvenile stages at 76%RH compared with 100%RH were detected on both genotypes ($p < 0.01$). The duration of the juvenile stages from egg to adult varied from 8.77 at 76%RH to 15.13 days at 100%RH and 9.04 at 76%RH to 13.06 days at 100%RH for the mites on M4 and M27, respectively.

Fig. 6.17. Developmental period from eggs to adults of TSSM females on M4(A) and M27(B) at 30°C and 171 lux.



According to the unpaired t-test, pre-reproductive periods of mites reared at 76% and 100%RH varied significantly (Fig. 6.18). The duration of egg-to-egg developmental period ranged from 9.53 at 76%RH to 15.67 days at 100%RH and 9.60 at 76%RH to 13.93 days at 100%RH for the mites on M4 and M27, respectively.

Fig. 6.18. Pre-reproductive period of TSSM females on M4(A) and M27(B) at 30°C and 171 lux.



The intrinsic rate of increase (r_m) of TSSM population on both M4 and M27 was higher at 76%RH than at 100%RH (Fig. 6.19). In contrast, the mean generation time (T) of the same mite population was higher at 100%RH than at 76%RH (Fig. 6.20). The r_m values ranged from 0.331 on

M4 to 0.378 days on M27 and 0.182 on M4 to 0.236 days on M27 for the mites reared at 76%RH and 100%RH, respectively (Fig. 6.19). For both genotypes, the T values varied from 9.33 days at 76%RH to 14.67 days at 100%RH (Fig. 6.20).

Fig. 6.19. Intrinsic rates of increases of TSSM on two genotypes of hops at 30°C and 171 lux.

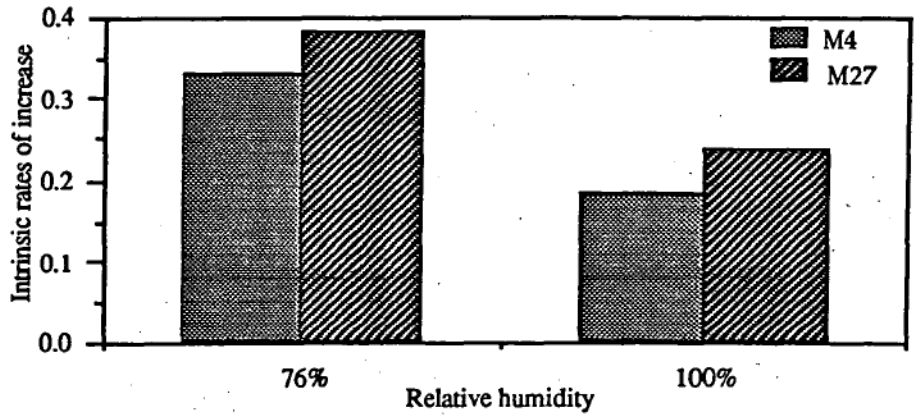
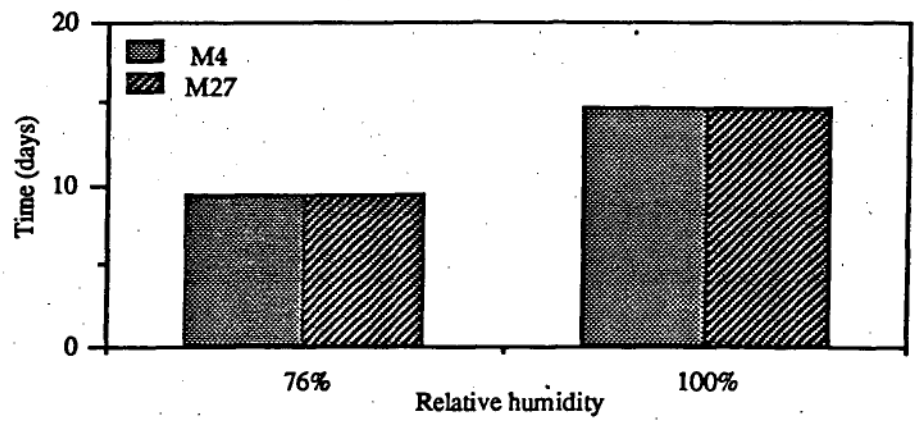


Fig. 6.20. Mean generation time of TSSM on two genotypes of hops at 30°C and 171 lux.



6.3.2.2. The second series of experiments: To determine whether the humidity levels controlled by the use of salt solutions would give different results from each other, a series of observations were conducted at 20°-30°C and a light intensity of 43 lux. The three humidity levels used were 55%, 76% and 85%RH. Comparisons of the survival of the mites reared at these humidity levels revealed that the percentage alive from

egg to adult varied with humidity (Table 6.13). The lowest and highest overall survival occurred at 55% and 76%RH, respectively. The survival of egg stage at 55% and 85%RH was nearly identical, whereas that of immatures was higher at 85%RH than at 55%RH. Nevertheless, at 76%RH the survival for both eggs and immatures was higher than at 55% and 85%RH. Generation mortality ranged from 71.43 to 81.43%, 58.57 to 34.28% and 65.71 to 55.71% at 55%, 76% and 85%RH, respectively.

Table 6.13. Life table of TSSM on two hop genotypes at 20-30°C, constant illumination (16L:8D; 46 lux) and three humidities.

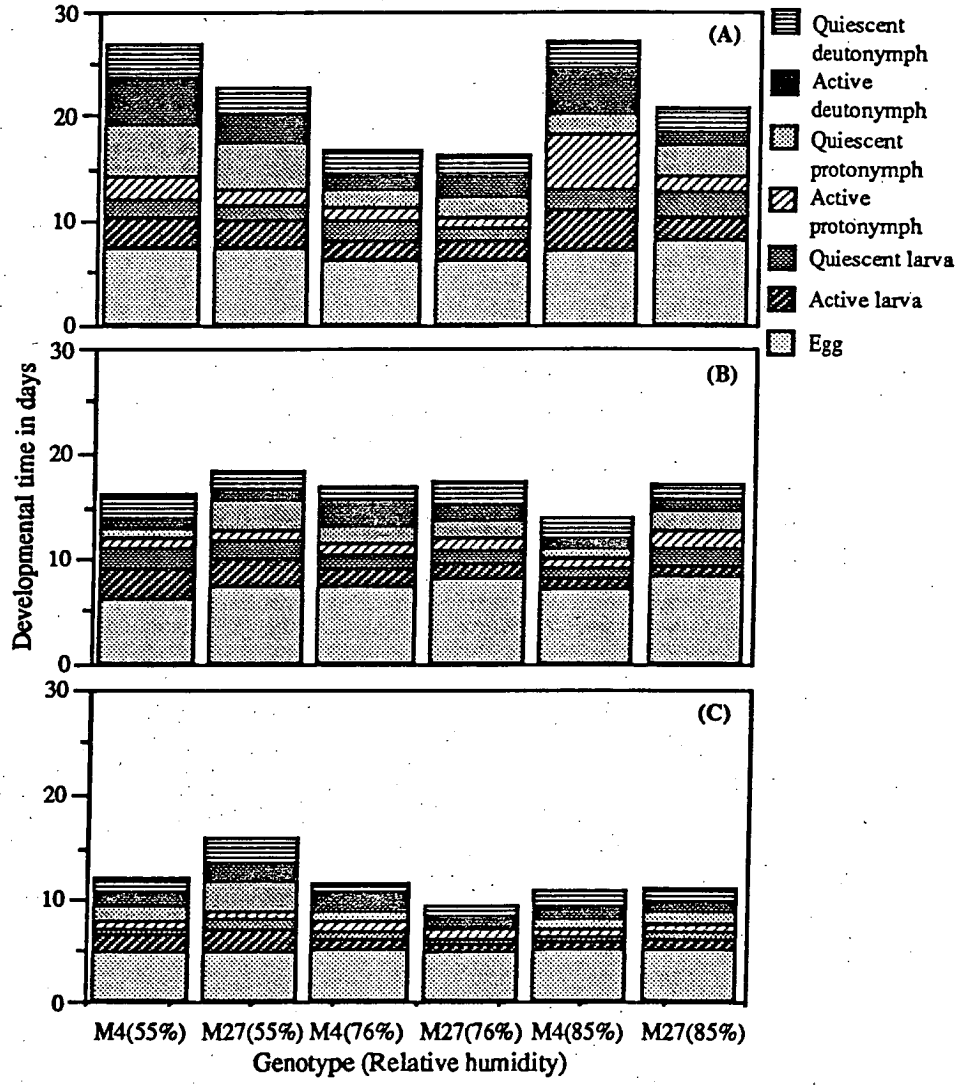
Humidity	Genotype	X[a]	l_x[b]	d_x[c]	q_x[d]	s_x[e]	Generation mortality (%)
55%RH	M4	Egg	70	37	.5286	.4714	
		Immature[f]	33	13	.3939	.6061	
		Adult[g]	20				71.43%
	M27	Egg	70	31	.4429	.5571	
		Immature	39	26	.6667	.3333	
		Adult	13				81.43%
76%RH	M4	Egg	70	14	.2000	.8000	
		Immature	56	27	.4821	.5179	
		Adult	29				58.57%
	M27	Egg	70	9	.1286	.8714	
		Immature	61	15	.2459	.7541	
		Adult	46				34.28%
85%RH	M4	Egg	70	36	.5143	.4857	
		Immature	34	10	.2941	.7059	
		Adult	24				65.71%
	M27	Egg	70	30	.4286	.5714	
		Immature	40	9	.2250	.7750	
		Adult	31				55.71%

a = Stage of life cycle.
b = Number living at beginning of stage in the x column.
c = Number dying within stage in the x column.
d = Probability of dying during x.
e = Probability of surviving interval x.
f = Larva + Protonymph + Deutonymph.
g = Female + Male.

Developmental time for each stage of the female juvenile stages on M4 and M27 under different relative humidity conditions is illustrated in Fig. 6.21. At 20°C the mites on both genotypes developed faster at 76%RH

than at 55% or 85%RH. At 25° and 30°C the humidity used in this study had little effect on the total developmental period of mites.

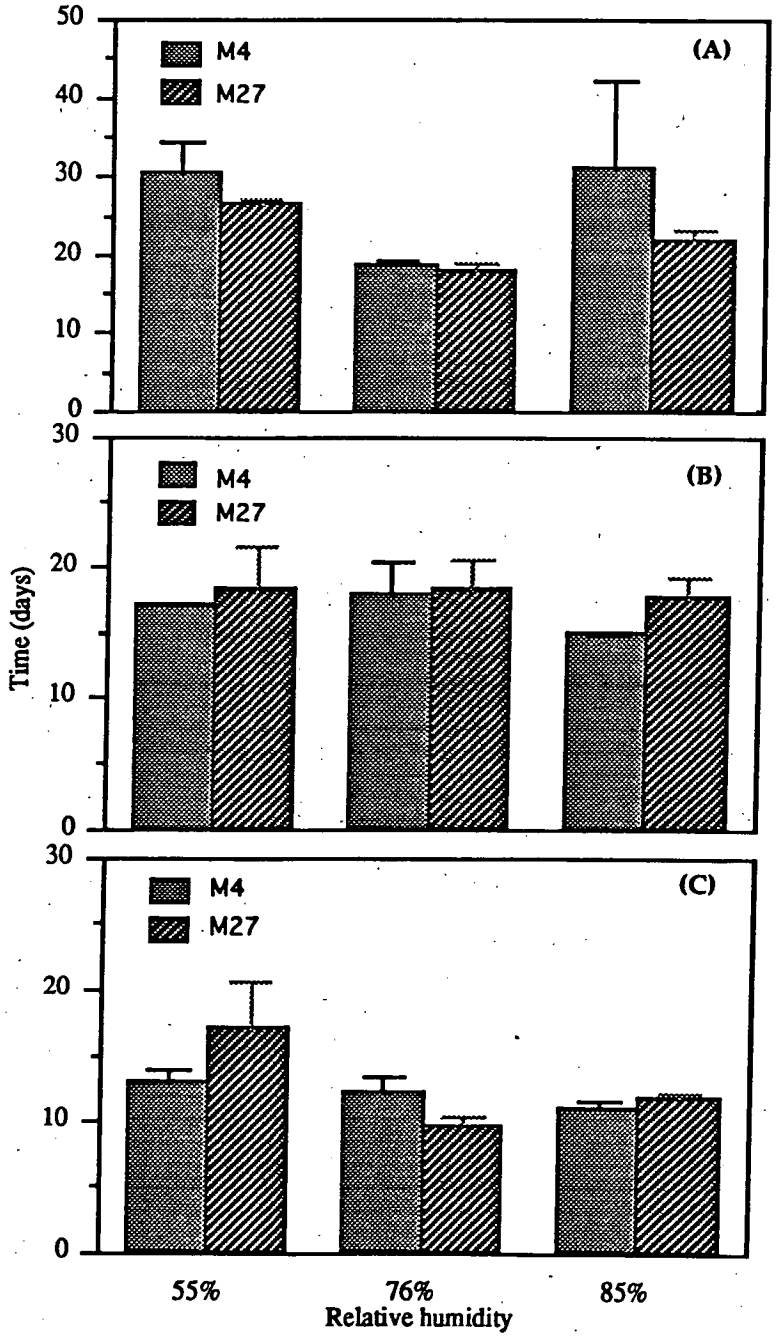
Fig. 6.21. Developmental time of TSSM females on M4 and M27 at 20°C(A), 25°C(B) and 30°C(C) at a light intensity of 43 lux.



The duration of egg-to-egg developmental period in the various humidity within each temperature is presented in Fig. 6.22. The difference in these pre-reproductive period due to humidity levels was

similar to those found in the developmental time of the juvenile stage as mentioned above.

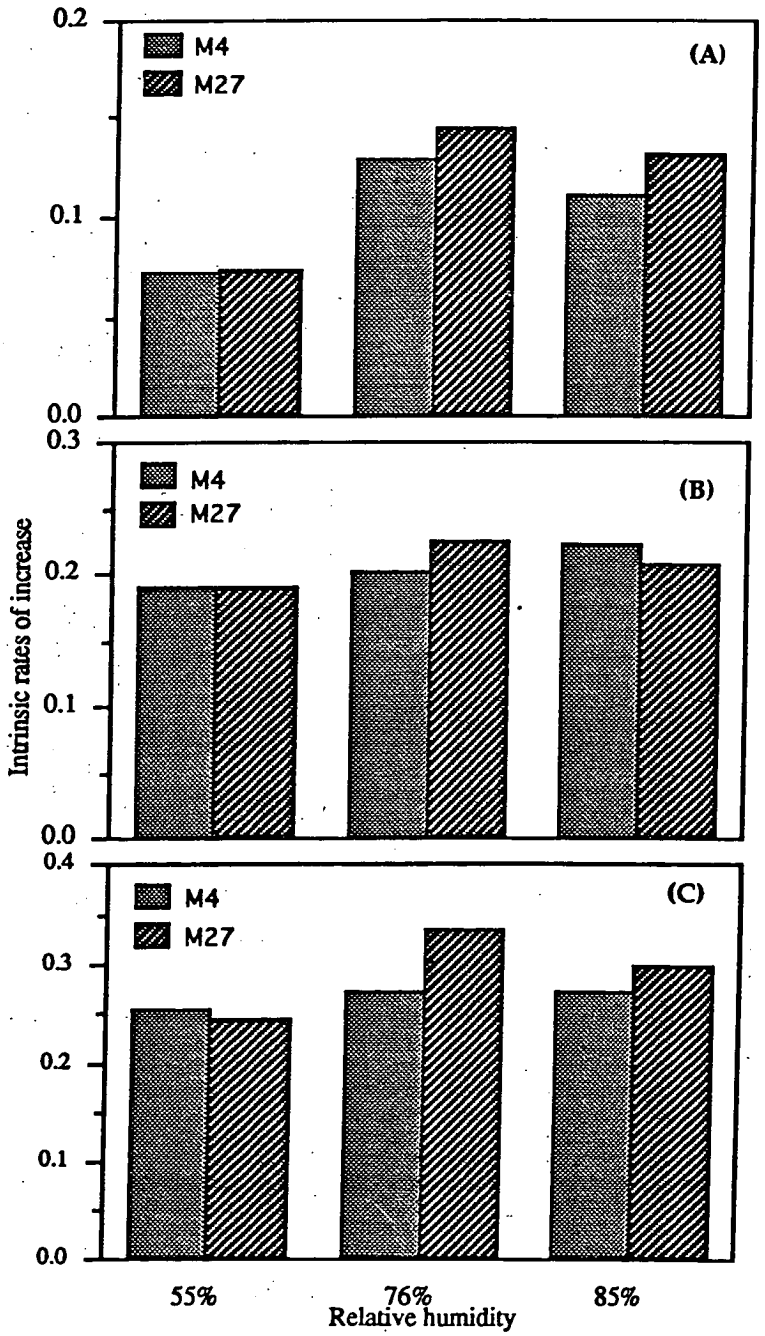
Fig. 6.22. Pre-reproductive period of TSSM on two genotypes of hops at 20°C(A), 25°C and 30°C at a light intensity of 43 lux.



The intrinsic rate of increase of TSSM at the various conditions is presented in Fig.6.23. At 20°C moderate relative humidity was shown to

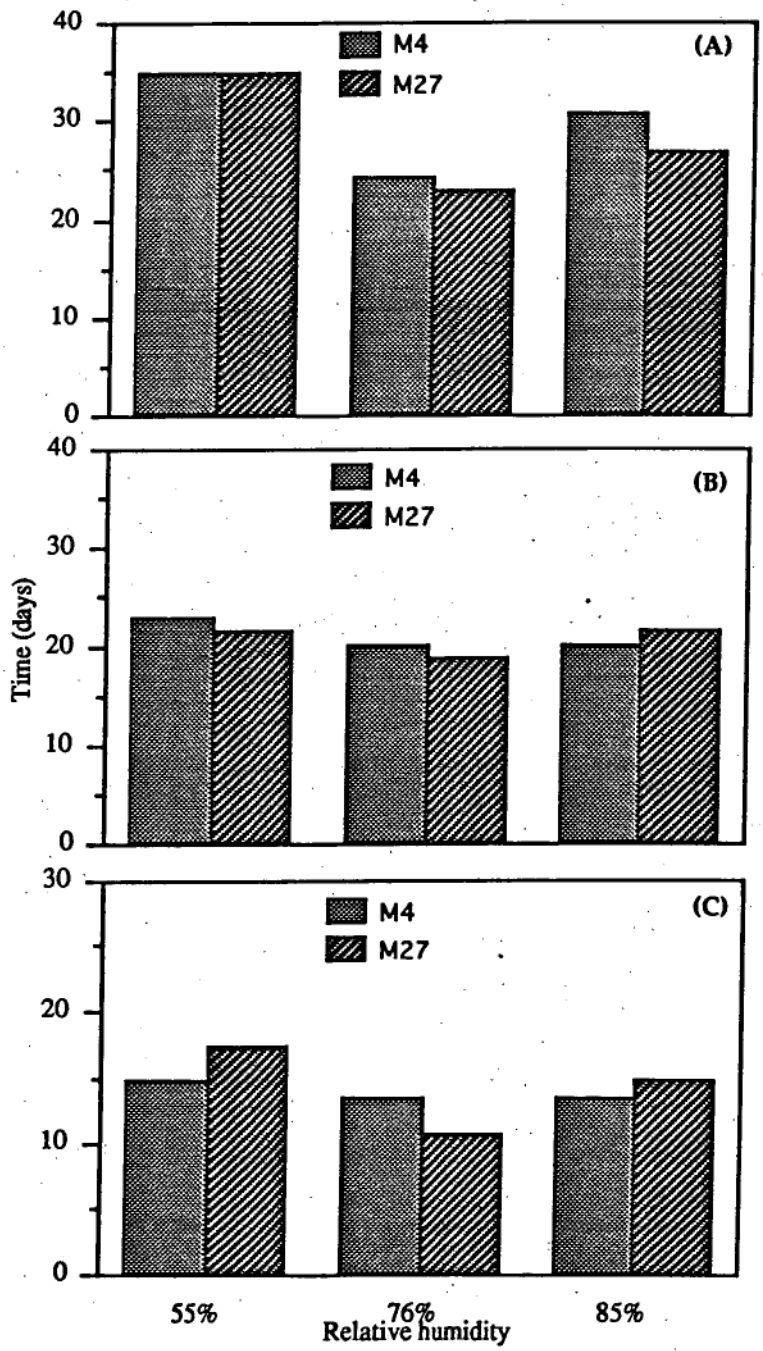
be superior to high and low relative humidity. At 25° and 30°C little difference was shown among these humidity regimes.

Fig. 6.23. Intrinsic rates of increase of TSSM on two genotypes of hops at 20°C(A), 25°C(B) and 30°C(C) at a light intensity of 43 lux and three humidities.



The mean generation times of TSSM for the three humidity levels are shown in Fig. 6.24. These results tend to confirm those obtained from the life table parameters presented earlier.

Fig. 6.24. Mean generation times of TSSM on two genotypes of hops at 20°C(A), 25°C(B) and 30°C at a light intensity of 43 lux and three humidities.



A two-way analysis of variance was carried out using the average values of each of the egg periods for each of different combinations of temperature and humidity as mentioned previously (Table 6.14). The duration of egg periods among these humidity levels did not vary significantly ($p \geq 0.05$). Furthermore, there were no significant differences among different genotypes and no significant interaction between genotypes and temperatures was found ($p \geq 0.05$). The average egg periods of the mites reared at each humidity level ranged from a minimum of 6.37 days at 76%RH to a maximum of 7.12 days at 85%RH (Fig. 6.25).

Table 6.14. Analysis of variance of the developmental periods for eggs of TSSM on two genotypes of hops at three humidies.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Humidity (A)	2	2.195	1.098	0.501	.6183
Genotype (B)	1	0.264	0.264	0.120	.7346
AB	2	0.647	0.323	0.147	.8644
Error	12	26.313	2.193		

Fig. 6.25. Developmental periods for eggs of TSSM at 55%, 76%, and 85% RH.

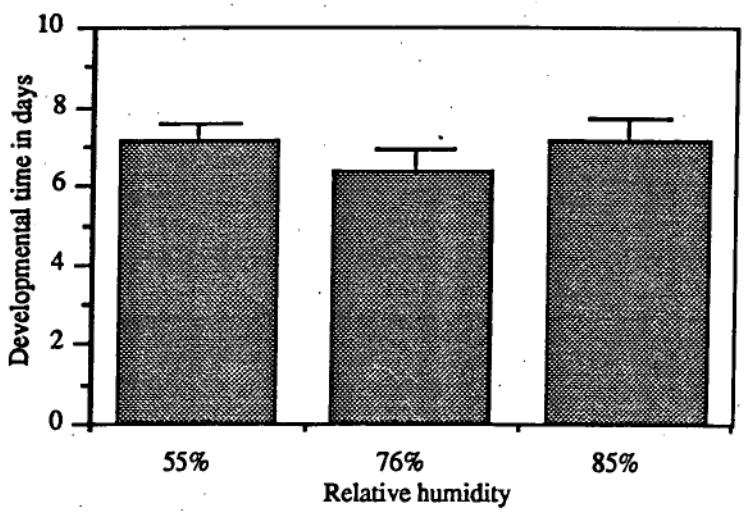
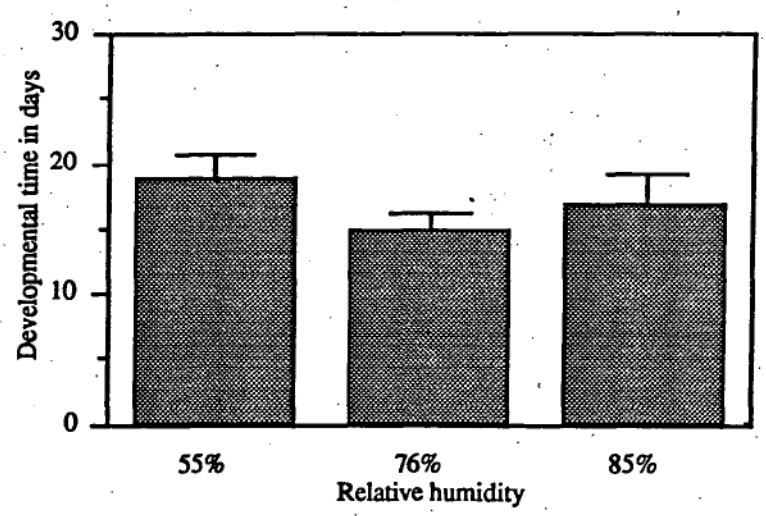


Table 6.15 shows that under various conditions the developmental period from egg to adult for females among humidity regimes did not differ significantly and that differences between genotypes as well as the interaction between temperatures and genotypes were not significant ($p \geq 0.05$). It was apparent that the mites at 76%RH had the shortest period (14.63 days) whilst the mites at 55%RH°C had the longest period (18.55 days; Fig. 6.26).

Table 6.15. Analysis of variance of the developmental periods from eggs to adults of TSSM on two genotypes of hops at three humidities.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Humidity (A)	2	46.207	23.103	0.703	.5142
Genotype (B)	1	0.360	0.360	0.011	.9184
AB	2	2.617	1.309	0.040	.9611
Error	12	394.117	32.843		

Fig. 6.26. Developmental periods from eggs to adults of TSSM at 55%, 76%, and 85%RH.

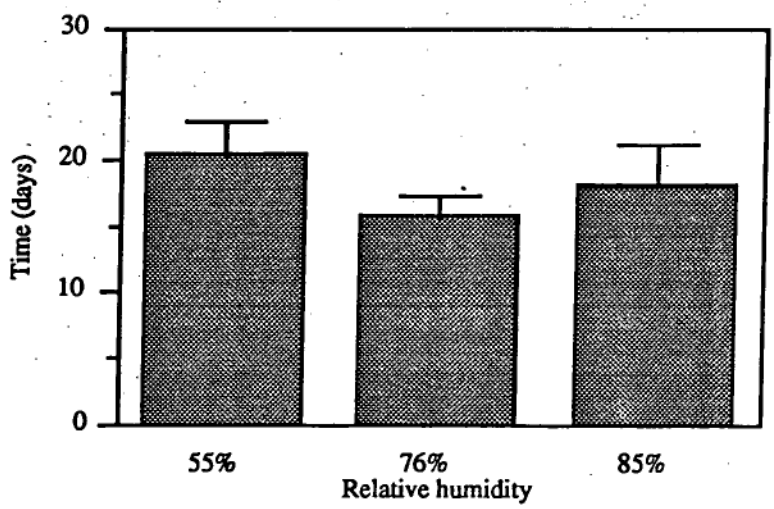


Analysis of variance of the pre-reproductive period showed no significant differences between humidity levels (Table 6.16). The duration of egg-to-egg developmental period at 20-30°C varied from a minimum of 15.74 days at 76%RH to a maximum of 20.32 days at 55%RH (Fig. 6.27). It was also apparent that the developmental period of mites reared on different genotypes did not vary significantly and that there was no significant interaction between temperatures and genotypes (Table 6.16).

Table 6.16. Analysis of variance of the pre-reproductive periods of TSSM on two genotypes of hops at three humidities.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Humidity (A)	2	63.068	31.534	0.665	.5320
Genotype (B)	1	2.494	2.494	0.053	.8224
AB	2	4.677	2.339	0.049	.9520
Error	12	568.693	47.391		

Fig. 6.27. Pre-reproductive periods of TSSM at 55%, 76%, and 85% RH.

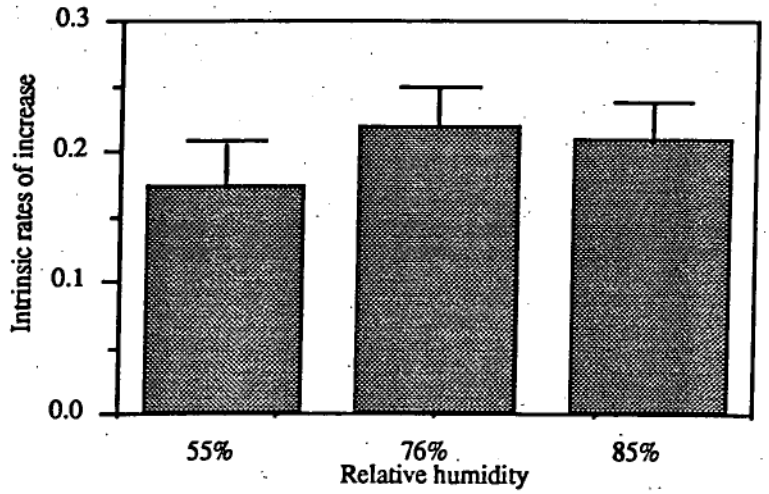


According to the analysis of variance, the intrinsic rate of increase of mites reared on both M4 and M27 at different humidity levels did not vary significantly (Table 6.17). In addition, there was no significant interaction of this value between humidities and genotypes. The highest value (0.217) was found at 76%RH and the lowest (0.170) at 55%RH (Fig. 6.28).

Table 6.17. Analysis of variance of the intrinsic rates of increase of TSSM on two genotypes of hops at three humidities.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Humidity (A)	2	0.007	0.0035	0.496	.6209
Genotype (B)	1	0.001	0.0010	0.113	.7425
AB	2	0.001	0.0005	0.071	.9323
Error	12	0.089	0.0074		

Fig. 6.28. Intrinsic rates of increase of TSSM at 55%, 76%, and 85% RH.

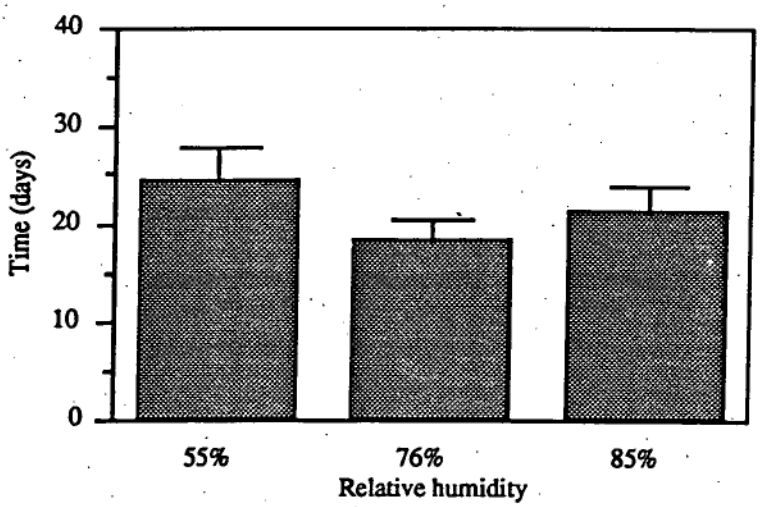


For mean generation times, analysis of variance showed no significant differences among the test humidity levels (Table 6.18). In addition, it can be seen from the table that there were no significant differences in the mean generation time between genotypes selected nor between genotypes and temperatures. Populations of TSSM at 76%RH had the shortest mean generation time, wheareas those at 55%RH had the longest (Fig. 6.29).

Table 6.18. Analysis of variance of the mean generation times of TSSM on two genotypes of hops at three humidities.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Humidity (A)	2	108.050	54.025	0.893	.4348
Genotype (B)	1	1.578	1.578	0.026	.8743
AB	2	3.724	1.862	0.031	.9698
Error	12	725.618	60.468		

Fig. 6.29. Mean generation time of TSSM at 55%, 76%, and 85% RH.



6.3.3. Light intensity

6.3.3.1. Open containers: Table 6.19 presents the number of TSSM individuals alive at each age interval when reared on two genotypes of hops at 25°C, and at three levels of light intensity. As can be seen from the table, the survival of the egg stage varied with the levels of light intensity. At all light intensities, the mortality rate of the egg stage was higher than that of the immature stage. For both stages, the mites reared at 61.5 lux suffered the highest mortality whilst those reared at 150 and 360 lux had nearly indentical mortalities. Generation mortality ranged from 54.17% on M4 to 41.67% on M27 at 61.5 lux, 33.33% to 25.00% at 150 lux and 33.33% to 20.83% at 360 lux.

Table 6.19. Life table of TSSM on two genotypes of hops at 25°C and three levels of light intensity.

Illumination	Genotype	X[a]	l_x[b]	d_x[c]	q_x[d]	s_x[e]	Generation mortality (%)
61.5 lux	M4	Egg	24	11	0.4583	0.5417	
		Immature[f]	13	2	0.1539	0.8461	
		Adult[g]	11				54.17%
	M27	Egg	24	6	0.2500	0.7500	
		Immature	18	4	0.2222	0.7778	
		Adult	14				41.67%
150 lux	M4	Egg	24	7	0.2917	0.7083	
		Immature	17	1	0.0588	0.9412	
		Adult	16				33.33%
	M27	Egg	24	6	0.2500	0.7500	
		Immature	18	0	0.0000	1.0000	
		Adult	18				25.00%
360 lux	M4	Egg	24	5	0.2083	0.7917	
		Immature	19	3	0.1579	0.8421	
		Adult	16				33.33%
	M27	Egg	24	3	0.1250	0.8750	
		Immature	21	2	0.0952	0.9048	
		Adult	19				20.83%

a = Stage of life cycle.
b = Number living at beginning of stage in the x column.
c = Number dying within stage in the x column.
d = Probability of dying during x.
e = Probability of surviving interval x.
f = Larva + Protonymph + Deutonymph.
g = Female + Male.

Sex ratios of immatures reaching adulthood were observed to favour females for all 3 illumination regimes (Table 6.20). This favourability was most evident at 61.5 and 360.0 lux, which averaged approximately 4 females to one male. At 150.0 lux, sex ratio determinations indicated a shift towards a smaller female:male ratio.

Table 6.20. Sex ratio of TSSM in open containers at 20°C, and three levels of light intensity.

Illumination	Adult females	Adult males
61.5 lux	19	6
150.0 lux	22	12
360.0 lux	28	7

The developmental time in days for eggs of TSSM on both M4 and M27 did not vary significantly ($p \geq 0.05$) for the three levels of light intensity (Fig. 6.30). When the data taken from both genotypes was pooled together, the average time required for egg hatch at these light intensities was nearly identical (Fig. 6.31).

Fig. 6.30. Developmental period for eggs of TSSM on M4 (A) and M27 (B) at 25°C and the relative humidity of the ambient air in the incubator. Columns with the same letter are not significantly different ($p \geq 0.05$; PLSD).

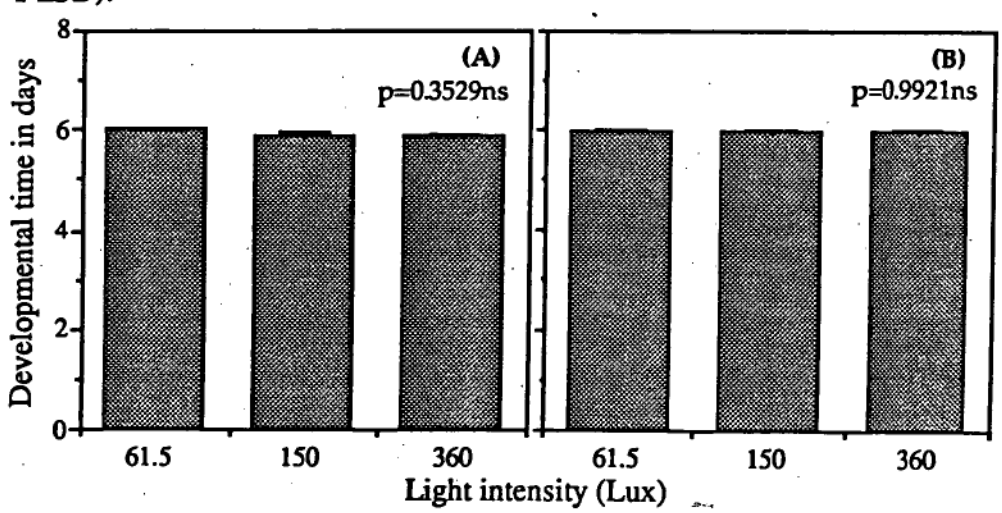
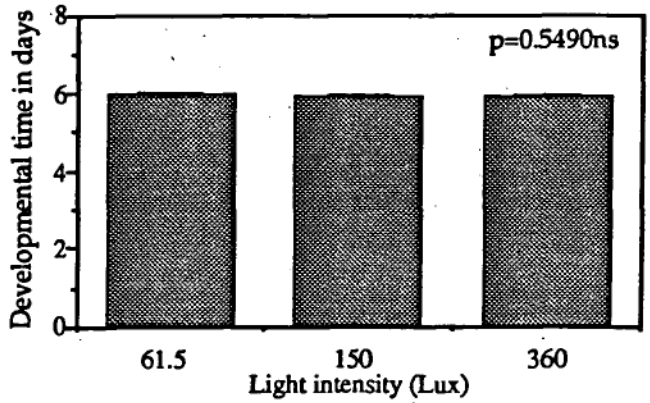
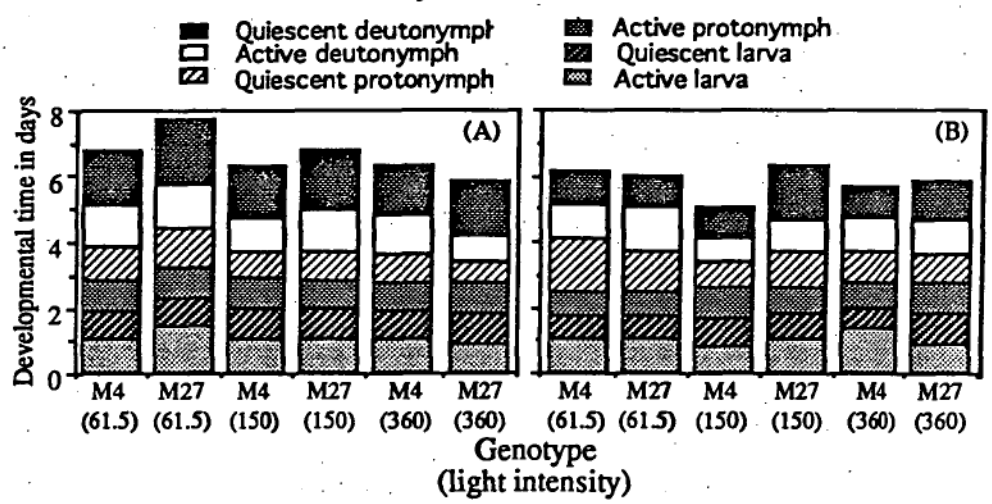


Fig. 6.31. Average developmental period for eggs of TSSM at 25°C and the relative humidity of the ambient air in the incubator. Columns with the same letter are not significantly different ($p \geq 0.05$; PLSD).



For females and males, the developmental periods of the active and quiescent periods for larva, protonymph and deutonymph reared on M4 and M27 within each light intensity are presented in Fig. 6.32A and B, respectively. Comparisons of the three rearing light intensities show that the length of the developmental periods for females and males on both genotypes was similar. At all light intensities, the developmental period from active larva to quiescent deutonymph of females on both genotypes was longer than that of males.

Fig. 6.32. Developmental period from active larva to quiescent deutonymph of females(A) and males(B) on M4 and M27 at 25°C and the relative humidity of the ambient air in the incubator.



Developmental periods from eggs to adults of TSSM females on M4 and M27 at the different light intensities are presented in Fig. 6.33A and B, respectively. There were significant differences in the developmental period of the mites on M27, whereas that of the mites on M4 did not differ significantly. Highly significant decreases in the total developmental time on juvenile stages at 360 lux compared with 61.5 and 150 lux were detected on M27 ($p < 0.01$). It was apparent that the average duration of the juvenile stages varied significantly ($p < 0.01$) for the three light intensities when the data taken from both genotypes was pooled together (Fig. 6.34). At 61.5, 150, and 360 lux females took 13.21, 12.50, and 11.46 days, respectively, to reach adulthood.

Fig. 6.33. Developmental period from eggs to adults of TSSM females on M4 (A) and M27 (B) at 25°C and the relative humidity of the ambient air in the incubator. Columns with the same letter are not significantly different ($p \geq 0.05$; PLSD).

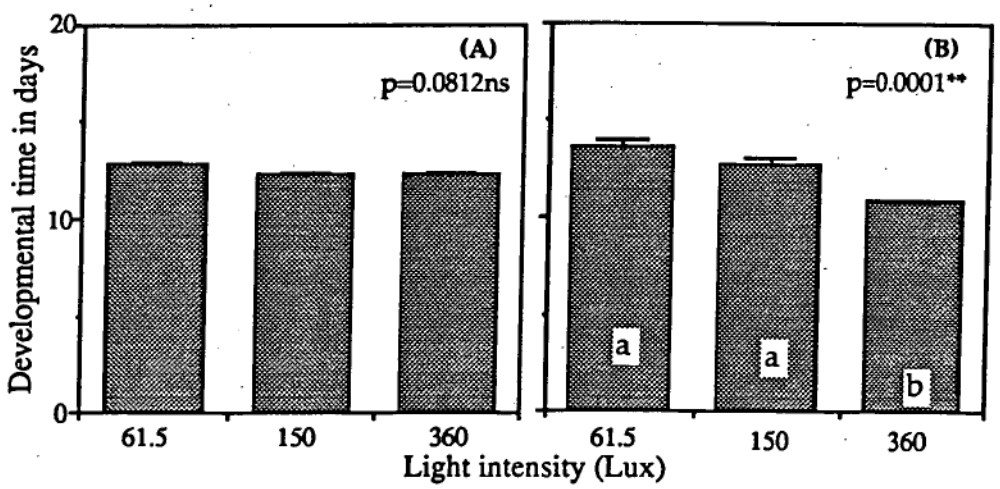
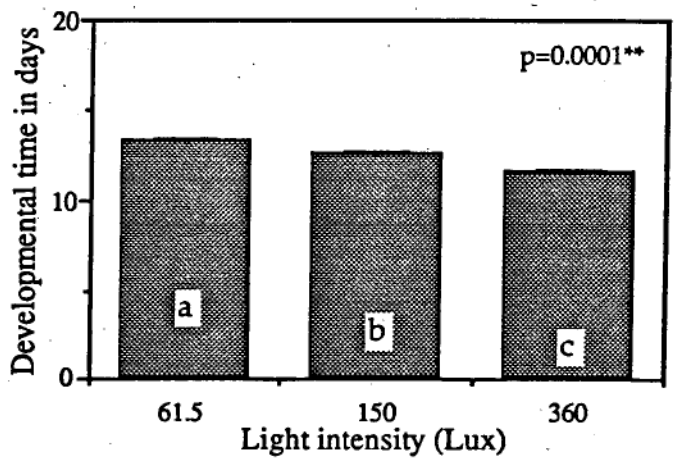


Fig. 6.34. Average developmental period from eggs to adutls of TSSM females at 25°C and the relative humidity of the ambient air in the incubator. Columns with the same letter are not significantly different ($p \geq 0.05$; PLSD).



According to analysis of variance, the pre-reproductive period of mites reared at these light intensities varied significantly (Fig. 6.35). At 61.5 lux the duration of egg-to-egg developmental period of the mites on both M4 and M27 was significantly longer than at 150 and 360 lux. It was also found that this period of mites on M4 was significantly shorter at 360 lux than at 150 lux. When the data taken from both genotypes was pooled, highly significant differences in average pre-reproductive periods were detected for the three light intensities ($p < 0.01$; Fig. 6.36). The pre-reproductive periods of the mites at 61.5, 150 and 360 lux were 14.24, 13.27 and 12.52 days, respectively.

Fig. 6.35. Pre-reproductive period of TSSM females on M4 (A) and M27 (B) at 25°C and the relative humidity of the ambient air in the incubator. Columns with the same letter are not significantly different ($p \geq 0.05$; PLSD).

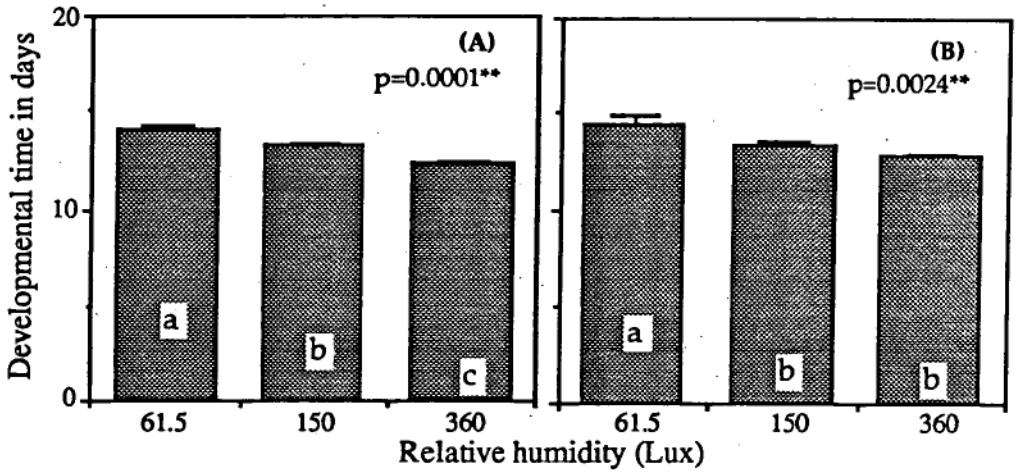
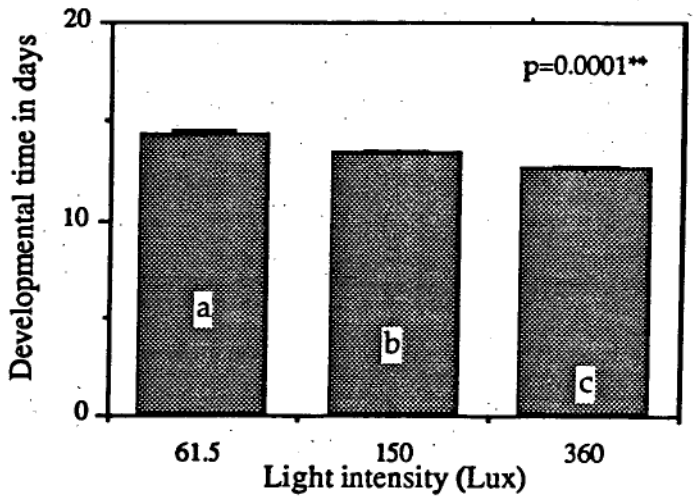
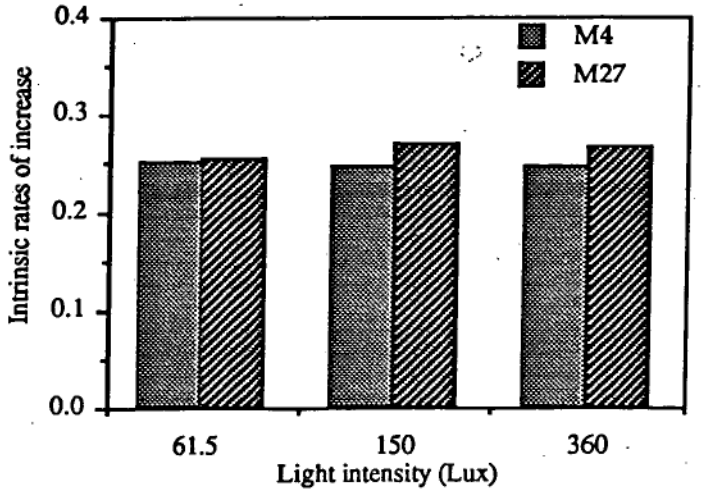


Fig. 6.36. Average pre-reproductive period of TSSM females at 25°C and the relative humidity of the ambient air in the incubator. Columns with the same letter are not significantly different ($p \geq 0.05$; PLSD).



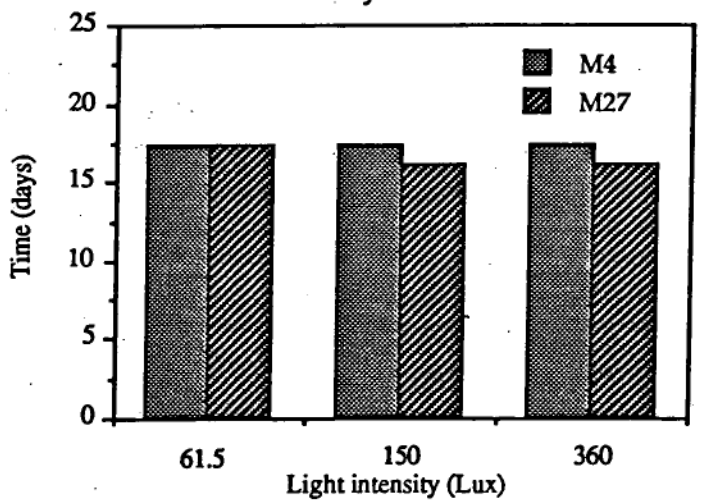
The intrinsic rate of increase of TSSM on M4 and M27 at the various light intensities is presented in Fig. 6.37. At all light intensities the mites on M27 were shown to increase at a greater rate than those on M4, with the greatest difference occurring at 150 and 360 lux.

Fig. 6.37. Intrinsic rates of increases of TSSM on different hop genotypes at 25°C and the relative humidity of the ambient air in the incubator.



The mean generation time (T) at the three light intensities at 25°C is shown in Fig. 6.38. Slight decreases in the T values resulted from an increase in light intensities.

Fig. 6.38. Mean generation times of TSSM on different hop genotypes at 25°C and the relative humidity of the ambient air in the incubator.



6.3.3.2. Closed containers: The following results show the effect of light intensity within given temperature and humidity environments on mite populations on different hop genotypes. Life tables were constructed at light intensities of 43 and 171 lux from the data collected on TSSM at

20° and 30°C under moderate (76%RH) and very high (100%RH) relative humidity conditions.

In the first life table, a comparison between the two light intensities at low temperature (20°C) under moderate humidity conditions (76%RH) indicated that the survival of immatures reaching adulthood incraesed with an increase in light intensity (Table 6.21). Generation mortality ranged from 60% on M4 to 30% on M27 and 30% on M4 to 10% on M27 at 43 and 171 lux, respectively.

Table 6.21. Life table of TSSM on two hop genotypes at 20°C, 76%RH and two light intensities.

Illumination	Genotype	X[a]	l_x[b]	d_x[c]	q_x[d]	s_x[e]	Generation mortality (%)
43.0 lux	M4	Egg	10	0	0.00	1.00	
		Immature[f]	10	6	0.60	0.40	
		Adult[g]	4				60.00%
	M27	Egg	10	0	0.00	1.00	
		Immature	10	3	0.30	0.70	
		Adult	7				30.00%
171.0 lux	M4	Egg	20	2	0.10	0.90	
		Immature	18	4	0.22	0.78	
		Adult	14				30.00%
	M27	Egg	20	0	0.00	1.00	
		Immature	20	2	0.10	0.90	
		Adult	18				10.00%

a = Stage of life cycle.
b = Number living at beginning of stage in the x column.
c = Number dying within stage in the x column.
d = Probability of dying during x.
e = Probability of surviving interval x.
f = Larva + Protonymph + Deutonymph.
g = Female + Male.

In the second life table, comparison between the two light intensities at low temperature under very high humidity conditions (100%RH) also shows that the overall survival (birth to adult) increased as the light intensity increased (Table 6.22). In addition, it was found that

the survival of the mites on M4 and M27 at both light intensities was lower in this life table as compared to the first because of the increase in relative humidity. Generation mortality ranged from 100% on M4 to 80% on M27 and 80% on M4 to 70% on M27 for the mites reared at 43 and 171 lux, respectively.

Table 6.22. Life table of TSSM on two hop genotypes at 20°C, 100%RH and two light intensities.

Illumination	Genotype	X[a]	l_x[b]	d_x[c]	q_x[d]	s_x[e]	Generation mortality (%)
43.0 lux	M4	Egg	10	1	.1000	.9000	
		Immature[f]	9	9	1.000	0.000	
		Adult[g]	0				100%
	M27	Egg	10	1	.1000	.9000	
		Immature	9	7	.7778	.2222	
		Adult	2				80%
171.0 lux	M4	Egg	10	1	.1000	.9000	
		Immature	9	7	.7778	.2222	
		Adult	2				80%
	M27	Egg	10	4	.4000	.6000	
		Immature	6	3	.5000	.5000	
		Adult	3				70%

a = Stage of life cycle.
b = Number living at beginning of stage in the x column.
c = Number dying within stage in the x column.
d = Probability of dying during x.
e = Probability of surviving interval x.
f = Larva + Protonymph + Deutonymph.
g = Female + Male.

In the third life table, comparison between the two light intensities indicated that the survival of the mites was not related to the effect of light intensity at high temperature (30°C) under moderate humidity conditions (Table 6.23). Generation mortality ranged from 30% on M4 to 15% on M27 and 27.69% to 36.92% at 43 and 171 lux, respectively.

Table 6.23. Life table of TSSM on two hop genotypes at 30°C, 76%RH and two light intensities.

Illumination	Genotype	X[a]	l_x[b]	d_x[c]	q_x[d]	s_x[e]	Generation mortality (%)
43.0 lux	M4	Egg	20	1	.0500	.9500	
		Immature[f]	19	5	.2632	.7368	
		Adult[g]	14				30.00%
	M27	Egg	20	0	.0000	1.000	
		Immature	20	3	.1500	.8500	
		Adult	17				15.00%
171.0 lux	M4	Egg	65	5	.0769	.9231	
		Immature	60	13	.2167	.7833	
		Adult	47				27.69%
	M27	Egg	65	11	.1692	.8308	
		Immature	54	13	.2407	.7593	
		Adult	41				36.92%

a = Stage of life cycle.
b = Number living at beginning of stage in the x column.
c = Number dying within stage in the x column.
d = Probability of dying during x.
e = Probability of surviving interval x.
f = Larva + Protonymph + Deutonymph.
g = Female + Male.

In the fourth life table, comparison between the two light intensities at high temperature under very high humidity conditions still shows that the survival of the mites increased as the light intensity increased (Table 6.24). Generation mortality varied from 95% on M4 to 100% on M27 and 56% on M4 to 24% on M27 at 43 and 171 lux, respectively.

Table 6.24. Life table of TSSM on two hop genotypes at 30°C, 100%RH and two light intensities.

Illumination	Genotype	X[a]	l_x[b]	d_x[c]	q_x[d]	s_x[e]	Generation mortality (%)
43.0 lux	M4	Egg	20	5	.2500	.7500	
		Immature[f]	15	14	.9333	.0667	
		Adult[g]	1				95%
	M27	Egg	20	7	.3500	.6500	
		Immature	13	13	.0000	1.000	
		Adult	0				100%
171.0 lux	M4	Egg	25	0	.0000	1.000	
		Immature	25	14	.5600	.4400	
		Adult	11				56%
	M27	Egg	25	0	.0000	1.000	
		Immature	25	6	.2400	.7600	
		Adult	19				24%

a = Stage of life cycle.
b = Number living at beginning of stage in the x column.
c = Number dying within stage in the x column.
d = Probability of dying during x.
e = Probability of surviving interval x.
f = Larva + Protonymph + Deutonymph.
g = Female + Male.

The sex ratios of immatures becoming adults were biased in favour of females for both light intensity regimes under controlled conditions (Table 6.25). This bias was most evident for the lower light intensity at moderate relative humidity, which averaged approximately four females to one male. It was also found that at a light intensity of 43 lux the male

immatures were not able to reach adulthood at both 20° and 30°C under very high relative humidity conditions.

Table 6.25. Sex ratio of TSSM at 20°and 30°C; 76% and 100%RH at light intensities of 43 and 171 lux.

Illumination (lux)	Temperature (°C)	Humidity (%RH)	Adult females	Adult males
43.0	20	76	9	2
		100	2	0
	30	76	24	7
		100	1	0
171.0	20	76	23	9
		100	5	0
	30	76	57	31
		100	24	6

Under the rearing conditions described above, two-way analysis of variance of average values obtained from the data collected on TSSM showed that there were no significant differences ($p \geq 0.05$) in developmental periods for eggs, overall developmental periods of female immatures, pre-reproductive periods, intrinsic rates of increase (r_m) and mean generation times (T) between the mites reared at light intensities of 43 and 171 lux (Table 6.26, 6.27, 6.28, 6.29 and 6.30). Furthermore, variation between the mites on different genotypes and interaction between the light intensity and genotypes were not significant ($p \geq 0.05$). Within these experimental regimes, means for egg stage duration and developmental period from egg to adult were approximately 6.5 and 16.5 days, respectively (Fig. 6.39 and 6.40). Mite populations demonstrated mean generation times ranging from 17.66 to 16.51 at 43 and 171 lux, respectively (Fig. 6.41). As can be seen in Fig. 6.42, the r_m value was higher at 171 lux (0.213) than at 43 lux (0.169). The mean generation times varied from 22.67 to 19.43 days at 43 and 171 lux, respectively (Fig. 6.43).

Table 6.26. Analysis of variance of the developmental periods for eggs of TSSM on two hop genotypes at 20°-30°C and 76%-100%RH.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Illumination (A)	1	5.063E-6	5.063E-6	1.899E-6	.9989
Genotype (B)	1	0.055	0.055	0.021	.8881
AB	1	0.402	0.402	0.151	.7045
Error	12	31.984	2.665		

Table 6.27. Analysis of variance of the developmental periods from eggs to adults of TSSM on two hop genotypes at 20°-30°C and 76%-100%RH.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Illumination (A)	1	0.357	0.357	0.008	.9316
Genotype (B)	1	0.339	0.339	0.007	.9333
AB	1	7.608	7.608	0.165	.6932
Error	10	461.424	46.142		

Table 6.28. Analysis of variance of the pre-reproductive periods of TSSM on two hop genotypes at 20°-25°C and 76-100%RH.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Illumination (A)	1	5.537	5.537	0.116	.7408
Genotype (B)	1	11.527	11.527	0.242	.6344
AB	1	0.586	0.586	0.012	.9141
Error	9	428.252	47.584		

Table 6.29. Analysis of variance of the intrinsic rates of increase of TSSM on two hop genotypes at 20°-30°C and 76-100%RH.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Illumination (A)	1	0.006	0.006	0.405	.5402
Genotype (B)	1	1.284E-6	1.284E-6	8.371E-5	.9929
AB	1	8.889E-8	8.889E-8	5.797E-6	.9981
Error	9	0.138	0.015		

Table 6.30. Analysis of variance of the mean generation times of TSSM on two hop genotypes at 20°-30°C and 76-100%RH.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Illumination (A)	1	37.941	37.941	0.432	.5258
Genotype (B)	1	17.422	17.422	0.200	.6653
AB	1	0.992	0.992	0.011	.9174
Error	9	783.964	87.107		

Fig. 6.39. Developmental periods for eggs of TSSM at 43 and 171 lux.

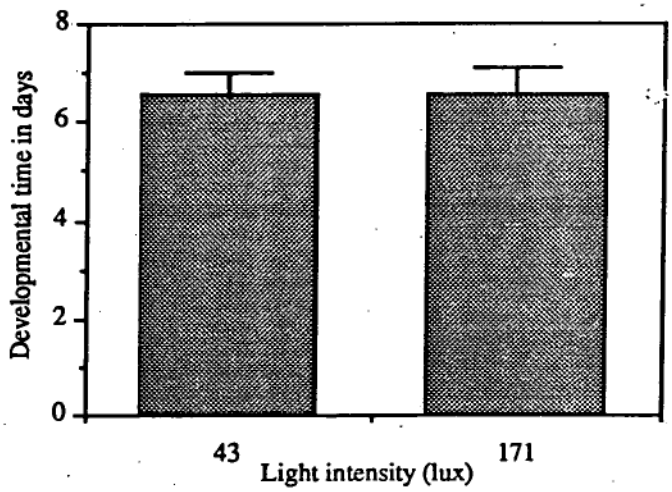


Fig. 6.40. Developmental periods from eggs to adults of TSSM at 43 and 171 lux.

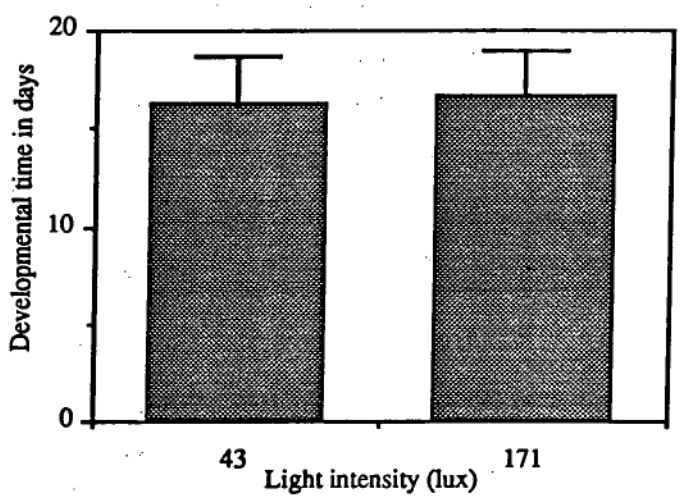


Fig. 6.41. Pre-reproductive periods of TSSM at 43 and 171 lux.

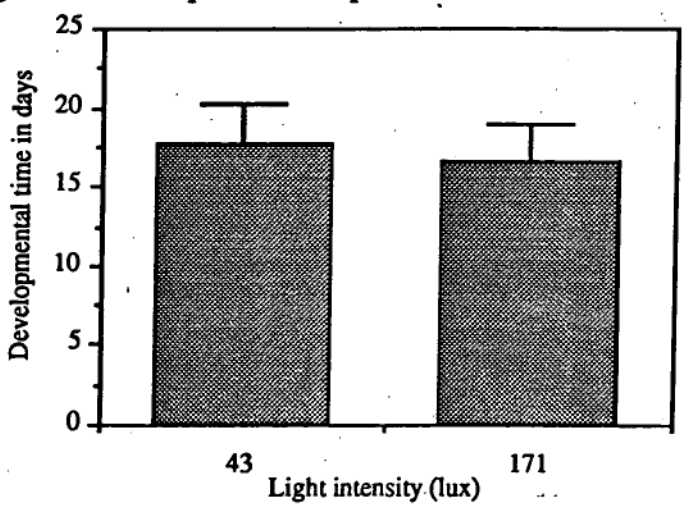


Fig. 6.42. Intrinsic rates of increase of TSSM at 43 and 171 lux.

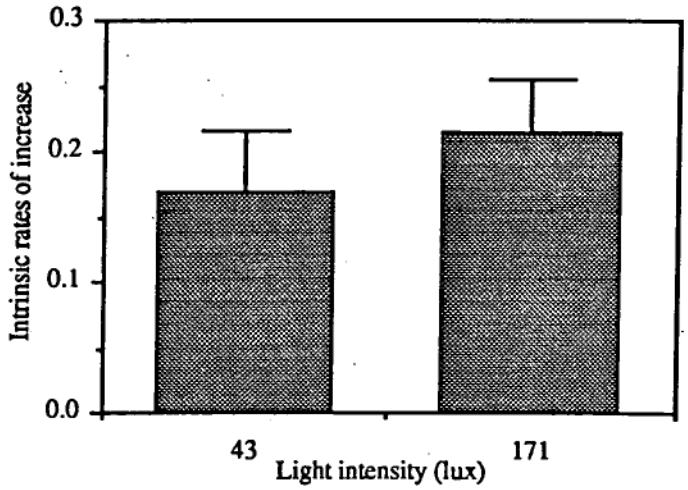
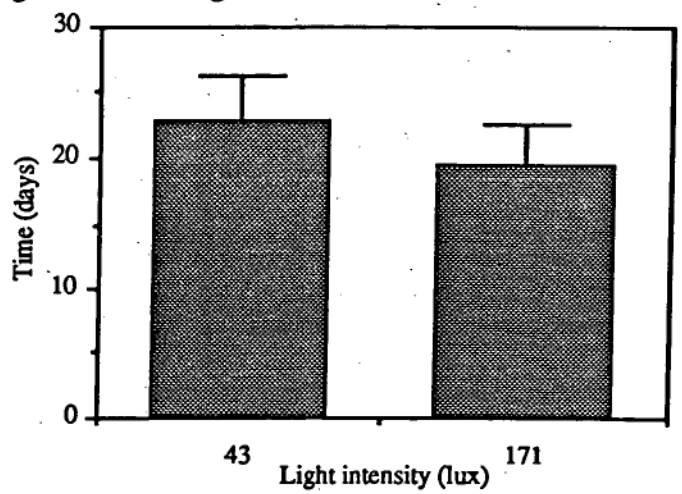


Fig. 6.43. Mean generation time of TSSM at 43 and 171 lux.



6.3.4. Plant variables

6.3.4.1. Leaf ages: The first series of experiments in this study was carried out at 20°C, 76%RH and a light intensity of 171 lux. A comparison of the mite survival between young and old leaves showed that the overall survival of juvenile stages did not vary with leaf age (Table 6.31). Under these controlled conditions, generation mortality was approximately 10%. Sex ratios of mite populations on young and old leaves were similar, which averaged about 4 females to one male (Table 6.32). The developmental times for the eggs of TSSM to hatch were

nearly identical for both young and old leaves of M4 and M27 (Fig. 6.44). According to unpaired t-tests, variation in the developmental period of juvenile stages as well as the pre-reproductive period between mites on young and old leaves of M4 was not significant, but variation between young and old leaves of M27 was highly significant (Fig. 6.45 and 6.46). The intrinsic rate of increase ranged from 0.165 on M4 to 0.160 on M27 and 0.128 on M4 to 0.106 on M27 for young and old leaves, respectively (Fig. 6.47), whereas the mean generation time varied from 22.7 days on M4 to 24.0 days on M27 and 26.7 days on M4 to 28.0 days on M27 for young and old leaves, respectively (Fig. 6.48).

Table 6.31. Life table of TSSM on two hop genotypes at 20°C, 76%RH and a light intensity of 171 lux for old and young leaves.

Leaf age	Genotype	X[a]	l_x[b]	d_x[c]	q_x[d]	s_x[e]	Generation mortality (%)
Young	M4	Egg	10	0	0.000	1.000	
		Immature[f]	10	0	0.000	1.000	
		Adult[g]	10				0%
	M27	Egg	10	0	0.000	1.000	
		Immature	10	1	0.100	0.900	
		Adult	9				10%
Old	M4	Egg	10	0	0.000	1.000	
		Immature	10	1	0.100	0.900	
		Adult	9				10%
	M27	Egg	10	0	0.000	1.000	
		Immature	10	1	0.100	0.900	
		Adult	9				10%

a = Stage of life cycle.
b = Number living at beginning of stage in the x column.
c = Number dying within stage in the x column.
d = Probability of dying during x.
e = Probability of surviving interval x.
f = Larva + Protonymph + Deutonymph.
g = Female + Male.

Table 6.32. Sex ratio of TSSM reared on young and old leaves at 20°C, 76%RH and a light intensity of 171 lux.

Leaf age	Adult females	Adult males
Young	15	4
Old	14	4

Fig. 6.44. Developmental period for eggs of TSSM on young and old leaves of M4(A) and M27(B) at 76% RH and 171 lux.

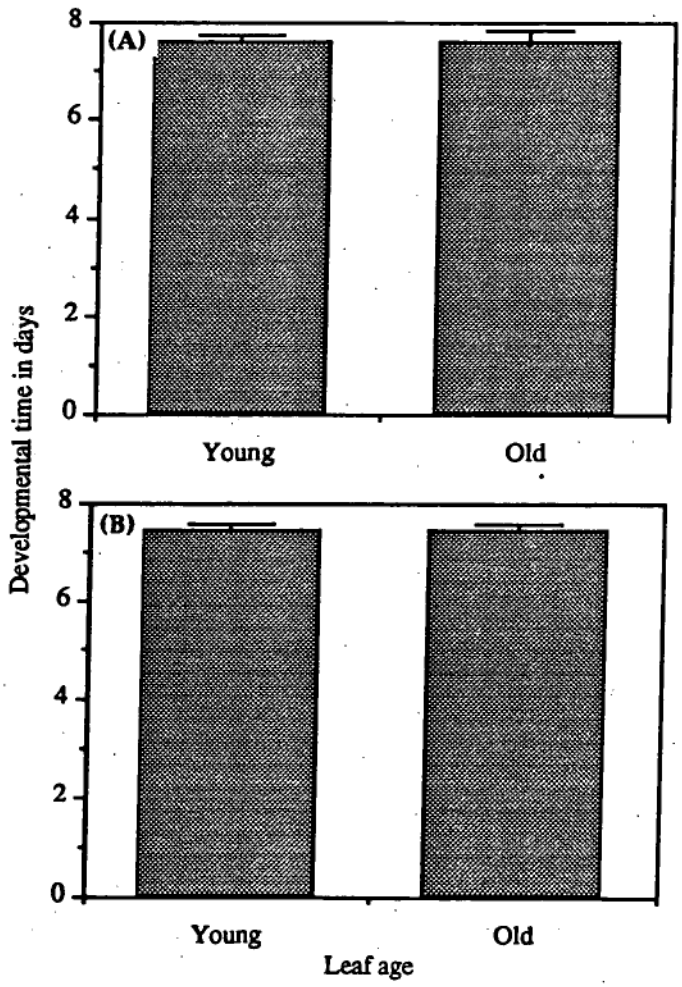


Fig. 6.45. Developmental period from eggs to adults of TSSM females on young and old leaves of M4(A) and M27(B) at 76%RH and 171 lux.

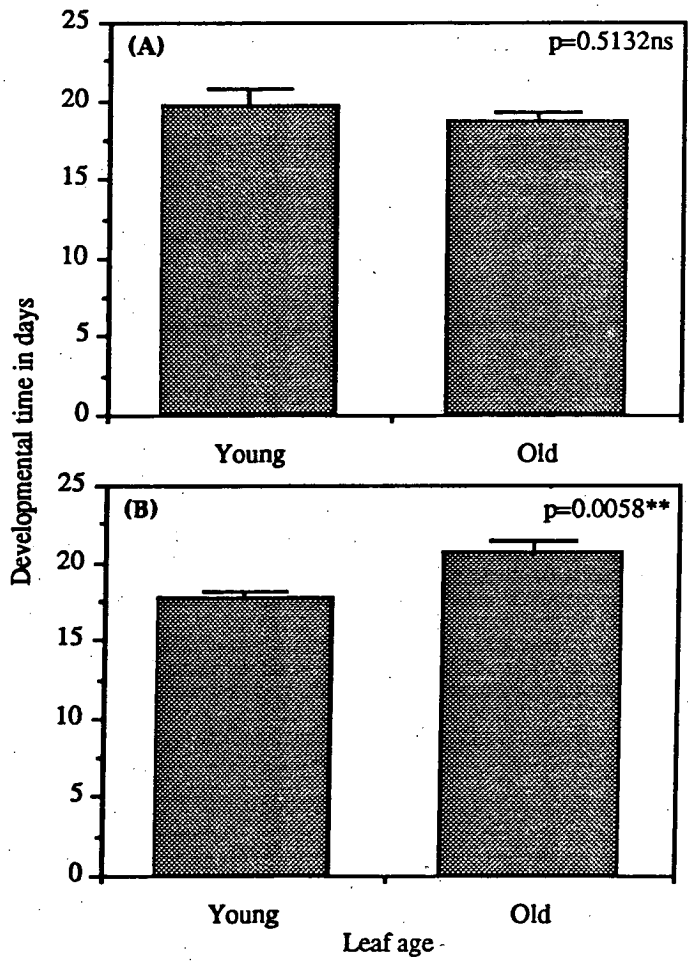


Fig. 6.46. Pre-reproductive period of TSSM on young and old leaves of M4(A) and M27(B) at 76%RH and 171 lux.

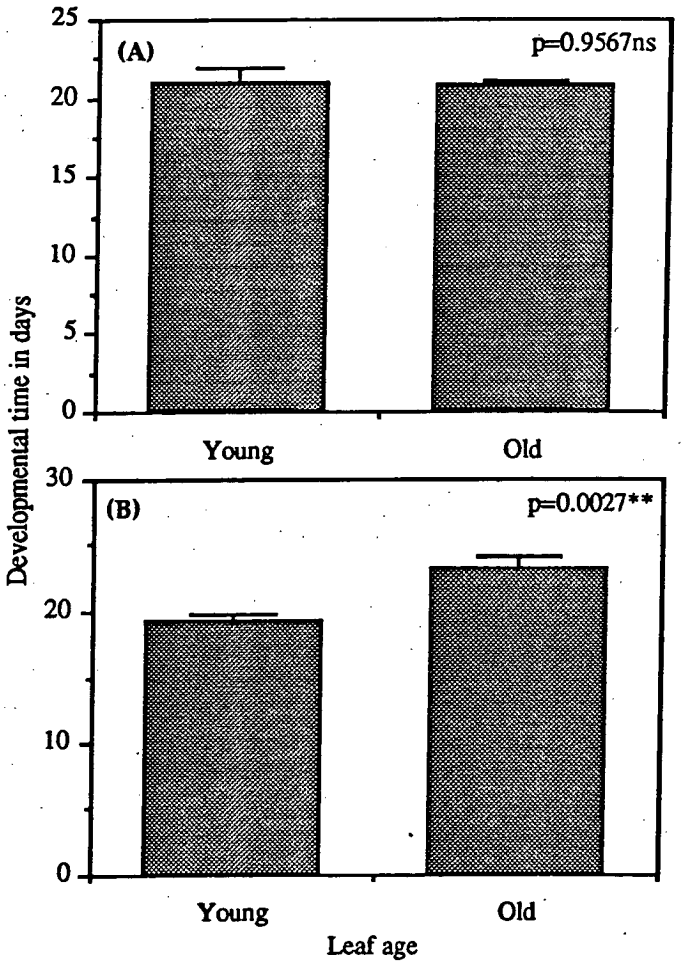


Fig. 6.47. Intrinsic rates of increases of TSSM on young and old leaves of different hop genotypes at 20°C, 76%RH and a light intensity of 171 lux.

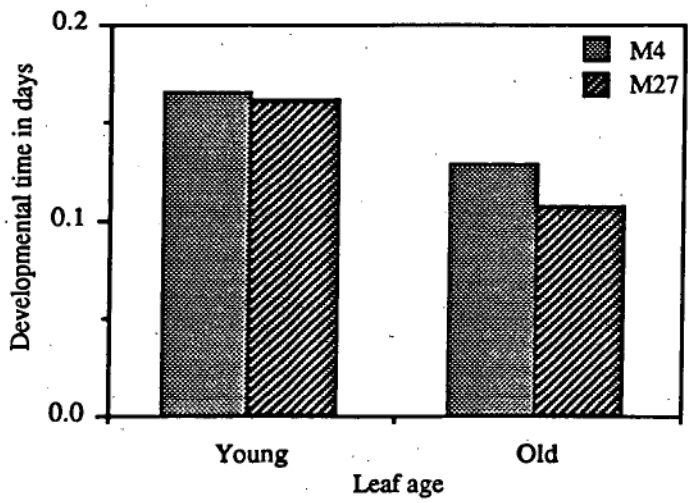
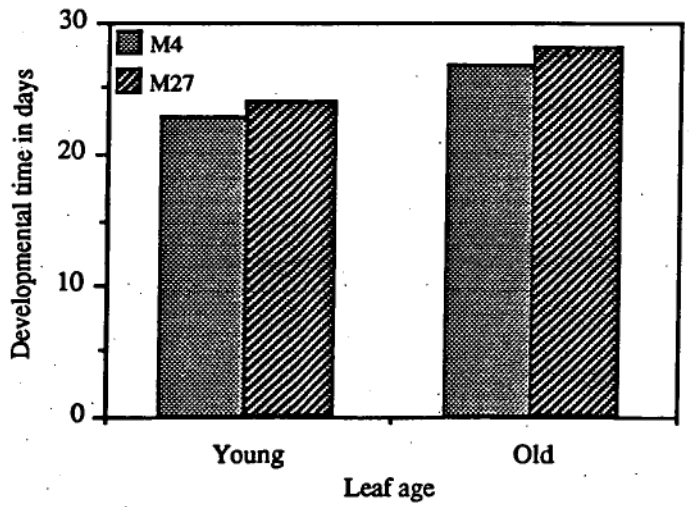


Fig. 6.48. Mean generation times of TSSM on young and old leaves of different hop genotypes at 20°C, 76%RH and a light intensity of 171 lux.



The second series of experiments in this study was carried out at 20°C, 55-100%RH and a light intensity of 43 lux. A comparison of mite survival between young and old leaves also showed that the overall survival of juvenile stages was not related to leaf age (Table 6.33).

Nevertherless, generation mortality of mite populations in this series was higher than that in the first run because the data used was collected on TSSM held at lower light intensities under various relative humidity conditions. On M4 the generation mortality varied from 65 to 45% for young and old leaves, respectively, whilst on M27 the mortality ranged from 30 to 45 for young and old leaves, respectively. The sex ratios of immatures becoming adults were observed to favour females for both leaf ages (Table 6.34). This favourability was most evident for the old leaves, which averaged about six females to one male. On older leaves, sex ratio determinations indicated a shift towards a smaller female:male ratio.

Table 6.33. Life table of TSSM on two hop genotypes at 20°C, 55-100%RH and a light intensity of 43 lux for old and young leaves.

Leaf age	Genotype	X^a	$l_x{}^b$	$d_x{}^c$	$q_x{}^d$	$s_x{}^e$	Generation mortality (%)
Young	M4	Egg	20	0	.0000	1.000	
		Immature[f]	20	13	.6500	.3500	
		Adult[g]	7				65%
	M27	Egg	20	2	.1000	.9000	
		Immature	18	4	.2222	.7778	
		Adult	14				30%
Old	M4	Egg	20	4	.2000	.8000	
		Immature	16	5	.3125	.6875	
		Adult	11				45%
	M27	Egg	20	3	.1500	.8500	
		Immature	17	6	.3529	.6471	
		Adult	11				45%

a = Stage of life cycle.
b = Number living at beginning of stage in the x column.
c = Number dying within stage in the x column.
d = Probability of dying during x.
e = Probability of surviving interval x.
f = Larva + Protonymph + Deutonymph.
g = Female + Male.

Table 6.34. Sex ratio of TSSM reared on young and old leaves at 20°C, 55-100%RH and a light intensity of 43 lux.

leaf age	Adult females	Adult males
Young	14	7
Old	19	3

Using average values obtained from the data collected on mite populations in the environmental regimes mentioned above, two-way analyses of variance were performed. No significant differences ($p \geq 0.05$) in developmental periods for eggs, overall developmental periods of female immatures, pre-reproductive periods, intrinsic rates of increase (r_m) and mean generation times (T) between the mites on young and old leaves were detected (Table 6.35, 6.36, 6.37, 6.38 and 6.39). Furthermore, variation between the mite populations on different genotypes and interaction between leaf ages and genotypes were not significant ($p \geq 0.05$). The means for duration of egg stage ranged from 8.20 to 7.68 days for young and old leaves, respectively (Fig. 6.49), whilst the developmental period from egg to adult varied from 22.63 to 21.27 days for young and old leaves, respectively (Fig. 6.50). The mean generation time for the mite population was approximately 24 days (Fig. 6.51). As can be seen in Fig. 6.52 and 6.53, the r_m value and mean generation times were nearly indentical for both young and old leaves.

Table 6.35. Analysis of variance of the developmental periods for eggs of TSSM on young and old leaves of two hop genotypes at 20°C, 55-100%RH and a light intensity of 43 lux.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Age (A)	1	1.076	1.076	1.029	.3304
Genotype (B)	1	1.238	1.238	1.183	.2981
AB	1	0.238	0.238	0.227	.6422
Error	12	12.554	1.046		

Table 6.36. Analysis of variance of the developmental periods from eggs to adults of TSSM females on young and old leaves of two hop genotypes at 20°C, 55-100%RH and a light intensity of 43 lux.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Age (A)	1	5.535	5.535	0.223	.6494
Genotype (B)	1	42.225	42.225	1.701	.2284
AB	1	0.330	0.330	0.013	.9110
Error	8	198.575	24.822		

Table 6.37. Analysis of variance of the pre-reproductive periods of TSSM females on young and old leaves of two hop genotypes at 20°C, 55-100%RH and a light intensity of 43 lux.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Age (A)	1	0.521	0.521	0.022	.8868
Genotype (B)	1	50.021	50.021	2.073	.1879
AB	1	0.521	0.521	0.022	.8868
Error	8	193.064	24.133		

Table 6.38. Analysis of variance of the intrinsic rate of increase of TSSM on young and old leaves of two hop genotypes at 20°C, 55-100%RH and a light intensity of 43 lux.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Age (A)	1	5.333E-8	5.333E-8	5.221E-5	.9944
Genotype (B)	1	0.002	0.002	1.668	.2326
AB	1	4.014E-4	4.014E-4	0.393	.5483
Error	8	0.008	0.001		

Table 6.39. Analysis of variance of the mean generation time of TSSM on young and old leaves of two hop genotypes at 20°C, 55-100%RH and a light intensity of 43 lux.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Age (A)	1	7.254	7.254	0.190	.6746
Genotype (B)	1	78.285	78.285	2.049	.1902
AB	1	33.300	33.300	0.871	.3779
Error	8	305.716	38.214		

Fig. 6.49. Developmental periods for eggs of TSSM on young and old leaves.

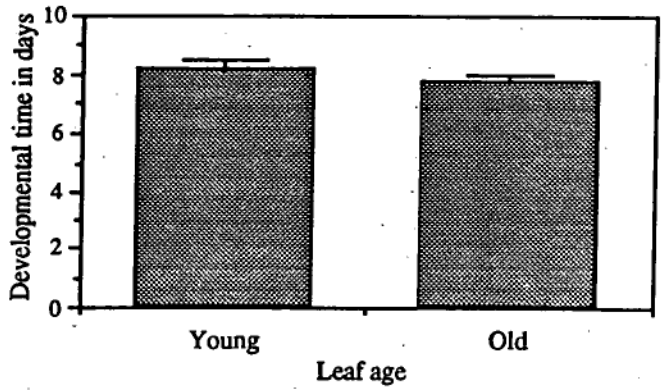


Fig. 6.50. Developmental periods from eggs to adults of TSSM females on young and old leaves.

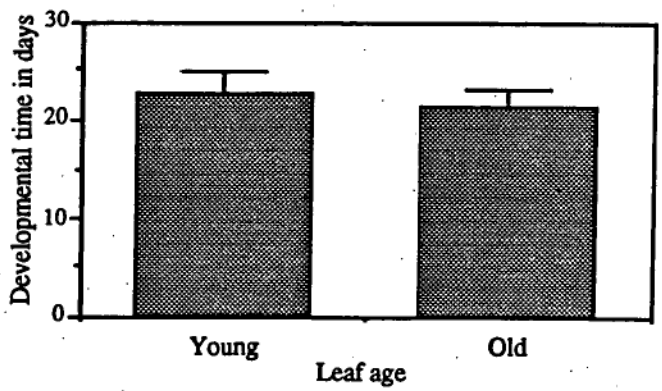


Fig. 6.51. Pre-reproductive periods of TSSM females on young and old leaves.

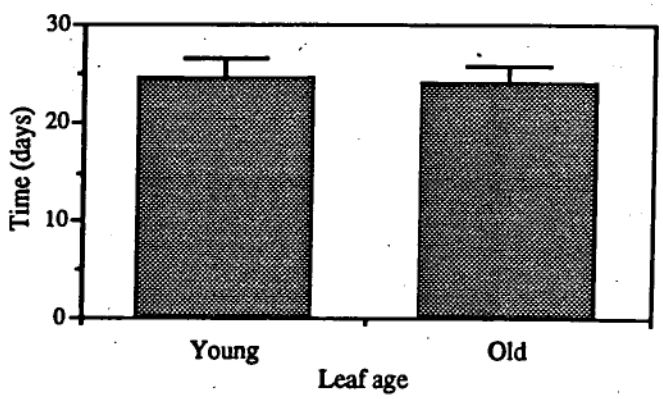


Fig. 6.52. Intrinsic rates of increase of TSSM on young and old leaves.

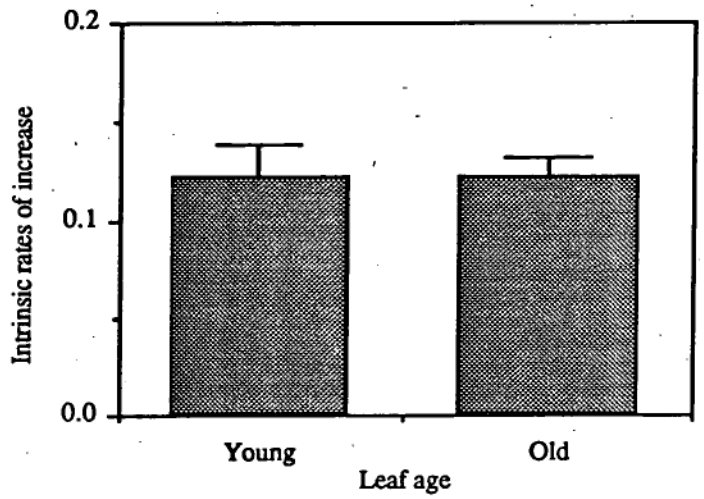
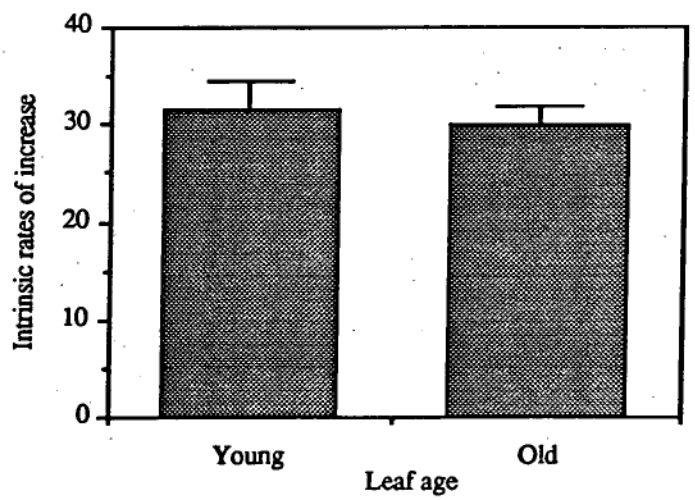


Fig. 6.53. Mean generation time of TSSM on young and old leaves.



6.3.4.2. Leaf regions: The survival of the juvenile stage on distal and basal regions of hop leaves is presented in Table 6.40. Comparison between the two regions of leaves shows that the percentage survival of the egg stage for both regions was similar, whereas that for the immature stages was higher on the basal regions.

Table 6.40. Life table of TSSM on distal and basal regions of leaves of two hop genotypes at 25°C, and the relative humidity of the ambient air in a incubator.

Portion	Genotype	X[a]	l_x[b]	d_x[c]	q_x[d]	s_x[e]	Generation mortality (%)
Distal	M4	Egg	36	9	.2500	.7500	
		Immature[f]	27	11	.4074	.5926	
		Adult[g]	16				55.56%
	M27	Egg	36	9	.2500	.7500	
		Immature	27	11	.4074	.5926	
		Adult	16				55.56%
Basal	M4	Egg	36	14	.3889	.6111	
		Immature	22	6	.2727	.7273	
		Adult	16				55.56%
	M27	Egg	36	6	.1667	.8333	
		Immature	30	8	.2667	.7333	
		Adult	22				38.89%

a = Stage of life cycle.
b = Number living at beginning of stage in the x column.
c = Number dying within stage in the x column.
d = Probability of dying during x.
e = Probability of surviving interval x.
f = Larva + Protonymph + Deutonymph.
g = Female + Male.

According to the unpaired t-tests, no significant differences in developmental periods for eggs occurred between these two regions of hop leaves for M4 and M27 (Fig. 6.54). It was also found that there were no significant differences in developmental periods from egg to adult as well as pre-reproductive periods occurred on M4, whereas significant differences were found on M27 (Fig. 6.55 and 6.56). For intrinsic rates of increase and mean generation times, nearly identical values were found on distal and basal regions of hop leaves of both M4 and M27 (Fig. 6.57 and 6.58).

Fig. 6.54. Developmental period for eggs of TSSM on distal and basal regions of leaves of M4(A) and M27(B) at 25°C under the relative humidity of the ambient air in the incubator .

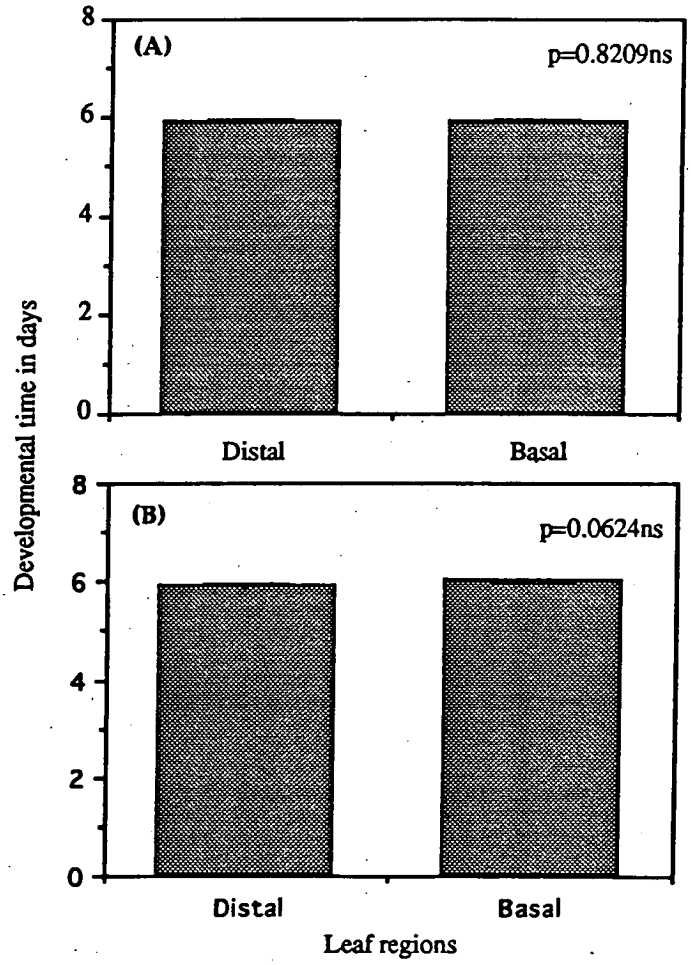


Fig. 6.55. Developmental period from eggs to adults of TSSM females on distal and basal regions of leaves of M4(A) and M27(B) at 25°C under the relative humidity of the ambient air in the incubator.

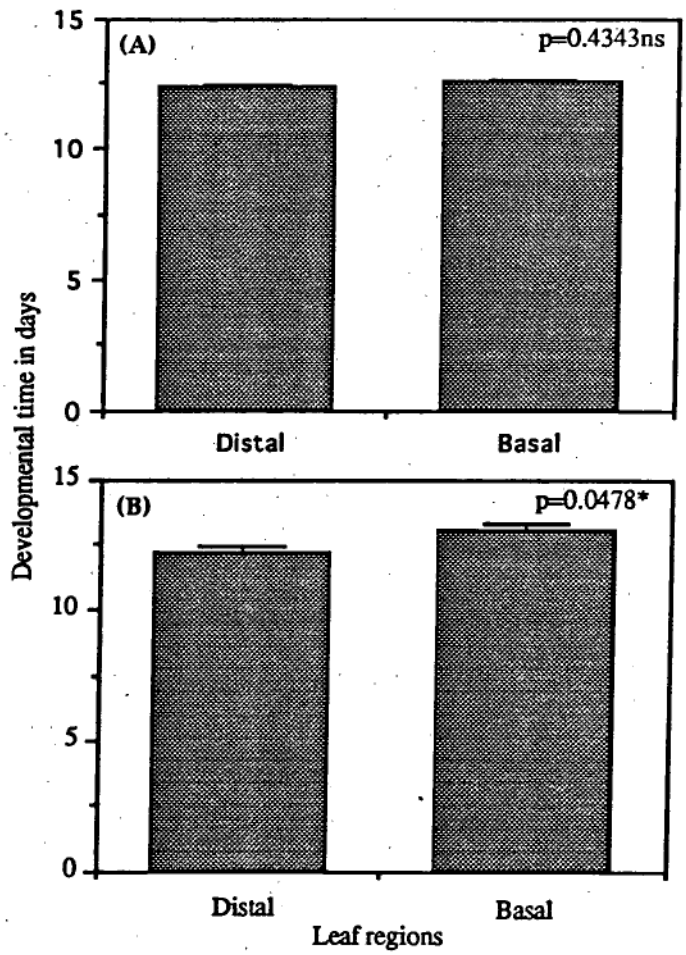


Fig. 6.56. Pre-reproductive period of TSSM females on distal and basal regions of leaves of M4(A) and M27(B) at 25°C and the relative humidity of the ambient air in the incubator.

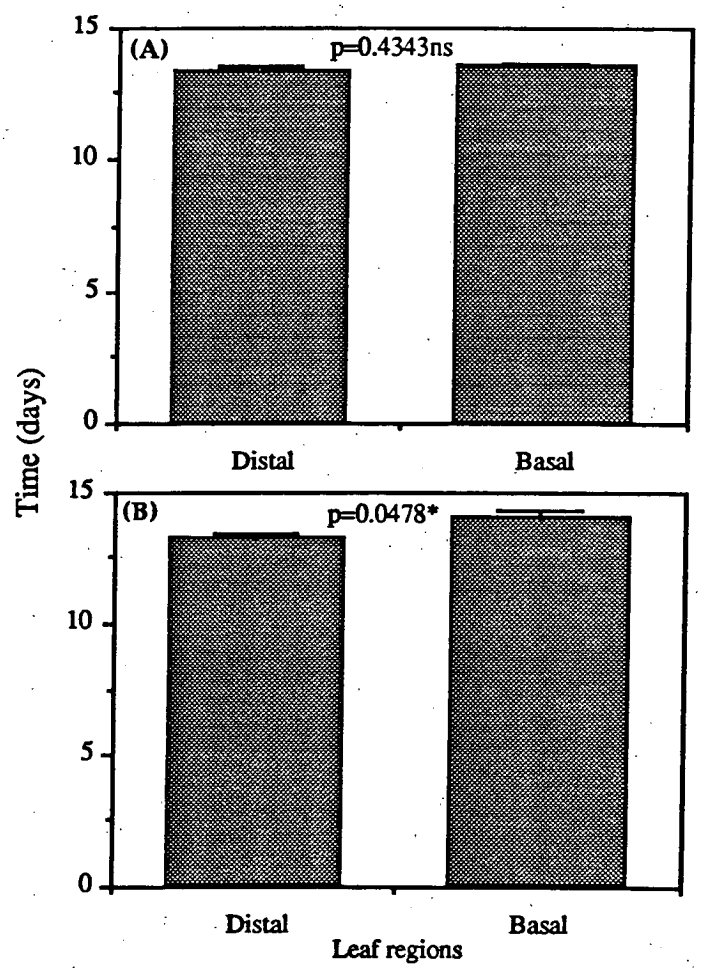


Fig. 6.57. Intrinsic rates of increase of TSSM on distal and basal regions of leaves of different hop genotypes at 25°C under the relative humidity of the ambient air in the incubator.

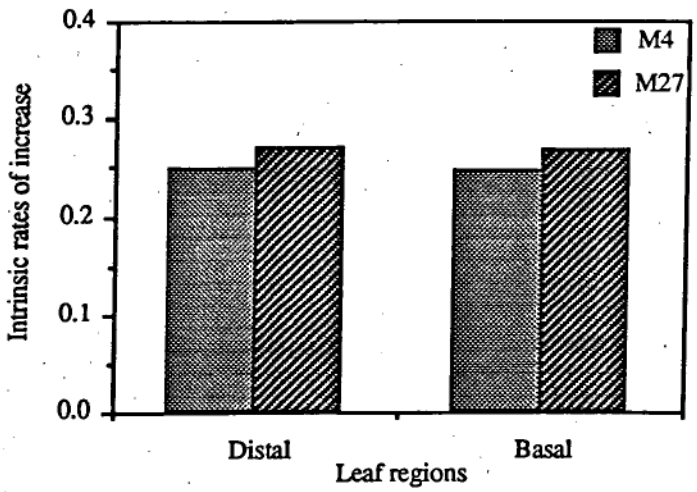
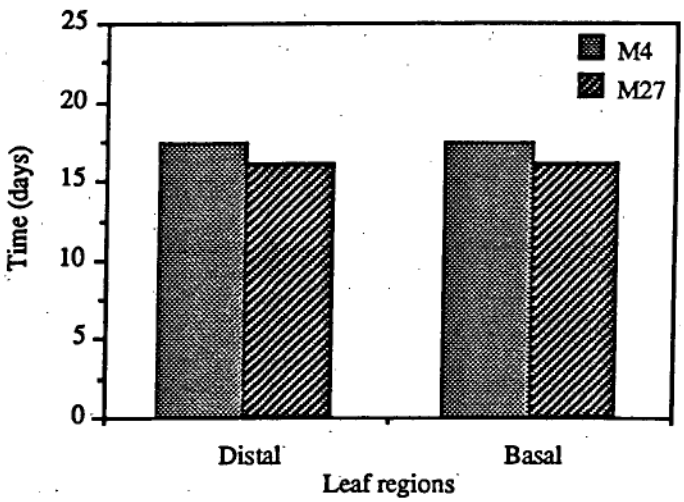


Fig. 6.58. Mean generation time of TSSM on distal and basal regions of leaves of different hop genotypes at 25°C under the relative humidity of the ambient air in the incubator.



6.4. DISCUSSION

6.4.1.Temperature

Since temperature is known to affect several physiological processes in plants and animals, it is not surprising that it should also affect the expression of resistance of plants to arthropod pests (McMurtry, 1962). The influence of environmental temperature on the resistance of plants has been the subject of several reports. Dahms and Painter (1940) demonstrated that the pea aphid had a higher reproductive capacity on resistant plants at low temperatures. Significant loss in expression of resistance in sorghums to the greenbug has also been reported at reduced temperatures (Wood and Starks, 1972). Nevertheless, Sosa and Foster (1976) working with four races of the Hessian fly on four wheat cultivars, showed that race-specific resistance of these cultivars generally decreased with rising temperature, as measured by per cent infestation.

According to Tingey and Singh (1980), the level and expression of genetic resistance in plants can be modified by temperature, i.e. either increased or reduced temperature can result in loss of resistance. Consequently, measurements of pest resistance and assessment of resistance mechanisms are frequently made in controlled environments at constant temperatures and it becomes necessary to include temperature records when presenting data indicating resistance in certain cultivars.

In the present study, the two hop genotypes selected generally had less resistance to mites with increasing temperature. However, there was no significant interaction between temperature and susceptibility, indicating that in general mites responded the same on these genotypes as far as temperature was concerned. The slightly susceptible genotype M4 could not be distinguished from the local susceptible genotype M27 at all constant temperature regimes studied. By the procedures employed, both genotypes appeared susceptible at these temperatures. It is therefore

likely that M4 and M27 are identified as susceptible genotypes. Sosa and Foster (1976) showed that infestation levels of the Hessian fly in susceptible wheat cultivars were unaffected by temperature.

From the economic point of view, the tendency of mites to survive better on resistant plants at low temperatures would not be expected to be of serious consequence, since at low temperatures TSSM populations build up relatively slowly and usually do not reach outbreak proportions. At higher temperatures, when populations have a greater tendency to reach economic levels, resistance would be displayed to a higher degree, making the resistant plants unfavourable for rapid increase in the mite populations.

Regardless of the influence on plant resistance, the present study supports the hypothesis that developmental rates in high-temperature environments contributed to TSSM outbreaks. The results show an increase in rate of development with increased temperature as is the rule for poikilothermous animals within the favourable temperature range (Nickel, 1960). The three temperatures studied appear to be inside the favourable range, as evidenced by the increased rates of development for all pre-adult stages at these temperatures. In addition, all the temperatures studied are within the range of summer temperatures at which mite outbreaks normally occur. Lewontin (1965) suggests that developmental rate is the single most important variable influencing the intrinsic rate of increase of colonizing species. Considering the relationship between temperature and developmental rates observed in this study, the importance of temperature as a factor involved in TSSM population explosions is apparent.

Furthermore, the series of experiments at constant temperatures provide useful information about the general life history of TSSM and the approximate duration of the various stages for each temperature

regime. It was found that growth rates of the mites was considerably higher at high than at low temperatures. Much recent work has shown that temperature is a dominant factor affecting the growth rate and development of many arthropod populations including tetranychids, especially in temperate climates (Tanigoshi et al., 1975; Perring et al., 1984).

Predicting the seasonal occurrence of pests is essential for accurately scheduling census samples and control tactics. The thermal requirements of development are often used as a basis for these predictions (Wagner et al., 1984).

The present study shows that the lower thermal threshold for TSSM development, can be estimated at 5.88°, 10.99° and 11.33°C for egg stage, female and male postembryonic stages, respectively. This is in agreement with the findings of other authors. In Japan, Mori (1961) demonstrated that the activity zone of temperature for TSSM ranged from 5-9°C to 41-44°C. In mainland Australia and Canada, the threshold temperature obtained from the regression of the developmental rates of TSSM at different temperatures was found to be ca. 10°C by Readshaw (1975) and Herbert (1981), respectively. In the United States, Carey and Bradley (1982) reported the threshold temperature for the development of TSSM to be 11.7°C. It is probable that the different threshold temperatures have been established because geographically separated populations of mites may differ with respect to the influence of temperature on developmental rates.

The present study demonstrated that the lengths of the egg stage, the egg to adult stage and the age at first oviposition varied with temperature. Similar phenomena have been observed by several researchers. Cagle (1949) reported that the incubation period of eggs ranged from 3 days at an average temperature 23.9°C to 21 days at 11.1°C.

Ferro and Chapman (1979) also showed that there was a decrease in incubation time for mean egg hatch with an increase in temperature. More precise temperature studies were performed by Herbert (1981), using degree-days (above 10°C). This author found that the durations from the beginning of the egg stage to adult for females were 141.3, 152.3, and 139.8; for males 134.2, 144.7, and 135.2 at 15°, 18°, and 21°C, respectively. Carey and Bradley (1982) reported a similar relationship between temperature and time required for TSSM development.

The developmental time required for egg hatch was approximately 40 percent of the total juvenile developmental time at the temperature regime studied. Shih et al. (1976) reported the longer time spent in the egg stage not only contributed to a longer period for predation by egg-feeding phytoseiid predators in a predator-prey interaction but also provided more time for the older stages to remain free of predation.

For survivorship and reproduction of TSSM, the present study confirmed that temperature influenced these two parameters. Among the temperatures studied, generation mortality was found to be the least at 25°C. This is in agreement with the statement by Boudreaux (1963) that the optimal temperature of many spider mite species occurs between 24° and 29°C. In general, both development and reproduction of TSSM are summarized by the value of r_m which was positively correlated with the temperature range employed. It was ascertained that values of r_m increased as generation times decreased.

In the present study, no effect of temperature on the ratio of females to males for mite populations reaching adulthood was observed. This indicated that survival of males was similar to that of females at the temperature regime used. Nevertheless, Hazan et al. (1973) reported that the numbers of adult males and females which emerged from tetranychid eggs was affected by temperature.

6.4.2. Humidity

Of the environmental factors studied, it appears that humidity is the second most important factor in modifying the growth rate of mite populations. Studies on the humidity relationships of TSSM by Andres (1957) showed this species to be favoured by low humidity. Nickel (1960), working with TSSM on cotton, also reported that the mites had a lower rate of reproduction and a slower rate of development at high, as compared with low, relative humidity. In terms of hygrokinetic behaviour, Mori and Chant (1966) found that TSSM chose dry conditions over moist ones, and that mite activity was reduced when they were placed in high humidities.

The results in the present study indicated that the embryonic development was influenced by humidity. A explanation may be in the physiology of the mite egg. Dittrich (1971) described the morphology of TSSM eggs as it relates to respiration. This author stated that a narrow duct system is present in the egg through which embryo respiration takes place. If the air flow system is saturated with water vapor, resistance to the movement of oxygen and carbon dioxide may contribute to the mortality of the embryo. By using saturation deficit (SD) as an index of humidity, Ferro and Chapman (1979) also demonstrated the effect of varying humidities at different temperatures on hatchability of TSSM.

Similar results have been reported in other members of the tetranychidae. Nickel (1960), working with *T. desertorum* Banks on cotton, found that the differences due to humidity level were most pronounced in the egg stage. Perring et al. (1984), working with *Oligonychus pratensis* (Banks) on corn, also indicated that humidity was an important variable in egg survival.

In addition to the effect of very high humidity, the results from the present work showed that the egg stage suffered high mortality at low

humidity (55%RH). This appeared to be due to the effect of desiccation on egg survival. There are apparent contradictions between the results reported in this study and the results reported by Nickel (1960), who reported that the mortality of the egg stage was lower at low humidities (25-30%RH) than at high humidities (85-90%RH). It appears possible that the temperature, as well as light intensity, used in these two studies might be involved. Nickel's observations related to saturated solutions however temperature and light intensity were not controlled. Results of this study is based on the use of three temperature levels and two light intensities.

In the present study, survival of postembryonic stages was affected by humidity. Boudreaux (1958) also reported a much higher nymphal mortality at very high humidity. This suggests that TSSM may be more easily controlled in glasshouses if a high relative humidity is maintained everything else being equal.

For the developmental time for each juvenile stage studied, there were significant differences in egg period, total juvenile developmental period and pre-reproductive period between moderately humid conditions (70-80%) and water-saturated atmospheres. However, no significant differences in these periods were detected among humidity conditions which were controlled by the use of the saturated solutions. Similar results were reported for TSSM on cotton by Boudreaux (1958) and Nickel (1960).

Using the value of r_m as the criterion for favourability, the most favourable humidity of those studied was shown to be 76%RH. The r_m determined at this humidity level was slightly greater than those recorded at the other humidity levels. In addition, at 76%RH a slight decrease in the mean generation time occurred.

The results from this study show that the sex ratio of immatures reaching adulthood was affected by humidity. At very high humidity, sex ratio determinations indicated a shift towards a higher female : male ratio, indicating that females were more tolerant to humidity than males.

Furthermore, the interaction between humidity and susceptibility was not significant. This indicated that as far as humidity was concerned, mites generally responded similarly irrespective of the genotype tested.

6.4.3. Light intensity

As with other variables of the physical environment, light intensity can modify fundamental physiological processes of pests and their host plants. Low light intensity has the greatest influence on expression and magnitude of plant resistance (Tingey and Singh, 1980). For example, Lowe (1974) reported that fecundity and population levels of *Myzus persicae* were significantly reduced on resistant and susceptible lines of sugar beets grown at light intensities reduced about 75 percent from incident intensities in a glasshouse environment.

For the plants, light has long been implicated as a factor in nitrate metabolism. In 1888, A.F.W. Shimper reported that shaded leaves contained a higher concentration of nitrate than leaves grown in the sun (Knipmeyer et al., 1962). Burstrom (1943) obtained evidence that wheat leaves might reduce nitrate in the light but not in the dark. Delwiche (1951), working with isotopic nitrogen, indicated that tobacco plants metabolized nitrate or ammonia in the dark as well as in the light. Other reseachers stated that some plant species can metabolize nitrate or hyponitrite in both light and dark; however, the rate is accelerated in the light (Mendel and Visser, 1951; Frear and Burrell, 1958). Candella et al. (1957) and Hageman and Flesher (1960) demonstrated that light was needed to maintain the enzyme nitrate reductase in an active state.

Since the variation in susceptibility of the two genotypes tested was not significant, the light intensity employed could not be shown to affect the mite populations on both genotypes of hops. In addition, the interaction between susceptibility and light intensity was not significant, indicating that mites generally responded the same on the genotypes tested as far as light intensity was concerned.

For the life-history parameters, the present study showed that light intensity had an influence on survival, development and reproduction of TSSM populations, especially those in open containers. It was noted that generation mortality of mites was generally greater at low light intensities than at high light intensities. There were significant differences in total juvenile development and pre-reproductive periods of mites reared at different light intensities. The intrinsic rate of increase tended to be greater for mites reared at higher light intensities, while the mean generation time tended to be longer for mites reared at lower light intensities. Wyatt and White (1977) and Wrensch (1985) stated that light intensity is a factor influencing fecundity. However, it was evident that the time required for egg hatch was not affected by the light intensity employed.

In the present study, the results obtained in open containers did not conform to those in closed containers. It seems probable that fresh air or purified air circulating in the rearing incubator enhanced the production of the mite. This may partly be the result of more favourable conditions for food utilization brought about by air change. Munger (1955; 1956), working with the citrus red mite on lemons in rearing rooms, found a similar effect.

Sex ratio of immatures becoming adults were observed to favour females for mites reared in both open and closed containers. It was found that at a light intensity of 43 lux the male immatures were not able to

reach adulthood at both 20° and 30°C under very high relative humidity conditions, whereas adult mites reared at the other environmental regimes consisted of males and females. This indicated that an interaction between light intensity, temperature and humidity affected mite populations.

6.4.4. Plant variables

6.4.4.1. Leaf age: The influence of leaf age on expression of genetic resistance could not be shown in this study because there were no significant differences in varietal susceptibility and the interaction between leaf ages and genotypes was not significant. However, numerous other observations of leaf age-related shifts in pest performance and levels of resistance have been reported (Henneberry, 1962; McMurtry, 1962; Watson, 1964; Tingey and Singh, 1980).

The results from the present study also show that very little difference occurred between survival, development and reproduction of mites on old and young leaf discs. There appeared to be no consistent pattern in generation mortality for mites reared on leaf discs cut from hop leaves at different ages. In general, the developmental period of mites on young leaf discs was very similar to that on old leaf discs. Nevertheless, it was apparent that total juvenile developmental time between young and old leaf discs of M27 differed significantly. The intrinsic rate of increase tended to be higher on young leaf discs than on old ones, indicating an apparent effect of leaf age upon fecundity. This was probably due to the decreasing availability of nitrogen in the older leaves. Similar results were reported by Watson (1964). However, Cates (1980) suggested that there is a general trend for young leaves to have higher toxin levels than mature leaves, and for nonspecialized herbivores to prefer mature leaves over young, expanding leaves.

Sex ratio of immatures reaching adulthood were observed to favour females for mites reared on both young and old leaf discs. From the present data it can be seen that sex ratio determinations on old leaf discs showed a shift towards a smaller female : male ratio. Wresnsch and Young (1983) suggested that the sex ratio of tetranychids is sensitive to leaf quality.

6.4.4.2. Leaf regions: Since the size of major veins in the basal zone of a hop leaf is usually larger than those in the distal region, the study on possible effects of leaf vein size on life history of mite populations was carried out using leaf discs cut from different regions of a leaf. Mitchell (1973) suggested that the feeding area of TSSM often lies close to a leaf vein. The results from this study show that survival and reproduction of mites were not signicantly affected by the size of leaf veins, whereas development was found to be influenced by this variable, especially on M27. This indicated that the possitively or negatively influence of leaf veins studied might depend on genotypes of hop plants. Some genotypes may have larger veins than other ones.

CHAPTER 7 RELATIONSHIP BETWEEN HOP LEAF MORPHOLOGY AND SUSCEPTIBILITY TO TSSM

7.1. INTRODUCTION

In continuing efforts to elucidate the parameters of hop genotypes which account for their TSSM resistance, roles of morphological factors in such resistance have been studied (Peters and Berry, 1980b). There is much evidence that plant morphological factors such as tissue toughness and trichomes (hairiness) act as barriers to some pests (Norris and Kogan, 1980). Several pest species, however, may respond differently to a given plant morphological trait (Chiang and Norris, 1985). Past research on these characteristics as they relate to TSSM has focussed mainly on trichomes.

This chapter, therefore, presents the results of a study designed to examine leaves from various hop genotypes for morphological differences and evaluate the relationship of the morphological characteristics to mite fitness traits. The morphological features studied were ventral trichomes, lupulin glands, stomata, cuticle thickness, leaf thickness, leaf veins and leaf moisture content. In addition, the effect of mite damage on leaf surface was examined and related to stomatal opening and stomatal size.

7.2. MATERIALS AND METHODS

7.2.1. Morphological features

7.2.1.1. Plant material: Leaves were collected from hop genotypes grown in the field at Bushy Park or in a glasshouse at the Department of Agricultural Science. All the 27 genotypes of hops mentioned in Chapter 5 were employed. For each genotype, the leaves were divided into two

portions; the first one for the bioassay test in Chapter 5 and the second one for the examination of morphological factors.

7.2.1.2. External characteristics of hop leaves: Fully expanded mature leaves of the 27 genotypes sampled from hop plants in the field or in the glasshouse were used in this study. In addition to the mature leaves, a leaf at the fourth node from the plant tip of each genotype in the field was also collected for comparing the morphological characteristics of young leaves with those of old ones.

Hop leaf surfaces were examined by scanning electron microscopy (Philips SEM505) at 1.5 kv and a spot size of 20 nm. Before the examination, samples were prepared as follows: (1) whole leaves were submerged into 4% gluteraldehyde in phosphate buffer (pH7) and the sample (ca. 0.75 cm. diam.) were cut out while being submerged to insure maximum penetration of the fix agent; (2) the samples placed abaxial side up were fixed on aluminum stubs with silver liquid paint; (3) the samples were then critically point dried, ultra-pure gold coated in a Balzers Union splutter coater to give a film thickness of 25 nm., and examined at 60X, 300X, 925X, and 5000X for densities of lupulin glands and ventral trichomes, diameters of gland and trichome bases, stomatal densities, and stomatal sizes, respectively. Images were recorded with Polaroid 667 and Ilford FP-Y120 Film. A total of eight samples was taken from each genotype. These samples included six from the mature leaves of field hop plants, another from the mature leaves of glasshouse hop plants, and the other from the young leaves of field hop plants.

7.2.1.3. Histological examinations: A razor blade was used for removing tissue samples from the basal regions of hop leaves. Then the tissue samples were sectioned using a plant microtome (Cat. No. 1225; Lab-Line Instruments, Inc.). These sections were stained with Sudan IV prior to microscopic examination. Using an ocular micrometer in a

binocular microscope, the measurement for trichome length, major vein size, upper and lower epidermal layer, and leaf thickness was carried out at 125X and for cuticle thickness at 500X. A total of six samples were examined for each genotype. These samples included three from the young leaves of glasshouse hops, two from the mature leaves of glasshouse hops, and the other from the mature leaves of field hops.

7.2.1.4. Leaf moisture content: Six fresh mature leaves collected from each genotype of field hop plants were weighed and placed in a 70°C drying oven. Two days later, the dried leaves were removed and reweighed to obtain a ratio of dry to wet weight.

7.2.2. Morphological responses of hop leaves to mite infestations

Feeding injuries caused by various levels of TSSM infestations between different hop genotypes was studied using the leaf disc technique. Mature leaves were collected from the genotypes M4 (slightly susceptible) and M26 (highly susceptible) under field conditions at Horticultural Research Centre. Four plants of each genotype were sampled, and one leaf of similar age was removed from each plant. Immediately after collection, three discs (1.35 cm. diam.) were cut from each leaf with a sharp mouth test tube. These three discs were placed abaxial side up on a filter paper surrounded by a water soaked cotton pad in the same petri dish. Mite densities of 0, 5, and 10 teneral females per disc, representing control, low, and high densities, respectively were randomly assigned to one disc on each petri dish. The experimental design then may be described as a two (genotypes) X three (densities) factorial experiment with 12 leaf discs tested on each genotype. The mite culture was kept in a constant temperature room maintained at 25°C, with a 16:8 h. L:D photoperiod. Each disc was observed daily under a binocular microscope (10X) and the number of eggs was counted. During this time, the number of females was adjusted to maintain those

densities in each disc. Three days after infestation all the mites and eggs were removed and the leaf discs were examined to estimate leaf area scarred in terms of the number of yellow specks occurring on the adaxial side under a binocular microscope (10X). Additionally, the number of open stomata and their sizes at four positions were determined using the electron microscopy at 925X and 5000X, respectively.

7.2.3. Data analyses

Analysis of variance was used to detect differences not only in morphological characteristics between different hop genotypes but also in mite daily fecundity among different densities. Means were compared using Fisher's protected least significant differences (PLSD) test with an alpha level of 5%. For the morphological features of leaves collected from different sources, the differences were analysed by the t-test. All the analyses were completed on Macintosh Classic II with MacSoftware Statview SE + Graphics. Linear regression employed to define the relationship of the morphological factors to mite fitness traits was obtained from the curve fit procedure of the Cricketgraph computer program. Since group variances tended to be proportional to the means, the daily egg counts were transformed as square root of x + 0.5 for statistical analysis (Zar, 1984), where x is the number of eggs per female per day.

7.3. RESULTS

7.3.1. Hop leaf morphology

7.3.1.1. Different genotypes: Scanning electron microscopy showed external morphological characteristics on the lower surface of hop leaves. These characteristics included ventral glands, trichomes and stomata (Plate 5).

Plate 5. The lower surface of hop leaves at 212X.

The mean density of ventral glands as well as the average diameter of the gland for each genotype is presented in Table 7.1. It was apparent that there were no significant differences in gland densities among the 27 hop genotypes studied ($p \leq 0.05$), whereas gland diameters between these genotypes differed significantly ($p \geq 0.05$). Maximum numbers of ventral glands per mm^2 were found on M16, M9, and M21 and minimum numbers on M6, M2, and M7. The diameters of ventral glands on M20 were significant longer than those on other genotypes with the exception of M18 and M22, whereas M1 had the shortest diameter compared with other genotypes.

Table 7.1. Average number of ventral glands and gland diameters found on each genotype tested.

Genotype	Means ± S.E.	
	Number of ventral glands per mm^2	Gland diameters (micron.)
M1	3.038 ± 0.538	128.72 ± 4.160 a
M2	2.333 ± 0.518	131.79 ± 3.785 ab
M3	3.472 ± 0.743	153.60 ± 3.930 efg
M4	4.178 ± 0.613	152.03 ± 3.895 def
M5	3.689 ± 0.348	132.01 ± 3.887 ab
M6	2.116 ± 0.224	134.47 ± 4.102 abc
M7	2.387 ± 0.492	144.10 ± 5.101 bcde
M8	2.767 ± 0.505	132.69 ± 4.059 ab
M9	5.046 ± 0.608	141.82 ± 5.189 abcde
M10	3.309 ± 0.357	141.64 ± 4.093 abcde
M11	2.930 ± 0.256	150.51 ± 2.885 def
M12	4.340 ± 1.397	151.50 ± 6.353 def
M13	4.829 ± 1.026	138.22 ± 2.379 abcd
M14	3.581 ± 1.330	149.07 ± 6.242 cde
M15	2.658 ± 0.445	138.18 ± 4.995 abcd
M16	5.642 ± 1.806	143.90 ± 9.397 bcde
M17	3.961 ± 0.810	154.10 ± 5.132 efg
M18	3.092 ± 0.265	167.21 ± 3.870 gh
M19	3.309 ± 0.434	144.79 ± 4.501 bcde
M20	2.767 ± 0.384	170.74 ± 8.349 h
M21	4.991 ± 1.437	153.82 ± 8.780 efg
M22	3.689 ± 1.205	164.58 ± 2.946 fgh
M23	3.364 ± 1.171	153.17 ± 4.243 efg
M24	2.441 ± 0.705	132.53 ± 4.281 ab
M25	4.395 ± 1.096	148.00 ± 7.254 cde
M26	4.557 ± 1.252	155.81 ± 4.195 efg
M27	2.984 ± 0.380	144.67 ± 7.871 bcde
p-value	0.276ns	0.0001**

Means with the same letter in a column are not significantly different (p>0.05) using Fisher PLSD.

For both densities and basal diameters of trichomes, significant differences ($p \leq 0.01$) were detected among the genotypes studied (Table 7.2). M4 had the highest number of trichomes per mm^2 followed by M9 and M19 with M7, M13 and M27 having the lowest densities. In terms of trichome basal diameters, M1 had the longest diameter followed by M20 and M18 with M12 having the shortest.

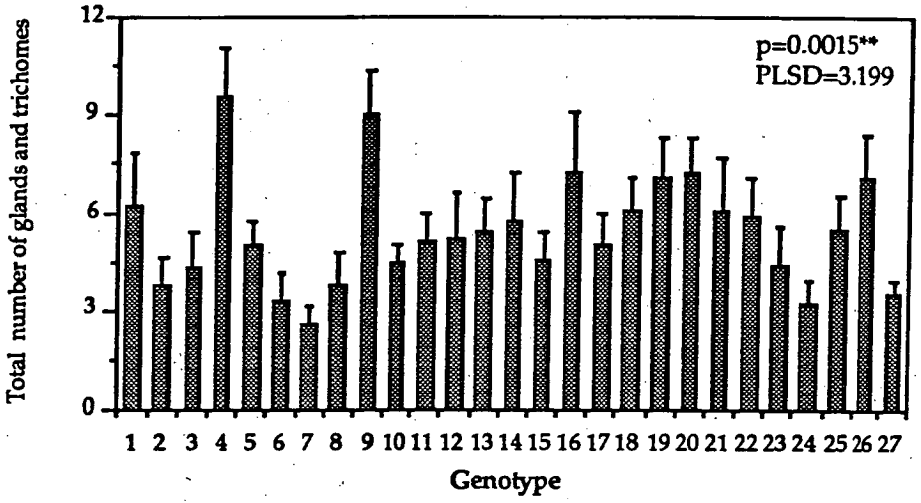
Table 7.2. Average number of trichomes and trichome basal diameters found on each genotype tested.

Genotype	Means ± S.E.	
	Number of trichomes per mm ^{2}	Trichome basal diameters (micron.)
M1	3.147 ± 1.283 def	73.593 ± 7.519 f
M2	1.465 ± 0.646 abcd	58.578 ± 2.165 abcdef
M3	0.814 ± 0.397 ab	49.778 ± 2.288 abcd
M4	5.371 ± 1.166 g	59.722 ± 7.553 bcdef
M5	1.356 ± 0.638 abcd	58.056 ± 6.672 abcdef
M6	1.139 ± 0.832 abcd	63.704 ± 5.342 cdef
M7	0.217 ± 0.082 a	54.444 ± 1.111 abcd
M8	0.977 ± 0.732 abc	57.778 ± 4.157 abcdef
M9	3.961 ± 1.261 efg	57.569 ± 2.909 abcde
M10	1.139 ± 0.580 abcd	55.208 ± 2.446 abcde
M11	2.170 ± 0.782 abcde	62.593 ± 5.931 cdef
M12	0.814 ± 0.322 ab	41.667 ± 8.813 a
M13	0.597 ± 0.357 ab	49.409 ± 2.319 abcd
M14	2.170 ± 0.608 abcde	65.903 ± 8.840 def
M15	1.899 ± 0.676 abcde	45.694 ± 4.626 ab
M16	1.573 ± 0.824 abcd	53.333 ± 2.222 abcd
M17	1.031 ± 0.666 abcd	64.333 ± 6.948 cdef
M18	2.984 ± 0.896 cdef	72.476 ± 6.535 ef
M19	3.743 ± 1.124 efg	53.397 ± 2.918 abcd
M20	4.449 ± 1.010 fg	73.056 ± 4.188 f
M21	1.085 ± 0.525 abcd	61.852 ± 6.244 cdef
M22	2.170 ± 1.079 abcde	58.444 ± 8.802 abcdef
M23	1.031 ± 0.492 abcd	54.519 ± 5.160 abcd
M24	0.760 ± 0.365 ab	61.244 ± 6.590 bcdef
M25	1.085 ± 0.358 abcd	49.286 ± 4.979 abc
M26	2.496 ± 1.069 bcdef	54.756 ± 7.611 abcd
M27	0.543 ± 0.304 ab	55.556 ± 0.000 abcde
p-value	0.0001**	0.0113**

Means with the same letter in a column are not significantly different ($p>0.05$) using Fisher PLSD.

When the numbers of ventral glands and trichomes per unit area were pooled, it was found that there were highly significant differences ($p \leq 0.01$) in the density among these genotypes (Fig. 7.1). The highest density of these morphorlogical characteristics was found on M4 followed by M9, M16 and M20 with M7, M24 and M27 having the lowest density.

Fig. 7.1. Total number of ventral glands and trichomes within 1 mm^2 of hop leaves for each genotype studied.



The sizes of ventral glands and trichome bases, expressed as surface areas, are presented in Fig. 7.2. It was apparent that the surface area for each ventral gland and trichome base among the 27 genotypes differed significantly ($p \leq 0.05$). The average surface areas varied from 23287.598 to 13225.018 μm^2 and 4477.401 to 1669.239 μm^2 for ventral glands and trichome bases, respectively. Fig. 7.3 shows the percentages of hop leaf surface areas within 1 mm^2 for ventral glands and trichome bases. Significant differences were detected in the percentage of ventral gland areas on each genotype (Fig. 7.3A), M26 having the highest and M6 the lowest percentage, respectively. The percentage of trichome basal areas also varied significantly among these genotypes, with M20 having the highest percentage, followed by M18 and M4. M7 had the lowest percentage compared with other genotypes (Fig. 7.3B).

Fig. 7.2. Average areas of ventral glands (A) and trichome bases (B) found on each genotype tested.

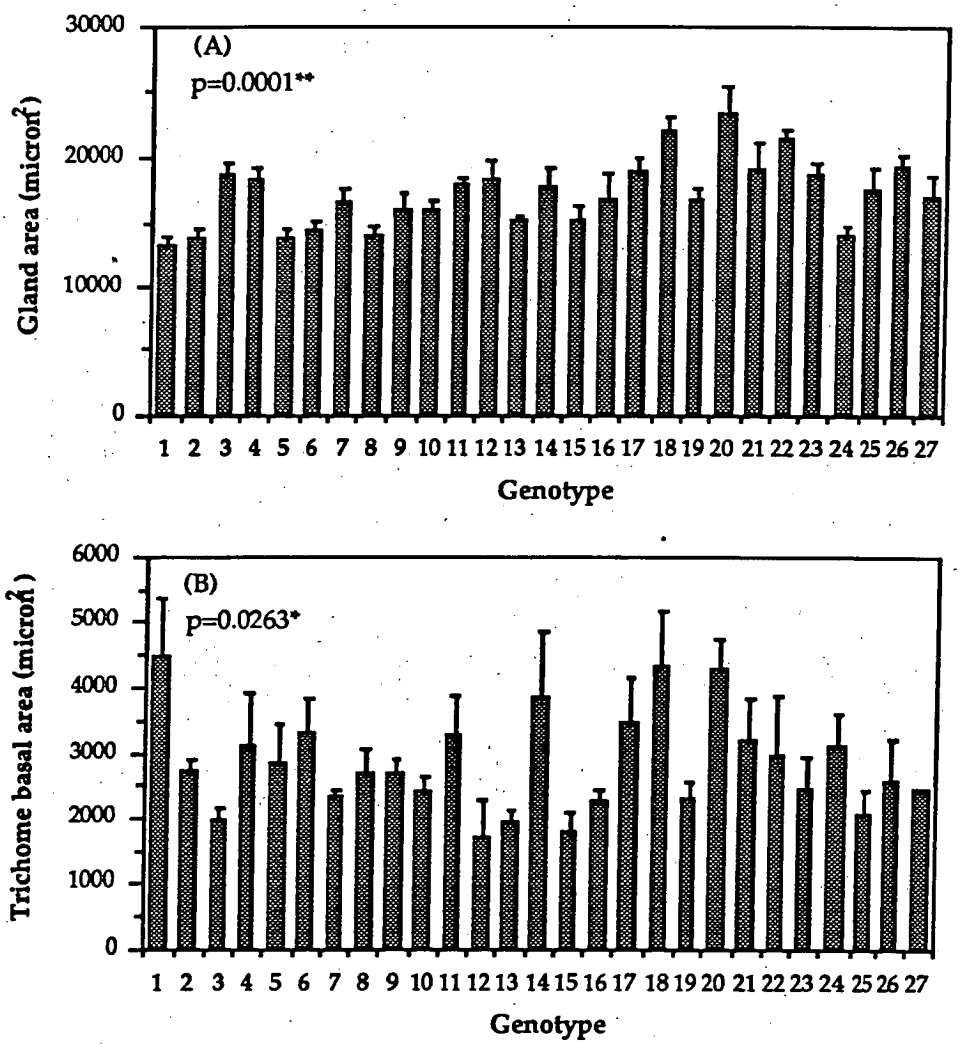
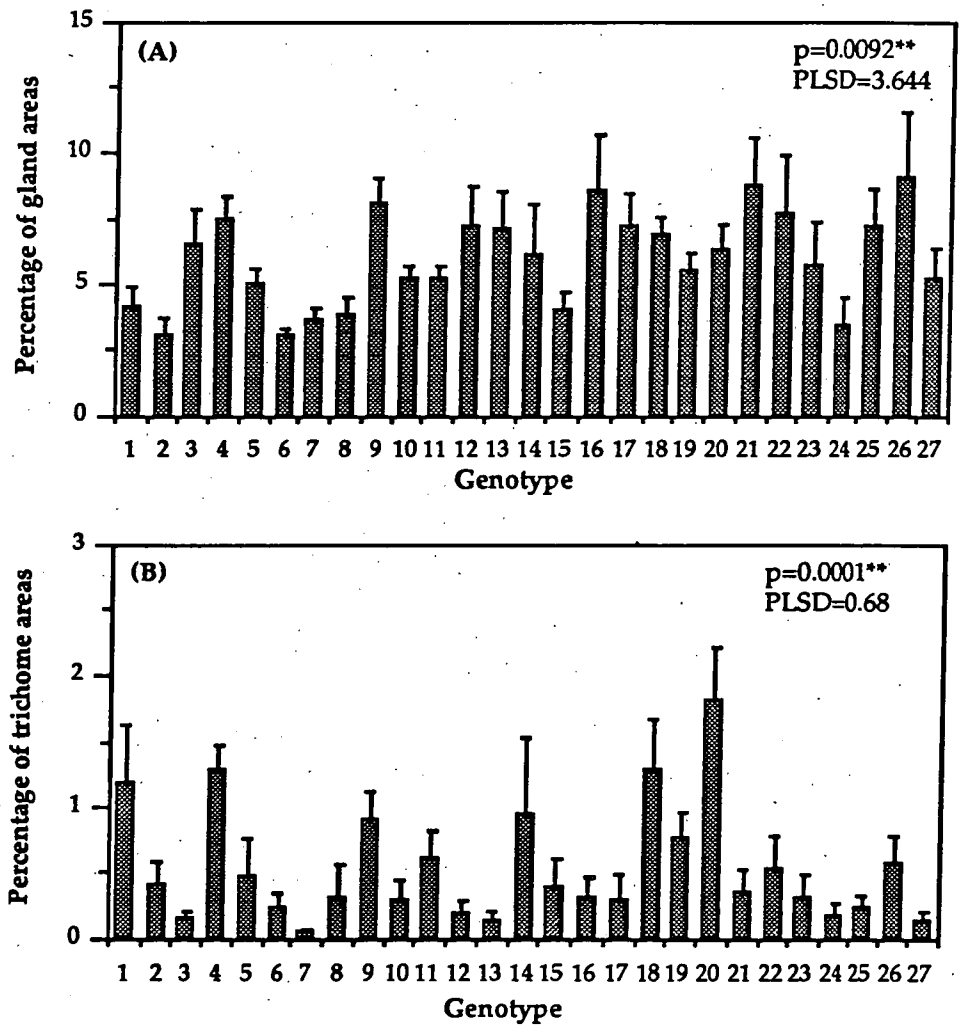
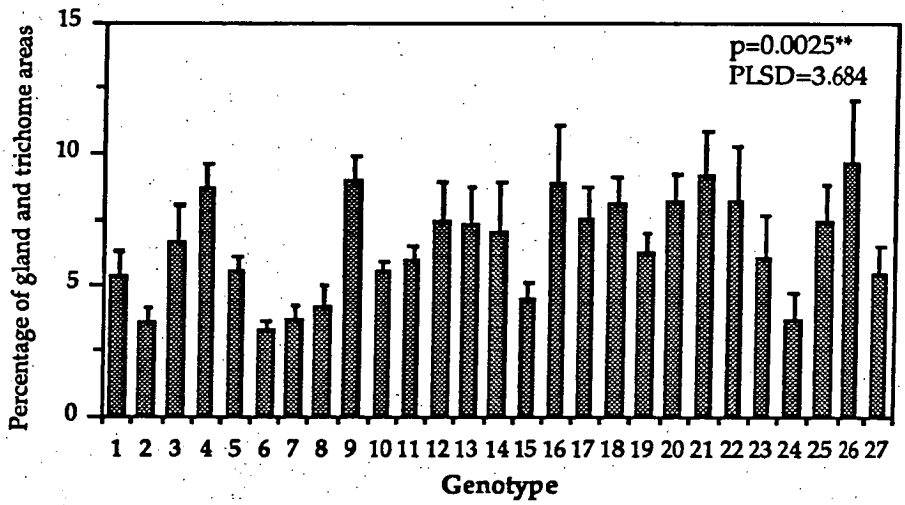


Fig. 7.3. Percentage of ventral gland areas (A) and trichome areas (B) within 1mm^2 of hop leaves for each genotype studied.



When the percentages of surface area found on hop leaves within 1 mm^2 for ventral glands and trichome bases were pooled, highly significant differences ($p \leq 0.01$) were detected among the genotypes studied (Fig. 7.4). M20 had the highest percentage of gland and trichome areas, followed by M4 and M9, with M6 and M7 having the lowest percentage.

Fig. 7.4. Pooled percentage of gland and trichome areas within 1 mm^2 of hop leaves for each genotype studied.



From studying the cross sections of hop leaves, the length of trichomes on each genotypes is presented in Table 7.3. Significant differences ($p \leq 0.05$) in the trichome length were found among the 27 genotypes, with M2 having the longest trichomes followed by M6, M15, and M26. M10 had shorter trichomes than other genotypes, although not differing significantly from trichome lengths of M23, M4, M8, M25, M16, M24, M21, M7, M12, M9, M19, M5, M22, M14, M3, M13, M27, and M20 ($p \geq 0.05$).

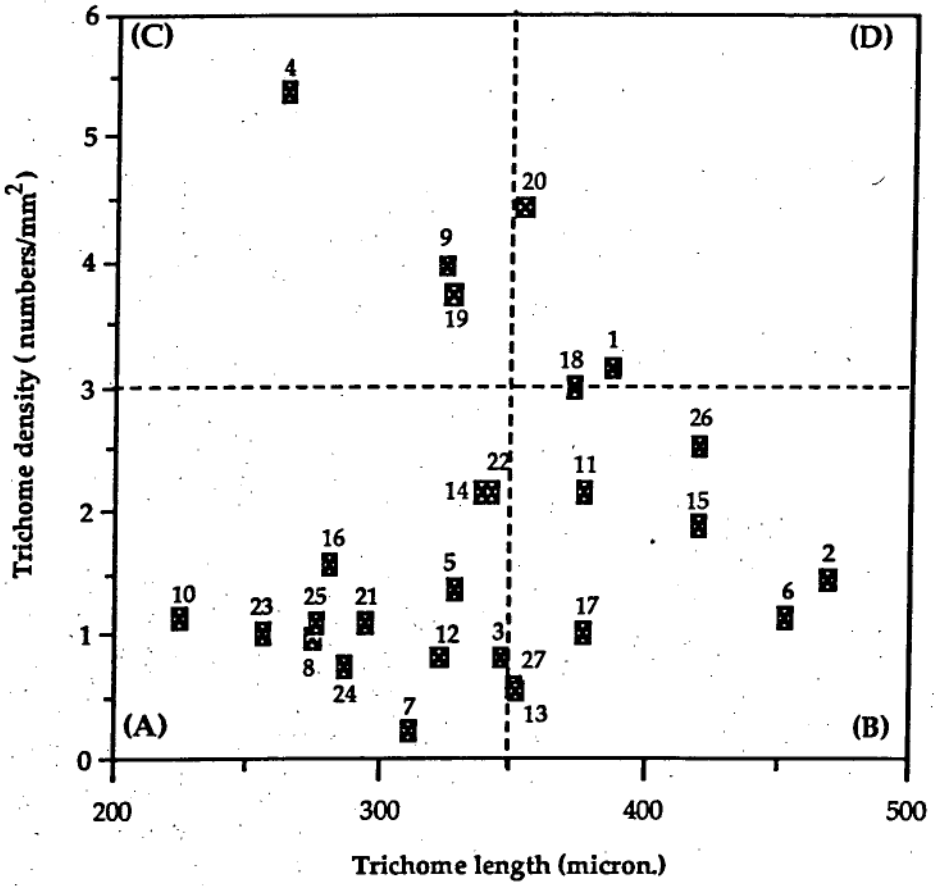
Table 7.3. Average length of trichome on leaves of 27 hop genotypes studied.

Genotype	Trichome length (micron.) Means + S.E.
M1	387.10 ± 42.63 bcde
M2	468.77 ± 56.89 e
M3	346.27 ± 57.79 abcde
M4	262.97 ± 35.01 ab
M5	328.30 ± 35.67 abcd
M6	452.43 ± 69.41 de
M7	311.97 ± 24.98 abc
M8	274.40 ± 46.99 ab
M9	325.03 ± 41.53 abcd
M10	223.77 ± 29.88 a
M11	377.30 ± 47.39 bcde
M12	323.40 ± 22.63 abcd
M13	351.17 ± 66.25 abcde
M14	343.00 ± 63.71 abcde
M15	419.77 ± 46.34 cde
M16	280.93 ± 68.44 ab
M17	377.30 ± 42.02 bcde
M18	372.40 ± 45.62 bcde
M19	326.67 ± 61.55 abcd
M20	354.43 ± 44.80 abcde
M21	295.63 ± 23.25 abc
M22	338.10 ± 38.69 abcde
M23	256.43 ± 36.62 ab
M24	287.47 ± 56.68 abc
M25	276.03 ± 34.18 ab
M26	419.77 ± 62.16 cde
M27	352.80 ± 14.97 abcde
p-value	0.0465*

Fig. 7.5 shows the plots of hop trichome density to length of 27 genotypes. From this figure, it can be seen that four basic trichome profiles were observed: (1) few-short trichomes represented by M10, M23, M8, M25, M16, M24, M21, M7, M12, M5, M14, M22, and M3; (2) few-long trichomes by M27, M13, M17, M11, M26, M15, M6, and M2; (3) many-short trichomes by M4, M9, and M19; and (4) many-long trichomes by M20, M18 and M1. According to the results obtained from the preference test in Chapter 4, it was found that most of the hop genotypes in few-long and

many-short trichomes were identified as highly susceptible and slightly susceptible genotypes, respectively.

Fig. 7.5. Trichome density and length of 27 hop genotypes and the respective trichome profile region: (A) few-short trichomes; (B) few-long trichomes; (C) many-short trichomes; and (D) many-long trichomes.



There were highly significant differences ($p \leq 0.01$) in stomatal density and stomatal size (based on the length and width of stomatal pores) among the 27 genotypes studied (Table 7.4). The highest number of stomata per mm^2 was found on M13, followed by M9, M8 and M10. M7 and M14 had the lowest density compared with other genotypes.

Table 7.4. Average number of stomata per mm^2 and stomatal sizes found on leaves of 27 hop genotypes.

Genotype	Means ± S.E.		
	Number of stomata per mm^2	Stomatal length (micron.)	Stomatal width (micron.)
M1	548.212 ± 36.547 abcdef	11.70 ± 1.01 abc	4.95 ± 0.28 hi
M2	548.212 ± 44.880 abcdef	11.11 ± 0.84 ab	3.13 ± 0.39 abc
M3	572.577 ± 56.582 abcdefgh	11.35 ± 1.34 abc	3.46 ± 0.44 abcde
M4	548.212 ± 51.891 abcdef	11.58 ± 0.99 abc	4.36 ± 0.41 efghi
M5	523.847 ± 55.062 abcd	14.08 ± 0.39 cdef	4.41 ± 0.25 efghi
M6	572.577 ± 42.948 abcdefgh	12.54 ± 0.74 abcd	3.99 ± 0.32 bcdefgh
M7	426.387 ± 17.833 a	15.68 ± 1.39 ef	5.17 ± 0.49 i
M8	694.402 ± 72.366 fgh	10.64 ± 0.59 a	2.93 ± 0.25 a
M9	706.584 ± 63.134 gh	11.98 ± 0.72 abc	3.73 ± 0.29 abcdef
M10	682.219 ± 36.836 efgh	13.25 ± 0.63 abcde	4.12 ± 0.37 cdefgh
M11	487.300 ± 31.901 ab	12.59 ± 0.75 abcd	3.85 ± 0.47 abcdefg
M12	487.300 ± 61.086 ab	11.46 ± 1.09 abc	3.82 ± 0.33 abcdefg
M13	718.767 ± 51.891 h	11.15 ± 0.83 abc	3.06 ± 0.27 ab
M14	426.387 ± 44.880 a	13.92 ± 0.94 bcdef	3.96 ± 0.47 bcdefgh
M15	670.037 ± 74.673 defgh	11.32 ± 1.09 abc	3.18 ± 0.27 abcd
M16	657.854 ± 44.165 cdefgh	11.29 ± 0.73 abc	3.13 ± 0.19 abc
M17	572.577 ± 83.265 abcdefgh	12.24 ± 1.65 abcd	3.26 ± 0.45 abcd
M18	487.300 ± 68.915 ab	15.16 ± 0.90 def	4.79 ± 0.30 ghi
M19	548.212 ± 82.240 abcdef	13.51 ± 0.88 abcdef	4.51 ± 0.13 fghi
M20	523.847 ± 55.062 abcd	12.07 ± 1.19 abc	3.66 ± 0.45 abcdef
M21	511.664 ± 35.667 abc	13.52 ± 1.08 abcdef	4.34 ± 0.37 efghi
M22	511.664 ± 44.165 abc	16.35 ± 1.53 f	4.05 ± 0.33 bcdefgh
M23	560.394 ± 51.274 abcdefg	15.71 ± 1.34 ef	4.13 ± 0.49 defgh
M24	560.394 ± 24.365 abcdefg	12.55 ± 0.74 abcd	3.75 ± 0.23 abcdef
M25	584.759 ± 45.115 bcdefgh	13.87 ± 1.04 bcdef	4.08 ± 0.25 cdefgh
M26	536.029 ± 52.095 abcde	15.05 ± 0.86 def	3.65 ± 0.41 abcdef
M27	670.037 ± 22.083 defgh	13.44 ± 1.90 abcdef	3.47 ± 0.39 abcde
p-value	0.0004**	0.0006**	0.0001**

Means with the same letter in a column are not significantly different ($p>0.05$) using Fisher PLSD.

In addition, the histological examinations displayed internal morphological characteristics of hop leaves for each genotype. No significant differences in thickness of leaves (Fig. 7.6A), major veins (Fig. 7.6B), cuticle layer, upper and lower epidermis (Table 7.5) among the 27 genotypes were detected ($p \geq 0.05$). The thickness ranged from 94.733 to 111.067 µm., 0.503 to 0.761 mm., 2.480 to 2.687 µm., 9.637 to 14.21 µm., and 8.003 to 10.13 µm. for leaves, major veins, cuticle, upper and lower epidermis, respectively.

Fig. 7.6. Thickness of leaves (A) and major leaf veins (B) of 27 hop genotypes studied.

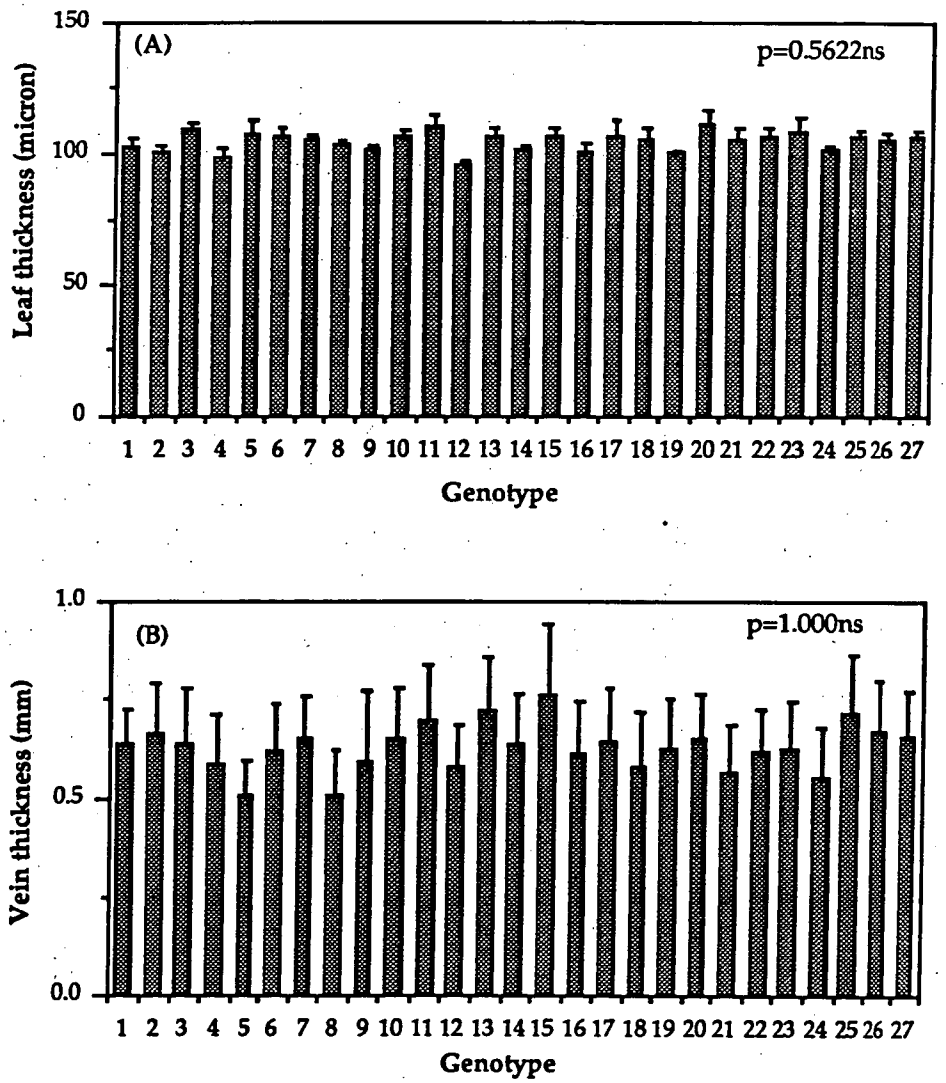


Table 7.5. Thickness of cuticle, upper and lower epidermis in leaves of each genotype studied.

Genotype	Means ± S.E.		
	Cutical thickness (micron.)	Upper epidermis (micron.)	Lower epidermis (micron.)
M1	2.687 ± 0.207	12.25 ± 1.67	9.147 ± 0.41
M2	2.521 ± 0.041	11.43 ± 1.63	9.473 ± 0.33
M3	2.521 ± 0.041	14.21 ± 1.86	9.473 ± 0.33
M4	2.480 ± 0.000	11.43 ± 1.63	8.657 ± 0.78
M5	2.687 ± 0.207	12.25 ± 1.67	9.473 ± 0.33
M6	2.521 ± 0.041	11.43 ± 1.63	9.637 ± 0.16
M7	2.521 ± 0.041	10.94 ± 0.82	9.310 ± 0.34
M8	2.563 ± 0.083	13.07 ± 2.07	9.637 ± 0.16
M9	2.480 ± 0.000	10.94 ± 0.82	9.800 ± 0.00
M10	2.480 ± 0.000	11.43 ± 1.63	9.473 ± 0.21
M11	2.480 ± 0.000	13.88 ± 1.97	9.473 ± 0.33
M12	2.480 ± 0.000	9.637 ± 0.16	9.310 ± 0.33
M13	2.480 ± 0.000	13.88 ± 1.97	8.003 ± 0.99
M14	2.480 ± 0.000	13.07 ± 2.07	9.228 ± 0.41
M15	2.521 ± 0.041	12.25 ± 1.67	9.147 ± 0.49
M16	2.563 ± 0.083	11.27 ± 1.67	8.738 ± 0.48
M17	2.521 ± 0.041	11.43 ± 1.63	10.13 ± 1.03
M18	2.521 ± 0.041	9.800 ± 0.00	9.637 ± 0.16
M19	2.521 ± 0.041	9.800 ± 0.00	9.473 ± 0.33
M20	2.687 ± 0.207	12.25 ± 1.67	9.800 ± 0.00
M21	2.563 ± 0.083	11.43 ± 1.63	9.147 ± 0.41
M22	2.480 ± 0.000	10.62 ± 0.82	9.800 ± 0.00
M23	2.687 ± 0.207	11.43 ± 1.63	9.473 ± 0.33
M24	2.480 ± 0.000	11.43 ± 1.63	9.392 ± 0.41
M25	2.480 ± 0.000	9.800 ± 0.00	9.800 ± 0.00
M26	2.480 ± 0.000	10.62 ± 0.82	9.637 ± 0.16
M27	2.480 ± 0.000	10.62 ± 0.82	9.800 ± 0.00
p-value	0.8846ns	0.8272ns	0.4356ns

Table 7.6 shows mean dry : wet weight ratios for each hop genotype. Highly significant differences in moisture content were found among these genotypes studied ($p \leq 0.01$). M2 had the highest percentage followed by M6, M13 and M24, with M22 having the lowest percentage compared with other genotypes.

Table 7.6. Mean ratio of dry : wet weight in leaves of 27 hop genotypes (expressed as a percentage).

Genotype	Percent dry weight (Means + S.E.)
M1	25.832 ± 0.678 ab
M2	30.276 ± 0.939 k
M3	28.540 ± 0.322 defghijk
M4	26.744 ± 0.556 abcde
M5	26.256 ± 0.411 abc
M6	29.919 ± 1.116 jk
M7	26.431 ± 1.193 abcd
M8	26.769 ± 1.184 abcde
M9	29.158 ± 0.879 ghijk
M10	27.809 ± 0.871 bcdefghij
M11	26.711 ± 0.610 abcde
M12	28.996 ± 0.891 fghijk
M13	29.665 ± 1.110 ijk
M14	27.264 ± 0.503 abcdefg
M15	27.401 ± 1.020 abcdefgh
M16	28.646 ± 0.507 efghijk
M17	27.081 ± 0.766 abcdefg
M18	28.531 ± 0.508 defghijk
M19	28.251 ± 0.369 cdefghijk
M20	26.161 ± 0.573 abc
M21	29.137 ± 0.929 ghijk
M22	25.457 ± 0.419 a
M23	27.746 ± 0.600 bcdefghi
M24	29.441 ± 0.476 hijk
M25	26.900 ± 0.768 abcdef
M26	27.830 ± 0.751 bcdefghij
M27	27.216 ± 0.728 abcdefg
p-value	0.0001**

7.3.1.2. Different sources of leaves: A comparison of morphological characteristics between field and glasshouse hop leaves is summarized in Table 7.7 which shows the means for each feature. According to t-tests, significant differences ($p \leq 0.05$) between these two sources of leaves were found for ventral gland density, trichome density, total density of glands and trichomes, percentage of trichome areas, total percentage of gland and trichome areas, stomatal density, stomatal sizes, leaf thickness, vein thickness, and thicknesses of both the upper and lower epidermis. It was also apparent that there were no significant differences in gland

diameters, gland areas, trichome basal diameters, trichome basal areas, percentage of gland areas, trichome lengths and cuticle thickness between glasshouse and field hop leaves ($p \geq 0.05$).

Table 7.7. Comparison of morphological characteristics between field and glasshouse hop leaves.

Morphological characteristics	Source of leaves (Means + S.E.)		p-value
	Glasshouse	Field	
Density of ventral glands per mm^2	3.745 ± 0.369	2.867 ± 0.109	0.0046**
Density of trichomes per mm^2	3.424 ± 0.550	1.546 ± 0.180	0.0002**
Gland diameter (micron.)	143.222 ± 3.448	148.389 ± 1.426	0.1717ns
Gland area (micron.^{2})	16359.931 ± 775.829	17558.085 ± 340.899	0.1815ns
Trichome basal diameter (micron.)	62.863 ± 2.379	59.722 ± 1.561	0.3704ns
Trichome basal area (micron.^{2})	3211.730 ± 245.285	3015.092 ± 162.540	0.5894ns
Number of ventral glands and trichomes per mm^2	7.169 ± 0.618	4.413 ± 0.217	0.0001**
Percentage of gland area per mm^2	6.092 ± 0.583	5.044 ± 0.212	0.0677ns
Percentage of trichome area per mm^2	4.330 ± 0.758	1.833 ± 0.234	0.0002**
Pooled percentage of gland and trichome area per mm^2	10.422 ± 1.011	6.877 ± 0.331	0.0001**
Density of stomata per mm^2	418.717 ± 23.156	600.401 ± 12.157	0.0001**
Length of stomata (micron.)	16.492 ± 0.537	12.451 ± 0.239	0.0001**
Width of stomata (micron.)	4.295 ± 0.173	3.766 ± 0.089	0.0228*
Leaf thickness (micron.)	101.72 ± 1.036	113.244 ± 2.359	0.0001**
Vein thickness (mm)	0.735 ± 0.018	1.127 ± 0.032	0.0001**
Thickness of upper epidermis (micron)	9.963 ± 0.112	15.970 ± 0.721	0.0001**
Thickness of lower epidermis (micron.)	8.902 ± 0.127	9.981 ± 0.181	0.0001**
Trichome length (micron.)	362.963 ± 16.669	376.756 ± 22.652	0.6298ns
Cuticle thickness (micron.)	2.544 ± 0.019	2.664 ± 0.086	0.0754ns

Between old and young leaves, significant differences ($p \leq 0.05$) were detected for ventral gland density, gland diameters, gland area, trichome basal area, total density of glands and trichomes, percentage of

gland area, total percentage of gland and trichome areas, stomatal density, vein thickness, trichome length, cuticle thickness, and thicknesses of both the upper and lower epidermis (Table 7.8). Nevertheless, the variation in trichome density, stomatal size and leaf thickness was not significant ($p \geq 0.05$).

Table 7.8. Comparison of morphological characteristics between young and old hop leaves.

Morphological characteristics	Source of leaves (Means + S.E.)		p-value
	Young	Old	
Density of ventral glands per mm^2	7.459 ± 0.778	2.867 ± 0.109	0.0001**
Density of trichomes per mm^2	2.170 ± 0.425	1.546 ± 0.180	0.1889ns
Gland diameter (micron.)	137.901 ± 2.543	148.389 ± 1.426	0.0045**
Gland area (micron^2)	15073.866 ± 571.794	17558.085 ± 340.899	0.0047**
Trichome basal diameter (micron.)	48.356 ± 2.005	59.722 ± 1.561	0.0012**
Trichome basal area (micron^2)	1913.030 ± 142.896	3015.092 ± 162.540	0.0021**
Number of ventral glands and trichomes per mm^2	9.629 ± 0.716	4.413 ± 0.217	0.0001**
Percentage of gland area per mm^2	11.148 ± 1.176	5.044 ± 0.212	0.0001**
Percentage of trichome area per mm^2	1.641 ± 0.345	1.833 ± 0.234	0.7443ns
Combined percentage of gland and trichome area per mm^2	12.789 ± 1.095	6.877 ± 0.331	0.0001**
Density of stomata per mm^2	523.396 ± 27.599	600.401 ± 12.157	0.0166*
Length of stomata (micron.)	12.238 ± 0.494	12.451 ± 0.239	0.7305ns
Width of stomata (micron.)	4.192 ± 0.195	3.766 ± 0.089	0.0692ns
Leaf thickness (micron.)	102.719 ± 0.863	101.720 ± 1.036	0.4621ns
Vein thickness (mm)	0.384 ± 0.010	0.735 ± 0.018	0.0001**
Thickness of upper epidermis (micron.)	11.191 ± 0.378	9.963 ± 0.112	0.0103*
Thickness of lower epidermis (micron.)	9.558 ± 0.111	8.902 ± 0.127	0.0002**
Trichome length (micron.)	309.002 ± 12.918	362.963 ± 16.669	0.0108*
Cuticle thickness (micron.)	2.480 ± 0.000	2.544 ± 0.019	0.0001**

7.3.2. Leaf morphological characteristics and hop susceptibility to TSSM

The relationships between leaf morphological characteristics of the hop genotypes studied and their susceptibility to TSSM were investigated by using the results from the present work to correlate with those from Chpters 4 and 5. Table 7.9 presents the linear regression equations for each leaf morphology and the intrinsic rates of increase from the antibiosis test of the 27 genotypes in Chapter 4. It was found that these relationships were not significant.

Table 7.9. Linear regression of intrinsic rates of increase (Y) on morphological characteristics of leaves (X) for 27 hop genotypes.

Morphological characteristics	Equation (Y = a + bX)	Coefficient of determination (r^2)
Density of ventral glands per mm^2	Y = 0.25726 - 5.0907e-3X	0.066
Density of trichomes per mm^2	Y = 0.24572 - 3.5150e-3X	0.062
Gland diameter	Y = 0.27335 - 2.3329e-4X	0.019
Gland area	Y = 0.25629 - 1.0003e-6X	0.020
Trichome basal diameter	Y = 0.23962 - 7.4520e-6X	0.000
Trichome basal area	Y = 0.24250 - 2.9622e-7X	0.002
Number of ventral glands and trichomes per mm^2	Y = 0.25905 - 3.6725e-3X	0.112
Percentage of gland area per mm^2	Y = 0.25704 - 3.0063e-3X	0.084
Percentage of trichome area per mm^2	Y = 0.24205 - 1.3521e-3X	0.016
Combined percentage of gland and trichome area per mm^2	Y = 0.25433 - 1.8796e-3X	0.074
Density of stomata per mm^2	Y = 0.23082 + 1.4725e-5X	0.004
Length of stomata	Y = 0.22625 + 1.0006e-3X	0.008
Width of stomata	Y = 0.26875 - 7.6091e-3X	0.058
Leaf thickness	Y = 0.12975 + 1.0509e-3X	0.045
Vein thickness	Y = 0.22569 + 2.1600e-2X	0.005
Thickness of upper epidermis	Y = 0.19040 + 4.2133e-3X	0.081
Thickness of lower epidermis	Y = 0.22531 + 1.4743e-3X	0.001
Trichome length	Y = 0.23653 + 7.8495e-6X	0.001
Cuticle thickness	Y = 0.28130 - 1.6633e-2X	0.004
Percentage of weight ratio	Y = 0.24207 - 1.0388e-4X	0.000

When the leaf morphology of the 27 genotypes were correlated with pre-reproductive period and net reproductive rates, similar results

were also obtained (Table 7.10 and 7.11). The relationships between these reproductive parameters of TSSM and the leaf morphology of hops were not significant. The coefficient of determination (r^2) ranged from 0.000 to 0.108 and 0.000 to 0.193 for the pre-reproductive period and net reproduction rates, respectively.

Table 7.10. Linear regression of pre-reproductive period (Y) on morphological characteristics of leaves (X) for 27 hop genotypes.

Morphological characteristics	Equation (Y = a + bX)	Coefficient of determination (r^2)
Density of ventral glands per mm^2	Y = 12.068 - 1.7997e-2X	0.001
Density of trichomes per mm^2	Y = 11.807 + 0.10576X	0.076
Gland diameter	Y = 11.397 + 4.1426e-3X	0.008
Gland area	Y = 11.666 + 1.9749e-5X	0.010
Trichome basal diameter	Y = 10.776 + 2.1167e-2X	0.108
Trichome basal area	Y = 11.422 + 5.1918e-5X	0.102
Number of ventral glands and trichomes per mm^2	Y = 11.689 + 5.8245e-2X	0.038
Percentage of gland area per mm^2	Y = 11.962 + 7.0986e-3X	0.001
Percentage of trichome area per mm^2	Y = 11.844 + 7.5370e-2X	0.067
Combined percentage of gland and trichome area per mm^2	Y = 11.727 + 3.4320e-2X	0.034
Density of stomata per mm^2	Y = 12.247 - 4.2747e-4X	0.005
Length of stomata	Y = 11.944 + 4.5859e-3X	0.000
Width of stomata	Y = 11.410 + 0.15280X	0.032
Leaf thickness	Y = 13.007 - 9.6379e-7X	0.005
Vein thickness	Y = 13.522 - 2.4296X	0.083
Thickness of upper epidermis	Y = 12.392 - 3.3531e-2X	0.007
Thickness of lower epidermis	Y = 12.972 - 0.10288X	0.008
Trichome length	Y = 11.832 + 5.0854e-4X	0.004
Cuticle thickness	Y = 7.8423 + 1.6435X	0.054
Percentage of weight ratio	Y = 11.490 + 1.8478e-2X	0.002

Table 7.11. Linear regression of net reproductive rates (Y) on morphological characteristics of leaves (X) for 27 hop genotypes.

Morphological characteristics	Equation (Y = a + bX)	Coefficient of determination (r^2)
Density of ventral glands per mm^2	Y = 48.708 - 3.0682e-2X	0.000
Density of trichomes per mm^2	Y = 51.594 - 1.6116X	0.024
Gland diameter	Y = 51.276 - 1.8281e-2X	0.000
Gland area	Y = 50.423 - 1.0671e-4X	0.000
Trichome basal diameter	Y = 51.560 - 5.1063e-2X	0.001
Trichome basal area	Y = 52.784 - 3.7374e-4X	0.007
Number of ventral glands and trichomes per mm^2	Y = 53.903 - 0.98055X	0.015
Percentage of gland area per mm^2	Y = 47.288 + 0.22081X	0.001
Percentage of trichome area per mm^2	Y = 50.714 - 0.99715X	0.016
Combined percentage of gland and trichome area per mm^2	Y = 51.147 - 0.31618X	0.004
Density of stomata per mm^2	Y = 61.142 - 2.2081e-2X	0.018
Length of stomata	Y = 1.1176 + 3.6723X	0.193
Width of stomata	Y = 47.487 + 0.28611X	0.000
Leaf thickness	Y = -36.273 + 0.81498X	0.051
Vein thickness	Y = 13.522 - 2.4296X	0.083
Thickness of upper epidermis	Y = 56.065 - 0.64485X	0.004
Thickness of lower epidermis	Y = 11.174 + 3.9772X	0.016
Trichome length	Y = 33.626 + 4.4261e-2X	0.038
Cuticle thickness	Y = 129.96 - 32.133X	0.029
Percentage of weight ratio	Y = 127.63 - 2.8443X	0.077

Using the data of only four genotypes, M4, M9, M26, and M27 to represent varying levels of mite susceptibility, the relationships between the leaf morphology and the three reproductive parameters mentioned above were found to be better than those for all the 27 genotypes (Table 7.12, 7.13, and 7.14). The coefficient of determination (r^2) varied from 0.040 to 0.981, 0.004 to 0.983, and 0.001 to 0.964 for intrinsic rates of increase, pre-reproductive period and net reproductive rates, respectively. Nevertheless, the cuticle thickness could not be correlated with these

reproductive parameters because the four genotypes selected had the same thickness of cuticle layer. It was evident that trichome density was positively correlated with the pre-reproductive period and was negatively correlated with the intrinsic rates of increase as well as the net reproductive rates, indicating that TSSM populations grew faster on genotypes with sparse trichomes than on those with dense trichomes. Other morphological characteristics showed no consistent relationships with the three reproductive parameters.

Table 7.12. Linear regression of intrinsic rates of increase (Y) on morphological characteristics of leaves (X) for 4 hop genotypes.

Morphological characteristics	Equation (Y = a + bX)	Coefficient of determination (r^2)
Density of ventral glands per mm^2	Y = 0.29757 - 9.5179e-3X	0.291
Density of trichomes per mm^2	Y = 0.27839 - 6.6973e-3X	0.795
Gland diameter	Y = 0.16246 + 6.4082e-4X	0.071
Gland area	Y = 0.19683 + 3.4696e-6X	0.104
Trichome basal diameter	Y = 0.62344 - 6.4281e-3X	0.848
Trichome basal area	Y = 0.35133 - 8.9608e-6X	0.737
Number of ventral glands and trichomes per mm^2	Y = 0.29294 - 4.8420e-3X	0.723
Percentage of gland area per mm^2	Y = 0.27275 - 2.0347e-3X	0.044
Percentage of trichome area per mm^2	Y = 0.27809 - 7.1466e-3X	0.792
Combined percentage of gland and trichome area per mm^2	Y = 0.29286 - 3.4272e-3X	0.453
Density of stomata per mm^2	Y = 0.27220 - 2.3607e-5X	0.017
Length of stomata	Y = 0.14199 + 8.8906e-3X	0.817
Width of stomata	Y = 0.37289 - 3.0301e-2X	0.569
Leaf thickness	Y = -0.14891 + 3.9670e-3X	0.858
Vein thickness	Y = 3.6243e-2 +0.35571X	0.981
Thickness of upper epidermis	Y = 0.64136 - 3.5192e-2X	0.765
Thickness of lower epidermis	Y = 0.11107 + 1.5475e-2X	0.301
Trichome length	Y = 0.19016 + 1.9848e-4X	0.692
Cuticle thickness	-	-
Percentage of weight ratio	Y = 0.33993 - 2.9655e-3X	0.040

Table 7.13. Linear regression of pre-reproductive period (Y) on morphological characteristics of leaves (X) for 4 hop genotypes.

Morphological characteristics	Equation (Y = a + bX)	Coefficient of determination (r^2)
Density of ventral glands per mm^2	Y = 011.259 + 9.0316e-2X	0.246
Density of trichomes per mm^2	Y = 11.420 + 7.0346e-2X	0.824
Gland diameter	Y = 12.416 - 5.2415e-3X	0.045
Gland area	Y = 12.156 - 2.9573e-5X	0.071
Trichome basal diameter	Y = 7.7450 + 6.8409e-2X	0.902
Trichome basal area	Y = 10.626 + 9.6745e-5X	0.807
Number of ventral glands and trichomes per mm^2	Y = 11.274 + 4.9852e-2X	0.720
Percentage of gland area per mm^2	Y = 11.497 + 1.8990e-2X	0.036
Percentage of trichome area per mm^2	Y = 11.422 + 7.5338e-2X	0.826
Combined percentage of gland and trichome area per mm^2	Y = 11.274 + 3.5455e-2X	0.456
Density of stomata per mm^2	Y = 11.561 + 1.2396e-4X	0.004
Length of stomata	Y = 12.837 - 9.2206e-2X	0.825
Width of stomata	Y = 10.367 + 0.33416X	0.649
Leaf thickness	Y = 15.945 - 4.2026e-2X	0.904
Vein thickness	Y = 13.924 - 3.6735X	0.983
Thickness of upper epidermis	Y = 7.5004 + 0.37946X	0.836
Thickness of lower epidermis	Y = 13.344 - 0.18015X	0.383
Trichome length	Y = 12.360 - 2.130e-3X	0.744
Cuticle thickness	-	-
Percentage of weight ratio	Y = 11.153 + 1.7456e-2X	0.013

Table 7.14. Linear regression of net reproductive periods (Y) on morphological characteristics of leaves (X) for 4 hop genotypes.

Morphological characteristics	Equation (Y = a + bX)	Coefficient of determination (r^2)
Density of ventral glands per mm^2	Y = 90.547 - 10.484X	0.964
Density of trichomes per mm^2	Y = 56.962 - 3.3488X	0.542
Gland diameter	Y = 100.90 - 0.36545X	0.063
Gland area	Y = 68.972 - 1.2754e-3X	0.038
Trichome basal diameter	Y = 118.72 - 1.2673X	0.090
Trichome basal area	Y = 60.432 - 1.3228e-3X	0.044
Number of ventral glands and trichomes per mm^2	Y = 68.589 - 3.0182X	0.766
Percentage of gland area per mm^2	Y = 86.886 - 5.4371X	0.851
Percentage of trichome area per mm^2	Y = 56.478 - 3.4558X	0.505
Combined percentage of gland and trichome area per mm^2	Y = 76.123 - 2.8754X	0.870
Density of stomata per mm^2	Y = 29.950 + 2.7074e-2X	0.061
Length of stomata	Y = 35.217 + 0.8752X	0.022
Width of stomata	Y = 84.00 - 9.8349X	0.163
Leaf thickness	Y = -105.70 + 1.4860X	0.328
Vein thickness	Y = -12.257 + 94.559X	0.189
Thickness of upper epidermis	Y = 142.34 - 8.7814X	0.130
Thickness of lower epidermis	Y = 15.416 + 3.2923X	0.037
Trichome length	Y = 44.931 + 4.9242e-3X	0.001
Cuticle thickness	-	-
Percentage of weight ratio	Y = 179.90 - 4.8058X	0.287

In addition, the relationships between the leaf morphology and the results from the screening of hop genotypes for resistance to TSSM in Chapter 5 are presented in Table 7.15, 7.16, and 7.17. It was apparent that

relatively poor fits to the linear regression equations were noted for each test of resistance type and the leaf morphology. The coefficient of determination (r^2) ranged from 0.001 to 0.163, 0.000 to 0.124, and 0.003 to 0.271 for a tolerance test under glasshouse conditions, a preference test under glasshouse conditions, and an avoidance test under field conditions, respectively.

Table 7.15. Linear regression of tolerance test under glasshouse conditions in 1990/91 (Y) on morphological characteristics of leaves (X) for 26 hop genotypes.

Morphological characteristics	Equation (Y = a + bX)	Coefficient of determination (r^2)
Density of ventral glands per mm^2	Y = 2.4827 + 0.11249X	0.036
Density of trichomes per mm^2	Y = 3.2138 - 0.17243X	0.163
Gland diameter	Y = 1.4349 + 9.8959e-3X	0.040
Gland area	Y = 2.1060 + 4.5504e-5X	0.047
Trichome basal diameter	Y = 3.2119 - 5.6340e-3X	0.006
Trichome basal area	Y = 3.1011 - 1.9237e-5X	0.012
Number of ventral glands and trichomes per mm^2	Y = 3.2646 - 6.9319e-2X	0.043
Percentage of gland area per mm^2	Y = 2.3868 + 8.3451e-2X	0.073
Percentage of trichome area per mm^2	Y = 3.0558 - 7.8416e-2X	0.029
Combined percentage of gland and trichome area per mm^2	Y = 2.8425 + 5.1747e-3X	0.001
Density of stomata per mm^2	Y = 3.4447 - 9.9284e-4X	0.020
Length of stomata	Y = 1.8564 + 7.9643e-2X	0.055
Width of stomata	Y = 3.0053 - 3.0943e-2X	0.001
Leaf thickness	Y = -1.7547 + 4.4583e-2X	0.092
Vein thickness	Y = 3.1793 - 0.47242X	0.003
Thickness of upper epidermis	Y = 3.0105 - 1.0835e-2X	0.001
Thickness of lower epidermis	Y = 1.9493 + 9.9558e-2X	0.006
Trichome length	Y = 2.6787 + 6.0985e-4X	0.004
Cuticle thickness	Y = -1.1093 + 1.5761X	0.041
Percentage of weight ratio	Y = 1.2437 + 5.9015e-2X	0.020

Table 7.16. Linear regression of preference test under glasshouse conditions in 1990 (Y) on morphological characteristics of leaves (X) for 26 hop genotypes.

Morphological characteristics	Equation (Y = a + bX)	Coefficient of determination (r^2)
Density of ventral glands per mm^2	Y = 456.87 + 116.12X	0.043
Density of trichomes per mm^2	Y = 924.38 - 27.595X	0.005
Gland diameter	Y = -265.18 + 7.7602X	0.028
Gland area	Y = 290.57 + 3.3964e-2X	0.029
Trichome basal diameter	Y = 931.17 - 1.0238X	0.000
Trichome basal area	Y = 994.29 - 1.0892e-2X	0.004
Number of ventral glands and trichomes per mm^2	Y = 762.13 + 19.988X	0.004
Percentage of gland area per mm^2	Y = 324.47 + 91.743X	0.100
Percentage of trichome area per mm^2	Y = 898.29 - 12.186X	0.002
Combined percentage of gland and trichome area per mm^2	Y = 576.90 + 36.180X	0.035
Density of stomata per mm^2	Y = 1825.4 - 1.6906X	0.067
Length of stomata	Y = -585.75 + 112.89X	0.124
Width of stomata	Y = 731.81 + 35.851X	0.002
Leaf thickness	Y = -582.10 + 13.970X	0.010
Vein thickness	Y = 1452.6 - 931.20X	0.012
Thickness of upper epidermis	Y = 1566.6 - 59.830X	0.021
Thickness of lower epidermis	Y = -907.01 + 189.33X	0.024
Trichome length	Y = 92.825 + 2.3062X	0.071
Cuticle thickness	Y = 569.52 + 119.24X	0.000
Percentage of weight ratio	Y = 1410.3 - 19.369X	0.002

Table 7.17. Linear regression of avoidance test under field conditions in 1991/92 season (Y) on morphological characteristics of leaves (X) for 24 hop genotypes.

Morphological characteristics	Equation (Y = a + bX)	Coefficient of determination (r^2)
Density of ventral glands per mm^2	Y = 0.13880 + 0.25066X	0.039
Density of trichomes per mm^2	Y = 1.5626 - 0.28511X	0.103
Gland diameter	Y = 1.8794 - 5.9161e-3X	0.003
Gland area	Y = 1.4962 - 2.8270e-5X	0.004
Trichome basal diameter	Y = 3.1872 - 3.7063e-2X	0.062
Trichome basal area	Y = 2.1085 - 9.5223e-5X	0.063
Number of ventral glands and trichomes per mm^2	Y = 1.5576 - 0.10010X	0.021
Percentage of gland area per mm^2	Y = 0.59933 + 7.1849e-2X	0.011
Percentage of trichome area per mm^2	Y = 1.3841 - 0.16535X	0.083
Combined percentage of gland and trichome area per mm^2	Y = 1.3455 - 4.1153e-2X	0.009
Density of stomata per mm^2	Y = -0.71533 + 3.0662e-3X	0.046
Length of stomata	Y = 2.1808 - 9.1189e-2X	0.016
Width of stomata	Y = 3.2160 - 0.56356X	0.084
Leaf thickness	Y = -2.5138 + 3.3949e-2X	0.013
Vein thickness	Y = -2.7954 + 6.1626X	0.095
Thickness of upper epidermis	Y = -2.4998 + 0.29961X	0.096
Thickness of lower epidermis	Y = 14.456 - 1.4347X	0.271
Trichome length	Y = -0.11818 + 3.3649e-3X	0.028
Cuticle thickness	Y = 9.0930 - 3.1820X	0.038
Percentage of weight ratio	Y = -8.0492 + 0.32556X	0.142

7.3.3. Morphological responses of hop leaves to mite infestations

The upper and lower surface of leaf discs infested by TSSM are presented in Plate 6 and 7, respectively. A two-way analysis of variance showed no significant differences ($p > 0.05$) in mean daily egg deposition between different hop genotype (Table 7.18). It was also found that the mite density studied had no significant effects on fecundity and the interaction between genotype and density was not significant ($p > 0.05$).

Mean number of eggs per female per day ranged from 9.271 on M4 to 10.133 on M26 (Fig. 7.7A). Under different densities, the mean number of eggs was 9.238-10.167 at densities of 10-5 mites per leaf disc, respectively (Fig. 7.7B).

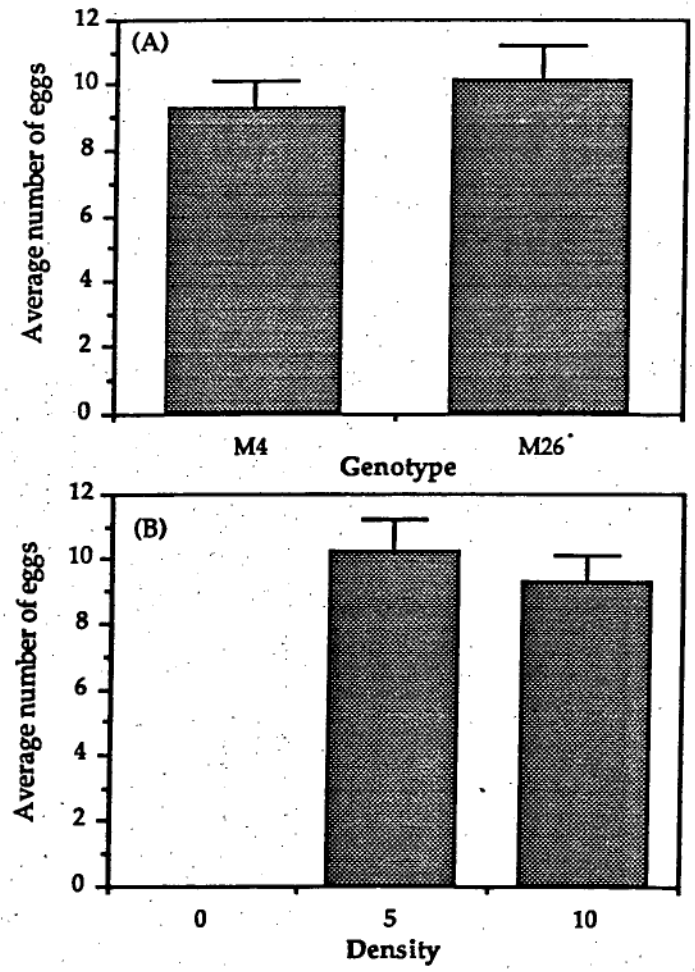
Plate 6. The upper surface of leaf discs infested by TSSM at 287X.

Plate 7. The lower surface of leaf discs infested by TSSM at 163X.

Table 7.18. Analysis of variance of number of eggs laid per female per day on two hop genotypes under different densities.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Genotype (A)	1	0.113	0.113	0.176	.6768
Density (B)	1	0.203	0.203	0.317	.5763
AB	1	0.003	0.003	0.005	.9454
Error	44	28.199	0.641		

Fig. 7.7. Average number of eggs on each genotype (A) under different densities (B).



For external leaf scarring, there were significant differences ($p \leq 0.05$) in mean number of yellow specks between the two hop genotypes

studied (Table 7.19). Highly significant differences among different mite densities were detected for the number of yellow specks ($p \leq 0.01$). However, the interaction between genotypes and densities was not significant ($p \geq 0.05$). Average number of yellow specks varied from 64.583 to 83.250 on M4 and M26, respectively (Fig. 7.8A). It was evident that a significantly greater number of scarred leaf surface resulted from each increase in mite density (Fig. 7.8B).

According to analysis of variance, significant differences in stomatal opening stemming from the underlying tissue injury were found between M4 and M26 (Table 7.20). However, the average number of open stomata did not vary significantly ($p \geq 0.05$) among different mite densities. Fig. 7.9A shows that the average number of open stomata was approximately three times greater on leaf discs of M4 than on those of M26. Even though mean stomatal opening decreased with an increase in mite density (Fig. 7.9B), none of these differences were significant ($p \geq 0.05$), indicating that mite density is not an important factor in determining stomatal opening.

Two types of stomatal size studied include stomatal pore length and stomatal pore width. There were no significant differences in stomatal pore length between the genotypes selected (Table 7.21). It was also found that the variation in stomatal pore length among different mite densities was not significant. The average length of stomata ranged from 9.233 to 10.749 μm on M4 and M26, respectively (Fig. 7.10A). Mean stomatal pore lengths was 10.618, 10.341, and 8.964 at densities of 0, 5, and 10 mites per leaf disc, respectively (Fig. 7.10B). For stomatal pore width, the variation between different genotypes or densities was not significant (Table 7.22). In addition, average widths of stomata for each genotype or density are shown in Fig. 7.11.

Table 7.19. Analysis of variance of number of yellow specks on hop leaves between different genotypes under various densities.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Genotype (A)	1	2090.67	2090.67	4.542	.0471
Density (B)	2	87827.08	43913.54	95.412	.0001
AB	2	1425.58	712.79	1.549	.2395
Error	18	8284.50	460.25		

Fig. 7.8. Average number of yellow specks on hop leaves for each genotype (A) under different densities (B).

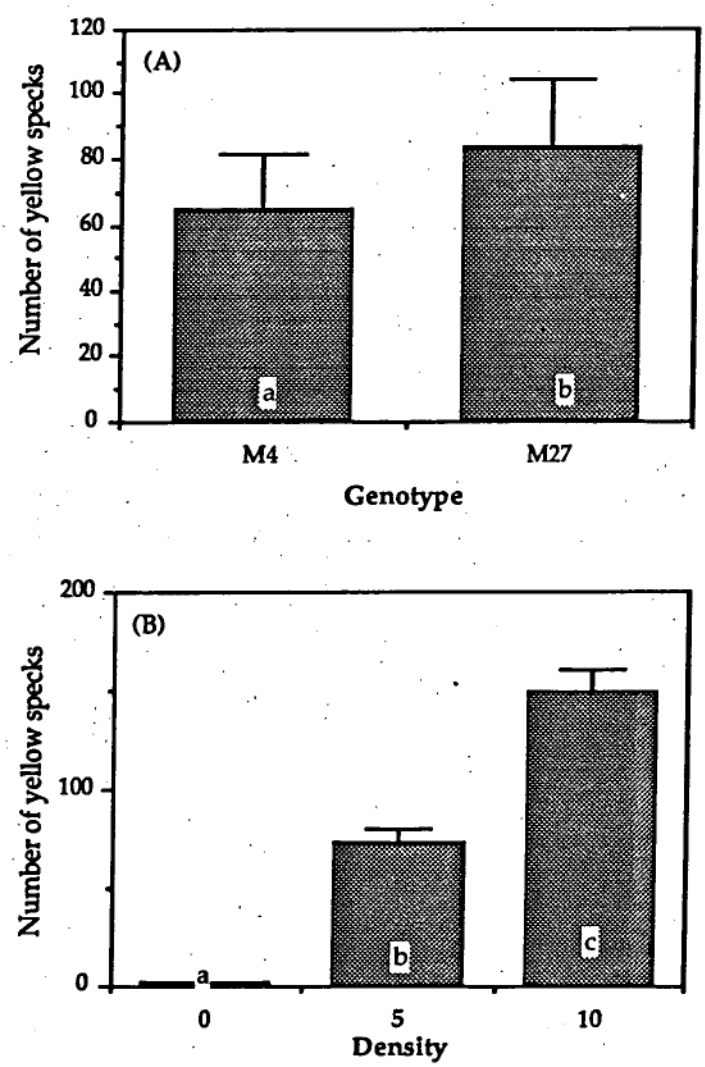


Table 7.20. Analysis of variance of number of open stomata on hop leaves between different genotypes under various densities.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Genotype (A)	1	299277.985	299277.985	43.63	.0001
Density (B)	2	39227.676	19613.838	2.86	.0835
AB	2	20825.790	10412.895	1.52	.2459
Error	18	123470.719	6859.484		

Fig. 7.9. Average number of open stomata on hop leaves for each genotype (A) under three different densities (B).

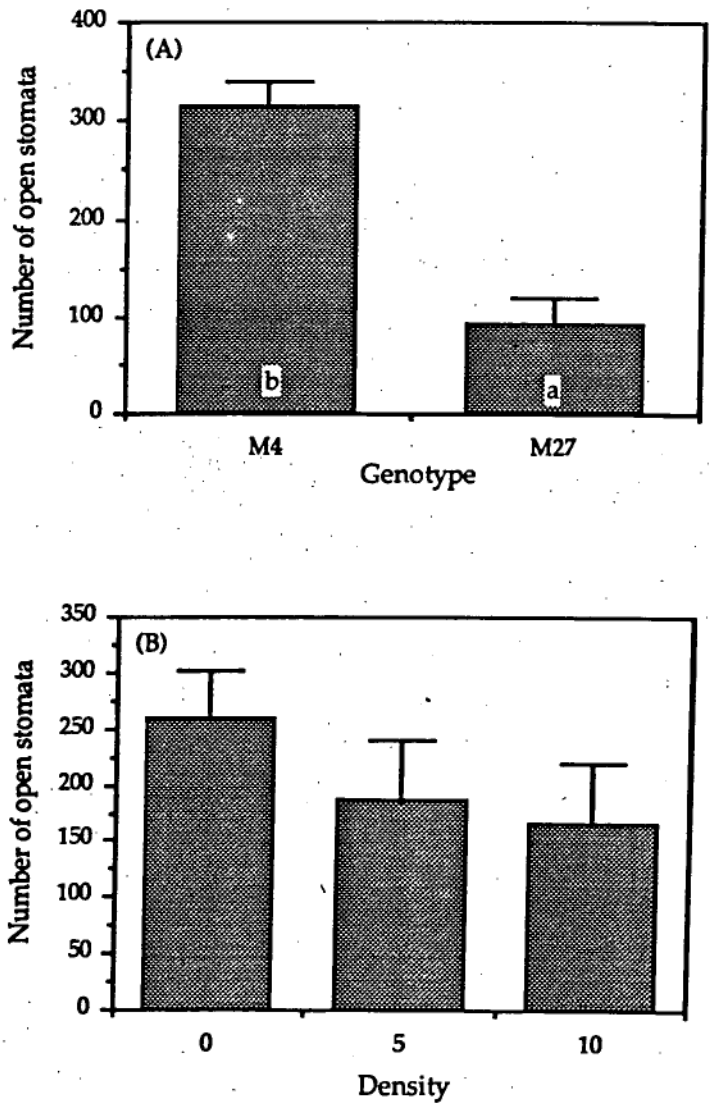


Table 7.21. Analysis of variance of length of stomata on hop leaves between different genotypes under various densities.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Genotype (A)	1	13.588	13.588	3.787	.0684
Density (B)	2	12.941	6.471	1.803	.1949
AB	2	4.362	2.181	0.608	.5559
Error	17	60.995	3.588		

Fig. 7.10. Average length of stomata on hop leaves for each genotype (A) under different densities (B).

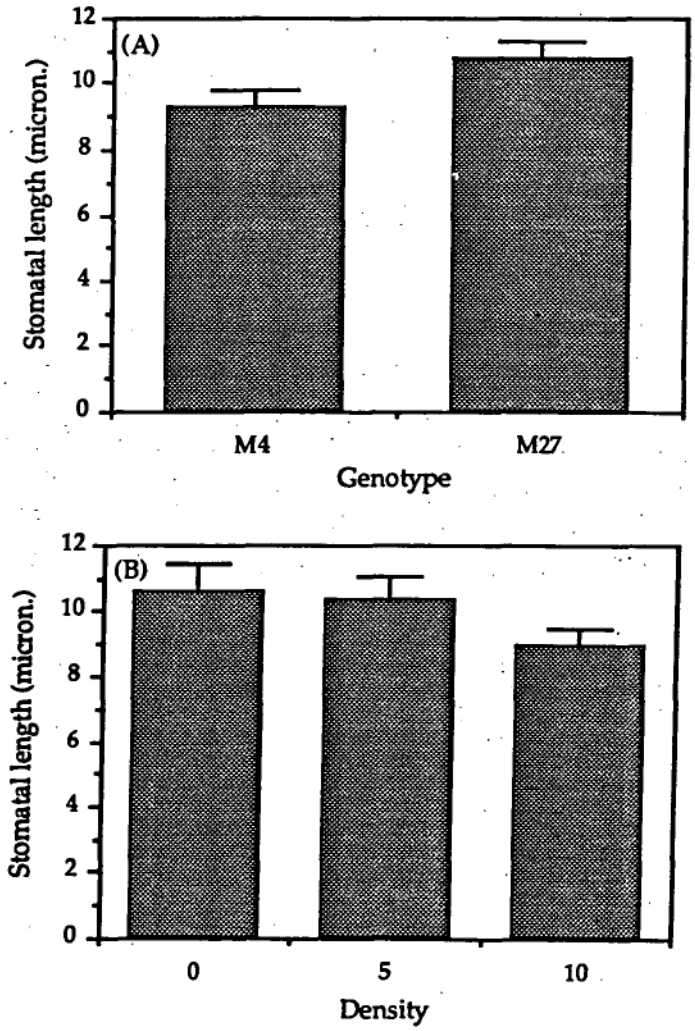
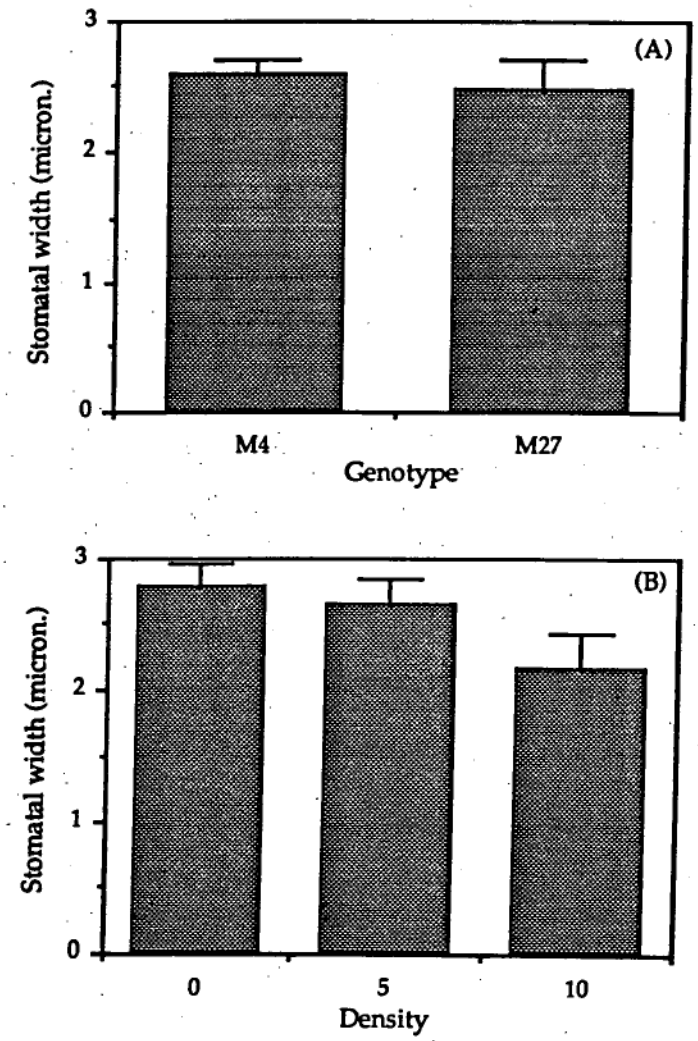


Table 7.22. Analysis of variance of width of stomata on hop leaves between different genotypes under various densities.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Genotype (A)	1	0.058	0.058	0.230	.6379
Density (B)	2	1.752	0.876	3.450	.0553
AB	2	2.153	1.076	4.239	.0321
Error	17	4.317	0.254		

Fig. 7.11. Average width of stomata on hop leaves for each genotype (A) under three different densities (B).



7.4. DISCUSSION

7.4.1. Leaf morphology

The present study has shown that there is morphological variation in external and internal characteristics of hop leaves among different genotypes. Significant differences were found in ventral gland size, trichome density, trichome size, length of trichomes, stomatal density, stomatal size and moisture content. Furthermore, it was apparent that some morphological characteristics of the hop leaves collected from the same genotype varied significantly according to leaf age and growing conditions. These were densities of ventral glands and trichomes, sizes of ventral glands and trichomes, trichome length, stomatal density, stomatal size, leaf thickness, major vein thickness, thicknesses of upper and lower epidermis and cuticle thickness.

According to Burgess (1964), ventral glands and trichomes have been reported to be more dense on some hop cultivars than others. A subsequent investigation by Peters and Berry (1980b), working with American and European hops, also confirmed this phenomenon.

Generally, lupulin glands containing resins and essential oils are found on the underside of hop leaves. These ventral glands vary from 120 to 190 microns in diameter (Brooks and Likens, 1962). This is in agreement with the results from the present study which show that the average diameters of ventral glands for the 27 genotypes used ranged from 128.72 to 170.74 microns.

In addition to the ventral glands, hop leaves are covered with nonglandular trichomes. These trichomes usually grow on the leaf surface and/or leaf veins. The venation of the leaves is palmate and the major veins protrude from the underside of the leaves. For anatomical structures, the hop leaves have a thin layer of mesophyll with a palisade parenchyma of only one stratum consisting of dilated cells with a

thickness to length ratio of 1 : 6. The upper epidermis is made up of large rectangular cells covered with a thin cuticle. The palisade layer consists of the cells transferring the assimilates and below it, the layers of spongy parenchyma have globular cells and large intercellular spaces. The lower epidermis contains small cells covered with thin cuticle penetrated in places by cellular pores (stomata). There are approximately 400 stomata per mm^2 on the underside of hop leaves providing for very intensive metabolism (Rybacek, 1991). In the present study, it was found that the average number of stomata for the genotypes used varied from 426.37 to 718.74 per mm^2. This variation in stomatal density may have resulted from differences in leaf surface areas among the hop genotypes as mentioned in Chapter 4.

The results from the present study also show differences in leaves collected from different sources according to leaf age and growing conditions. When comparing the morphological characteristics of glasshouse versus field hop leaves, it was found that the leaves collected from the glasshouse had more densely occurring ventral trichomes and glands than the leaves from the field, while the cell-layer thicknesses of the glasshouse leaves were less than those of the field leaves. For the comparison of morphological characteristics between young and old leaves, the numbers of ventral trichomes and glands per unit area were found more sparsely on old leaves than on young leaves, while the thicknesses of cell layer with the exception of epidermal cells were less in the young leaves than in the old ones.

In addition, it was apparent that the susceptibility of hop plants to TSSM was lowest on genotypes with the highest density of ventral trichomes and with the trichomes of the shortest average length, whereas it was highest on the genotypes with greatest length and the lowest density of trichomes, i.e., M4 < M9 < M26 < M27. However, other

genotypes showed intermediate situation. Hoxie et al. (1975), working with a cereal leaf beetle, *Oulema melanopus* (L.), on several wheat lines, demonstrated the relationship between length and density of wheat trichomes relative to the survival of newly hatched cereal leaf beetle larvae and relative to oviposition preference. Subsequently, Campbell et al. (1984) also found that trichome length and density within species of wheatgrasses (*Agropyron sp.*) were negatively correlated with feeding behaviour of the early instars of black grass bugs, *Labops hesperius* Uhler.

Esau (1965) suggests that trichomes are unicellular or pluricellular outgrowths from the epidermis of plant organs. In general, the trichome cover of individual plants varies in quantity (trichome size and density) and quality (trichome type) from organ to organ, and from tissue to tissue. A dense covering commonly develops on young organs. Since the organs expand through growth, the original trichomes are spaced further and further apart, and if no more new ones are produced, a sparse trichome cover of a plant surface will happen at maturity (Johnson, 1975).

Khan et al. (1986) also stated that the number of trichomes per unit area on the youngest leaves is higher than on their fully expanded older counterpart leaves because of their smaller size. Pillemer and Tingey (1976), working with broad beans *Vicia faba* L., found that mature leaves on the lower nodes had fewer hooked trichomes than mature leaves on the upper nodes and that this difference was consistent with increased leafhopper capture and capture mortality on the upper nodes. In their study, trichome density and capture mortality were found to be at a maximum on the unexpanded terminal leaves. This reveals the greatest pest protection for the tender and succulent plant tissues.

For hop plants, the young leaves were usually not attacked by TSSM (Cao, 1989). This may be due to the effect of trichome density as mentioned above. Johnson (1975) suggests that comparatively little

damage by insect pests takes place on young leaves still covered with pubescence.

7.4.2. Leaf morphological characteristics and hop susceptibility to TSSM

Numerous attempts have been made to establish a statistical correlation between the morphological characteristics of plants and resistance to their pests. It has long been assumed that several structural features of plant surfaces function to give the plant resistance to the attack of the pests (Gilbert, 1971). The features commonly found among resistant crop plants include trichomes and leaf toughness (Norris and Kogan, 1980).

Levin (1973) and Johnson (1975) discussed the ecological functions of trichomes as defence against plant pests. Dent (1991) suggested that when pubescence is present the mechanism of resistance may depend on one or more of four characteristics of the trichomes, their density, erectness, length, and shape. In addition some trichomes also possess glands, the exudates of which confer resistance against some pests.

Several investigators have identified significant relationships linking trichome density to pest resistance of crop plants. Gallun et al. (1973) found that pubescent varieties of wheat having more than 71 trichomes/mm^2 were less used for egg laying by the cereal leaf beetle *Oulema melanopus* L. than the plants with fewer trichomes. Wannamaker (1957) and Stephens (1959) reported that bud pubescence in cottons were correlated with both reduced oviposition and feeding preference in the boll weevil, *Anthonomus grandis* Boheman. Khan et al. (1986) demonstrated a negative correlation between trichome density on soybean leaves and the feeding and oviposition of cabbage looper, *Trichoplusia ni*.

The results from the present study show that there was a trend towards a significant positive correlation between pre-reproductive periods and trichome density. This is in agreement with the finding by Peters and Berry (1980b) that developmental time of immature mites was slowed on hop leaves with a high density of trichomes. There have been many reports which indicated that trichome differences among varieties were related to TSSM resistance of crop plants. Glandular hairs have been associated with resistance in tobacco (Patterson et al., 1974) and tomatoes (Rodriguez et al., 1972), and foliar pubescence has been related to resistance in strawberries (Kishaba et al., 1972). Good and Snyder (1988), working with *Lycopersicon hirsutum* Humb. & Bonpl., indicated that Type IV trichome density was inversely correlated with TSSM survival.

Leaf toughness reportedly contributed to interference with feeding and oviposition mechanisms of plant pests (Norris and Kogan, 1980). There is substantial evidence indicating that the leaf toughness is an important antiherbivore trait (Coley, 1983; Larsson and Ohmart, 1988). However, the TSSM susceptibility of hop palnts in the present study was unrelated to the leaf toughness expressed by cuticle thickness and thicknesses of epidermal cell layers which were similar for all genotypes used.

With regards to other characteristics of leaf morphology, Schuster et al. (1972) found that the presence of glands on cotton cultivars was associated with TSSM resistance. Nevertheless, the results from the present study showed inconsistent relationships between TSSM susceptibility of the hop genotypes used and ventral glands as well as moisture content. For the major vein thickness, there were a positive correlation with intrinsic rates of increase and a negative correlation with

pre-reproductive periods, indicating that hop genotypes with large leaf veins may enhance the development of TSSM.

7.4.3. Morphological responses of hop leaves to mite infestations

This study has shown that there is genetic variation in the morphological response of hop leaves to mites infestations and that this variation is related to leaf area scarred and stomatal opening. It was found that the average number of yellow specks was significantly greater on M27 than on M4, whereas the the mean number of open stomata was significantly less on M27 than on M4. In addition, there were significant differences in numbers of yellow specks between different mite densities. These data were consistent with Sances et al. (1979b) who indicated that percent leaflet area scarred by mite feeding was correlated with increasing mite infestation levels and that stomatal closure was an important host-plant response associated with TSSM infestation on strawberries .

Various densities of spider mites have been shown to strongly affect basic physiological processes of several plants (Andrews and LePre', 1979; Hall and Ferre, 1975). Sances et al. (1979b) also showed that mite feeding injury was mechanical and that no toxins were associated with its feeding.

Since leaves of mature crop plants have no meristematic tissues (Milthorpe, 1956), the possibility of leaf recovery from spider mite feeding is unlikely. Consequently, reductions in functional photosynthetic area caused by spider mite feeding would be permanent and could only be compensated for by the production of new foliage at the plant level. Such compensation may occur at low infestation levels, but when high spider mite populations are present, the reduction in photosynthetic assimilates, steming initially from stomatal closure and subsequently from internal injury, would ultimately have a detrimental effect on yield (Sances et al., 1979b).

CHAPTER 8 EFFECTS OF HOP-CANOPY MICROENVIRONMENTS ON MITE POPULATION DYNAMICS

8.1. INTRODUCTION

As shown above, rearing conditions influenced the population dynamics of TSSM. These conditions can be described by environmental factors, including temperature, relative humidity, light intensity and plant variables. The effect of temperature and relative humidity are clearly important; however light intensity and plant variables appear to have less effect on TSSM population growth rates. Additionally, increases in numbers of TSSM on field hops have been noted to be positively associated with hot and dry weather (Neve, 1991).

Thus, it is reasonable to hypothesise that fluctuations in canopy microenvironmental factors may be used as a cultural method for controlling TSSM populations infesting hop plants. Nevertheless, studies designed to investigate sensitivities of the TSSM and its predatory mite under different microenvironmental conditions found in hop plants are lacking. For this reason, the following experiments were carried out.

8.2. MATERIALS AND METHODS

8.2.1. Under field conditions

Field experiments were carried out in a hop yard at Bushy Park from November 18, 1992 to March 3, 1993. Two hop genotypes, M25 and M26, were selected because these genotypes were grown in the same area and because there was a significant difference in TSSM susceptibility between the two genotypes as mentioned in Chapter 4. The experiment was established in a single-hill plot replicated six times for each hop

genotype. Three strings were tied down at each hill. The vines of each hop plant were trained to one of the following foliage densities: 1, 3, and 5 vines per string. Consequently, the modification of foliage canopies provided contrasting microenvironments for naturally occurring TSSM. This experiment was a completely randomized factorial design with hop genotypes (2 levels) and foliage densities (3 levels) as the two main treatment factors.

After all the hop plants had been found to be infested with TSSM, the predatory mites (*Phytoseiulus persimilis*), imported from Biocontrol Ltd. in Queensland, were released onto hop plants at an infestation ratio of approximately 100 mites to two hills on January 27, 1993. Subsequently, some miticides (clofentezine and propargite) were applied in this hop yard during early February.

By using an examination level of one hop leaf per sampling unit, the assessment of mite infestation levels in each treatment was performed on the following dates:

On 30 December 1992, hop leaves at a height of 1.8 m above the ground were examined very closely with a 5 cm hand lens for adult females;

On 13 January 1993, the 1.8 m hop leaves were collected randomly and examined to determine the number of all mite stages under a binocular microscope (10X);

On 27 January 1993, the basal region of 1.8 m hop leaves were pressed on adhesive tape (1.2 x 3 cm) attached to pieces of sponge on microscope slides and the number of mites on the adhesive tape was counted under a binocular microscope (10X);

On 10 February 1993, both the adhesive tape method and the method employed to examine the samples on 13 January 1993 were used on the leaves collected from M26 at five vines per string in order to relate

the numbers of mites obtained from these two techniques, while the leaves from the other treatments were only examined using the latter technique;

On 17 February 1993, the hop leaves collected not only at 1.8 m but also at 3.6 m were examined to determine the number of mites at all stages under a binocular microscope (10X);

On 24 February and 3 March 1993, the examination of hop leaves was similar to that on 17 February 1993.

For monitoring the growth of hop plants at each foliage density, measurements of plant height were taken at 14-day intervals. Leaf surface areas were also determined by using a linear regression model that estimates area from measures of leaf length and width at the widest point: leaf area ($cm.^2$) = 7.903 + 0.67148 (width x length) r^2 = 0.957; n=93. Additionally, temperatures and relative humidities of plant canopy were measured with a handheld humidity and temperature meter (Vaisala HM 34, Vaisala Oy, Helsinki, Finland). The humidity and temperature measurements were made between 1200 and 1400 hours on March 3, 1993. After harvesting, cone production as well as percentage alpha acid in lupulin glands on the cones were also measured in order to evaluate quality and yield of hops obtained from each treatment.

8.2.2. Under glasshouse conditions

The glasshouse test was conducted in February and March, 1993 at temperature regime of 20-25°C with natural lighting conditions. Potted hop plants of four genotypes were placed on a glasshouse bench. The genotypes used were M7, M16, M17, and M24 and there was only one plant per genotype. The vines of these genotypes were trained to 1 and 3 vines per string. Each plant was infested with teneral female mites, taken from a culture maintained on dwarf beans in the growth chamber mentioned in Chapter 5, by using an infestation level of 6 mites per one

vine. This test was a completely randomized factorial design with hop genotypes (4 levels) and foliage densities (2 levels) as the two main treatment factors.

Hop leaves on the vines were inspected four and five weeks after inoculation. Three leaf pairs, one pair from the middle region and the others from the top, were removed from each string and the total number of mites at all mite stages on each leaf was counted under a binocular microscope (10X). Additionally, the leaves collected from M16 at one vine per string at the last inspection were also examined using the adhesive tape method as mentioned earlier for evaluating the relationship between the total mites on the leaf and those on the adhesive tape.

The temperatures and relative humidities of plant canopy were measured with the handheld humidity and temperature meter (Vaisala HM 34). The humidity and temperature measurements were made on March 3, 1993. In addition, the light intensity penetrating plant canopy was measured with a photometer (LI-185, Lambda Instruments) and the measurement was made on March 12, 1993.

8.2.3. Data analyses

Factorial analyses of variance provided statistical tests for differences between treatments. The calculations were completed using Macintosh software StatView ™ SE+. Simple linear regressions were performed using the curve fit procedure of the Cricketgraph computer program. In addition, data transformations were employed when necessary.

8.3. RESULTS

8.3.1. Under field conditions

Fig. 1 depicts graphically the average number of TSSM adult females on 1.8-m hop leaves of M25 and M26 at the various foliage densities on the first sampling date (30 December). The mite populations varied significantly between these two hop genotypes ($p < 0.05$), whereas there were no significant differences among foliage densities ($p \geq 0.05$). It was apparent that M26 at three vines per string had the highest populations of TSSM in early the growing season and that M25 at either one or five vines per string tended to have low population numbers.

Fig. 8.1. Average numbers of adult females per leaf on two genotypes of hops at three different foliage densities on December 30, 1992.

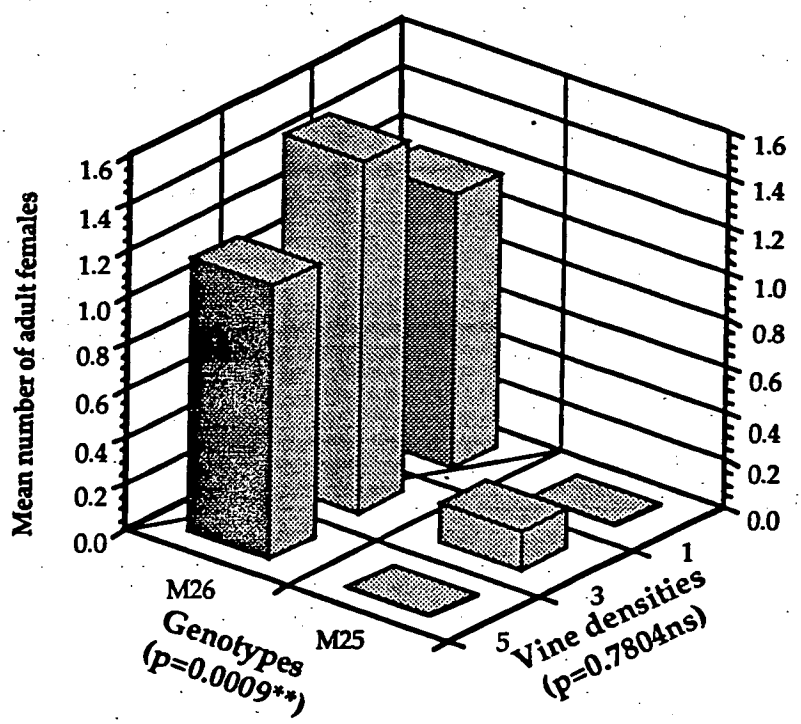


Table 8.1 indicates the average numbers of all mite stages per leaf on the two genotypes of hops at the three foliage densities on the second sampling date (13 January). Highly significant differences in mite densities prior to the release of predatory mites and the application of miticides were detected between these hop genotypes as well as among different foliage densities studied ($p < 0.01$). The total numbers of mites per leaf on M25 were lower than those on M26 at all foliage densities. It was also found that the average numbers of mites per leaf on M26 were reduced as the number of vines per string increased.

Table 8.1. Average numbers of total mites per leaf on two genotypes of hops at three vine densities on January 13, 1993.

Genotype (p=0.0001**)	Vine density (p=0.0076**)			Mean per leaf for each genotype
	1	3	5	
M25	4.333	19.333	6.833	10.167
M26	166.333	87.167	31.333	94.944
Mean per leaf for each vine density (PLSD = 58.348)	85.333	53.250	19.083	

The mite densities of individual stages at each foliage density, the mean numbers of adult females, adult males, immatures and eggs per leaf are illustrated in Fig. 8.2, 8.3, 8.4 and 8.5, respectively. Statistically significant differences in TSSM numbers per leaf were detected between the two genotypes of hops for all developmental stages of the mites, while the variation in mite densities among different hop vines per string was significant only in terms of adult females ($p < 0.05$).

Fig. 8.2. Average numbers of adult females per leaf on two genotypes of hops at three different foliage densities on January 13, 1992.

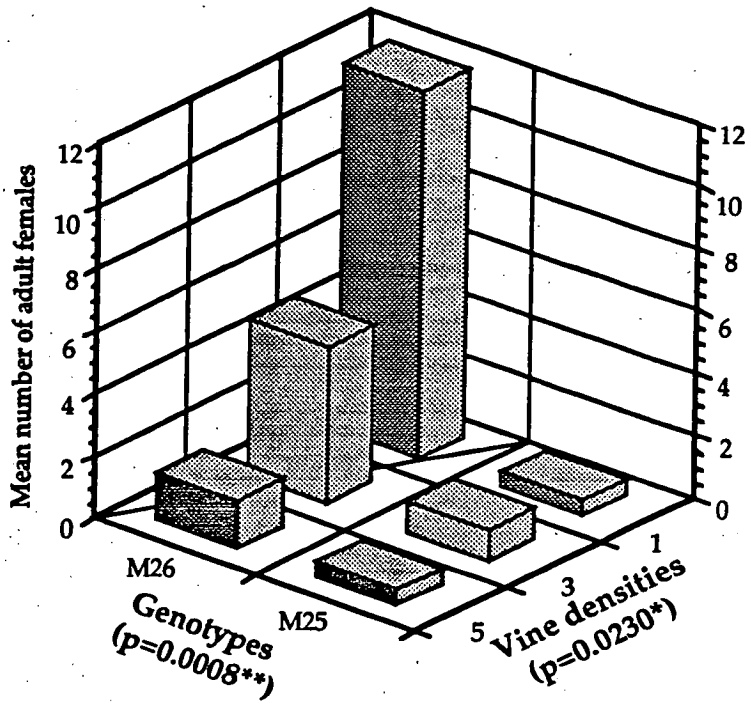


Fig. 8.3. Average numbers of adult males per leaf on two genotypes of hops at three different foliage densities on January 13, 1992.

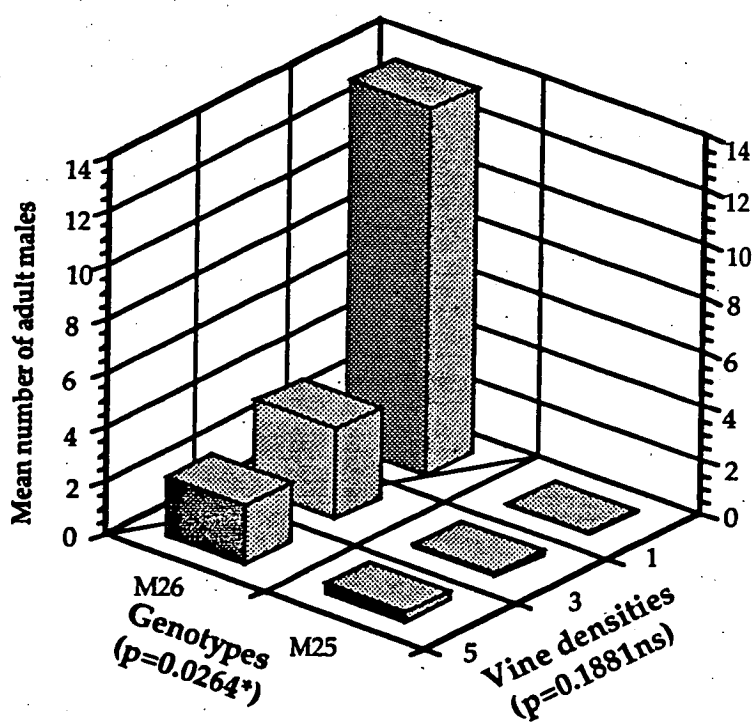


Fig. 8.4. Average numbers of immatures per leaf on two genotypes of hops at three different foliage densities on January 13, 1992.

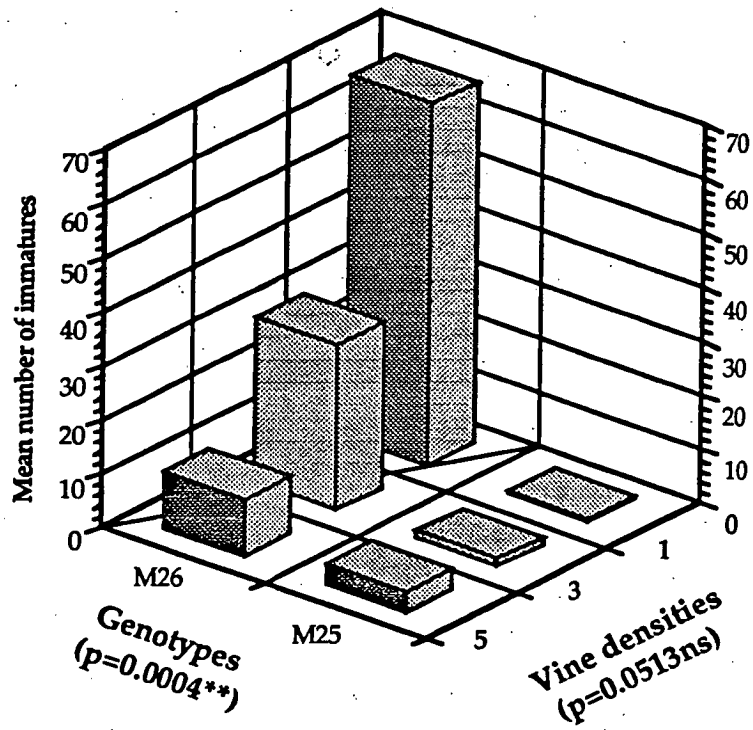
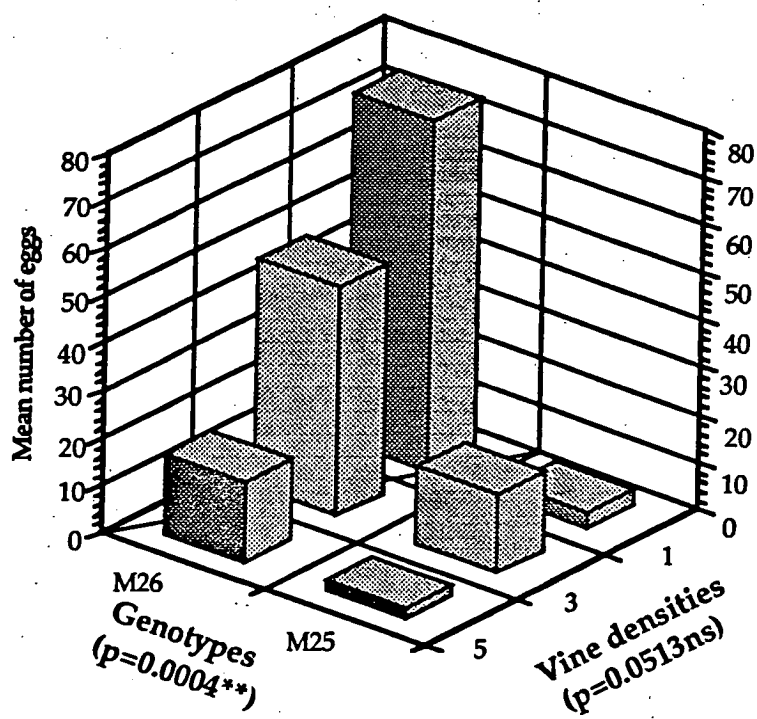


Fig. 8.5. Average numbers of eggs per leaf on two genotypes of hops at three different foliage densities on January 13, 1992.



Average numbers of total mites caught on sticky tapes on leaves of M25 and M26 at the three foliage densities on the third sampling date (27 January) are presented in Table 8.2. No significant differences in mite densities were found between the hop genotypes nor among different foliage densities ($p \geq 0.05$).

Table 8.2. Average numbers of total mites per adhesive tape on two genotypes of hops at three vine densities on January 27, 1993.

Genotype (p=0.0797ns)	Vine density (p=0.8319ns)			Mean per sticky tape for each genotype
	1	3	5	
M25	0.500	0.333	0.833	0.556
M26	4.667	4.833	2.000	3.833
Mean per sticky tape for each vine density	2.583	2.583	1.417	

The average numbers of TSSM and the predatory mites found on each hop leaf at the height of 1.8 m after the application of miticides are shown in Table 8.3 and 8.4, respectively. On the fourth sampling date (10 February), the populations of TSSM had been adversely affected by the miticide application and occurred at very low levels, while the predatory mites appeared to be unaffected by the miticides. There were no significant differences in TSSM densities either between the two hop genotypes or among different foliage densities ($p \geq 0.05$). In contrast, the density of predatory mites varied significantly between the hop genotypes as well as among different foliage densities ($p < 0.05$). In addition, it was also apparent that neither TSSM nor predatory mites were detected by using the sticky tape.

Table 8.3. Average numbers of total mites per leaf on two genotypes of hops at three vine densities on February 10, 1993.

Genotype (p=0.3533ns)	Vine density (p=0.3648ns)			Mean per leaf for each genotype
	1	3	5	
M25	3.500	1.000	0.167	1.556
M26	3.500	3.333	1.833	2.889
Mean per leaf for each vine density	3.500	2.167	1.000	

Table 8.4. Average numbers of predatory mites per leaf on two genotypes of hops at three vine densities on February 10, 1993.

Genotype (p=0.0230*)	Vine density (p=0.0067**)			Mean per leaf for each genotype
	1	3	5	
M25	2.667	0.500	0.333	1.167
M26	5.833	4.000	0.333	3.389
Mean per leaf for each vine density (PLSD = 2.501)	4.250	2.250	0.333	

Means for the mite numbers found on the leaves at the height of 1.8 m and 3.6 m on the fifth sampling date (17 February) are given in Table 8.5 for TSSM and Table 8.6 for the predatory mites. One week after the previous inspection, TSSM populations had increased. Meanwhile, the numbers of predatory mites still remained fairly static and only significant differences ($p < 0.05$) in average numbers of predatory mites between the genotypes were found (Table 8.6).

Table 8.5. Average numbers of total mites per leaf on two genotypes of hops at three vine densities on February 17, 1993.

Genotype (p=0.2739ns)	Vine density (p=0.3538ns)			Mean per leaf for each genotype
	1	3	5	
M25	5.667	9.500	4.000	6.389
M26	4.667	4.750	3.000	4.139
Mean per leaf for each vine density	5.167	7.125	3.500	

Table 8.6. Average numbers of predatory mites per leaf on two genotypes of hops at three vine densities on February 17, 1993.

Genotype (p=0.0060**)	Vine density (p=0.1317ns)			Mean per leaf for each genotype
	1	3	5	
M25	2.167	1.333	0.833	1.444
M26	3.917	2.417	2.750	3.028
Mean per leaf for each vine density	3.042	1.875	1.792	

The comparison of TSSM densities between different foliage heights on M25 and M26 is shown in Fig. 8.6. The average numbers of mites varied from 2.389 mites per leaf on M26 at the height of 1.8 m to 7.722 mites per leaf on M25 at the height of 3.6 m. With regard to the foliage densities, the density of TSSM ranged from 3.0 to 10.417 mites per leaf on the 1.8-m leaves at five vines per string and the 3.6-m leaves at three vines per string, respectively (Fig. 8.7). For the predatory mites, the mean densities at different foliage heights is illustrated in Fig. 8.8 for the two hop genotypes and Fig. 8.9 for the various foliage densities. The highest average number of predatory mites was detected on the 3.6-m leaves of M26 at one hop vine per string.

Fig. 8.6. Average numbers of total mites per leaf on two genotypes of hops at two height intervals on February 17, 1993.

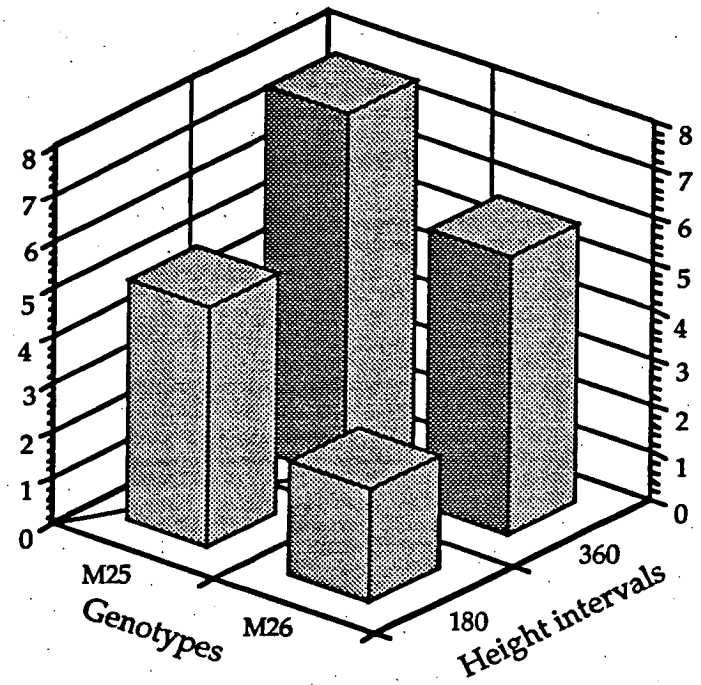


Fig. 8.7. Average numbers of total mites per leaf at three height intervals of three vine densities on February 17, 1993.

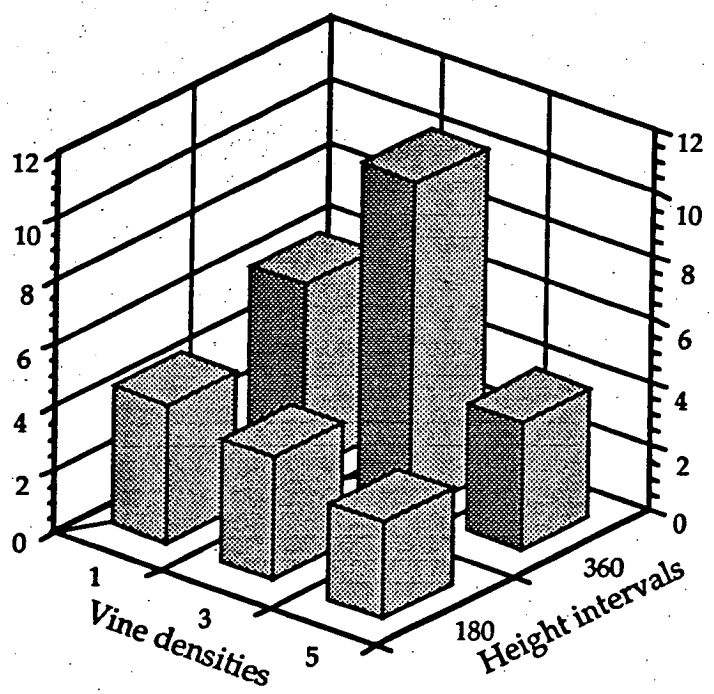


Fig. 8.8. Average numbers of predatory mites per leaf on two genotypes of hops at two height intervals on February 17, 1993.

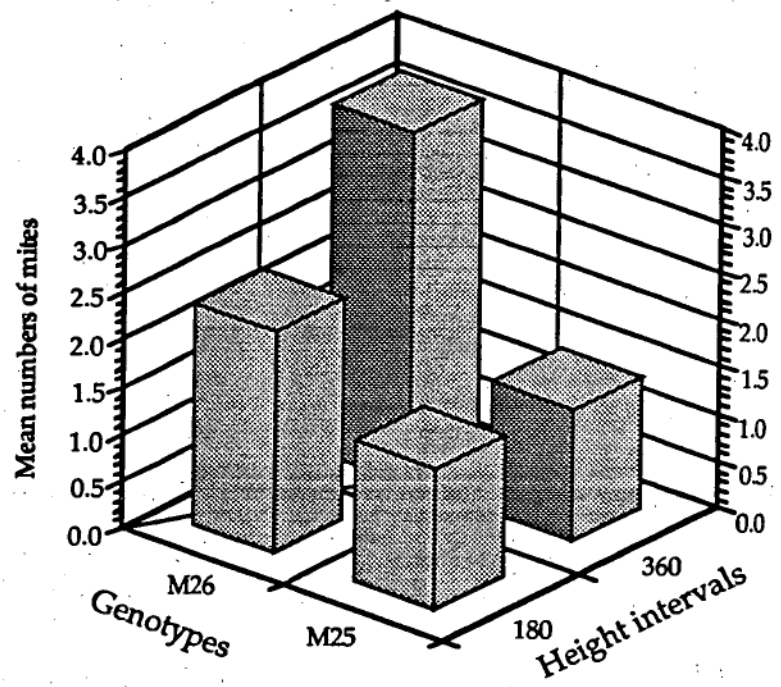
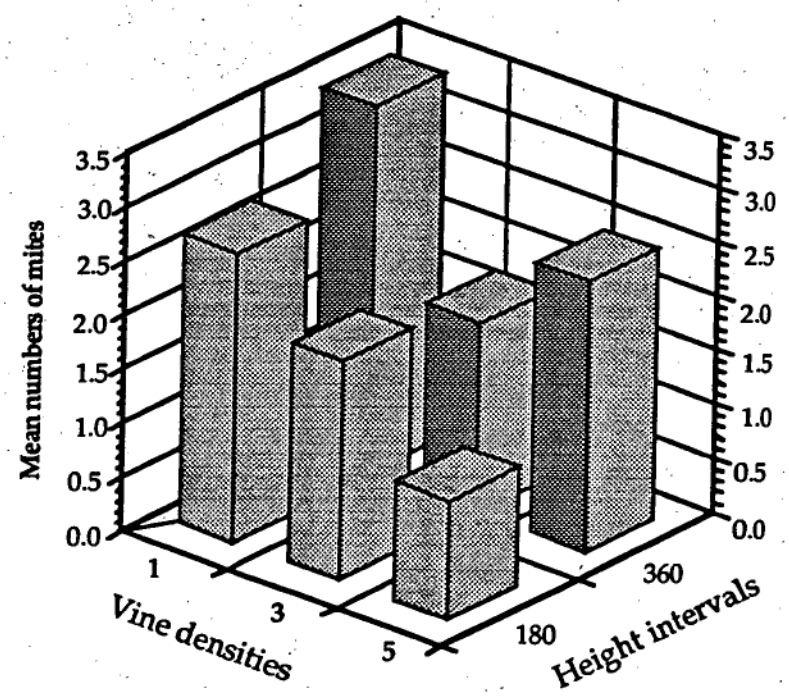


Fig. 8.9. Average numbers of predatory mites per leaf at three height intervals of three vine densities on February 17, 1993.



Even though the variation in average numbers of TSSM per leaf among different foliage densities was significant ($p < 0.05$) on the sixth sampling date (24 February), the variation in TSSM densities between the two hop genotypes was not significant ($p \geq 0.05$; Table 8.7). Significantly more mites were found on leaves at one vine per string than those at three and five vines per string. When the numbers of predatory mites per leaf were averaged over both hop genotypes and foliage densities, significant differences were detected ($p < 0.05$; Table 8.8). In addition, the average numbers of TSSM and predatory mites on leaves at each height interval for both hop genotypes and foliage densities are shown in Fig. 8.10 and 8.11, respectively.

Table 8.7. Average numbers of total mites per leaf on two genotypes of hops at three vine densities on February 24, 1993.

Genotype (p=0.7775ns)	Vine density (p=0.0184*)			Mean per leaf for each genotype
	1	3	5	
M25	44.583	17.750	23.000	28.444
M26	38.167	27.833	24.333	30.111
Mean per leaf for each vine density (PLSD = 14.188)	41.375	22.792	23.667	

Table 8.8. Average numbers of predatory mites per leaf on two genotypes of hops at three vine densities on February 24, 1993.

Genotype (p=0.0075**)	Vine density (p=0.0047**)			Mean per leaf for each genotype
	1	3	5	
M25	3.917	1.333	1.750	2.333
M26	7.833	4.000	2.917	4.917
Mean per leaf for each vine density	5.875	2.667	2.333	

Fig. 8.10. Average numbers of total mites per leaf on the leaves at two height intervals for the two hop genotypes (A) and the three foliage densities (B) on February 24, 1993.

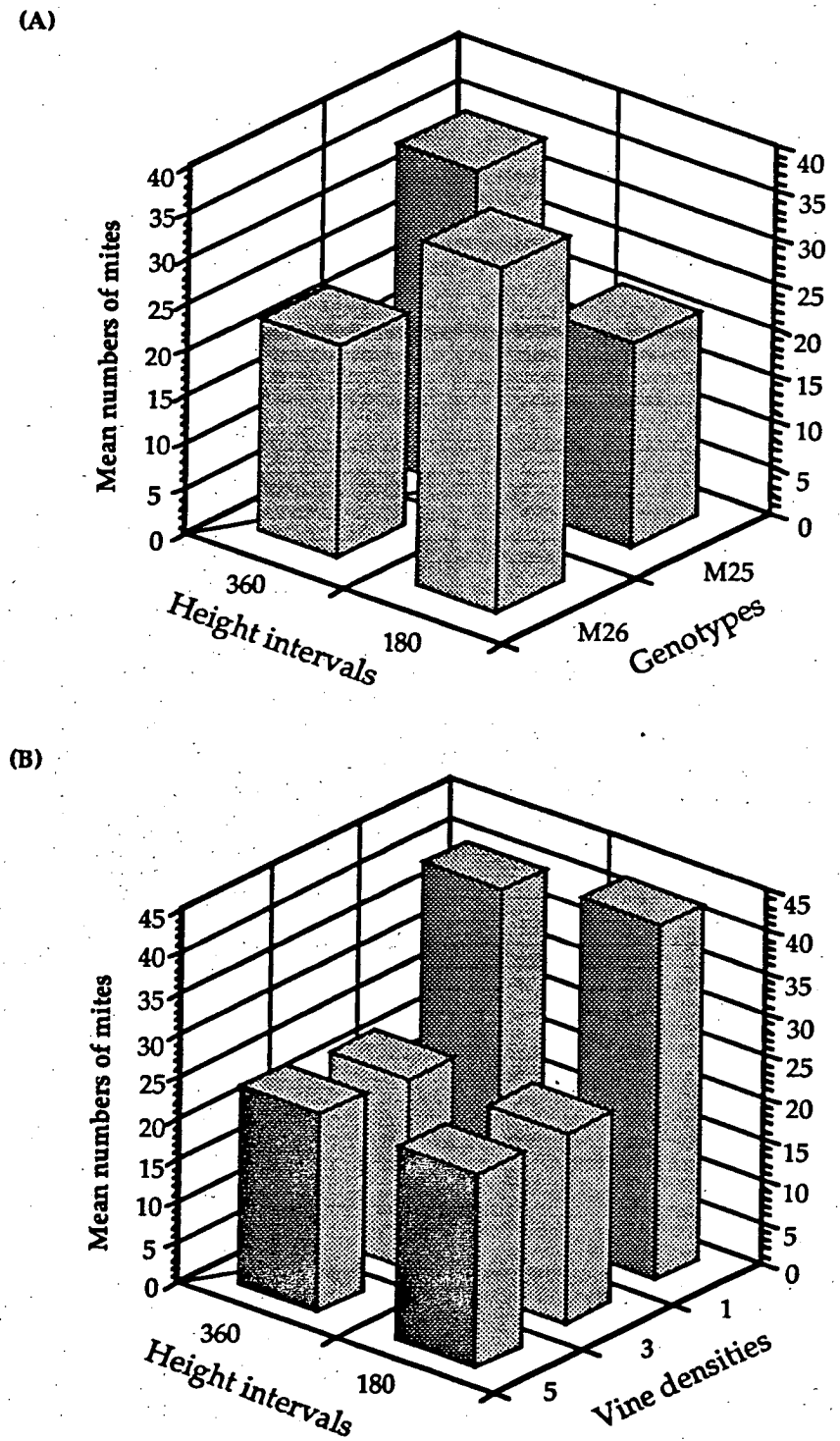
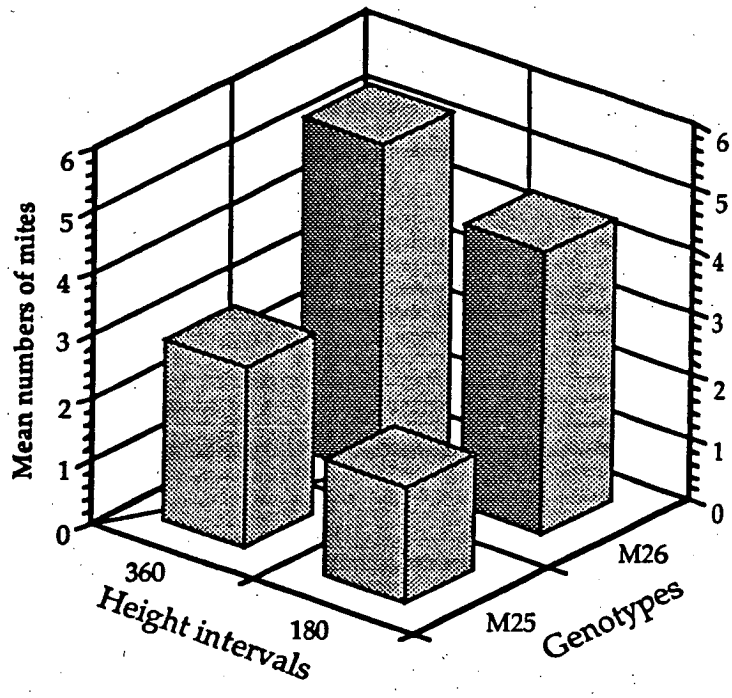
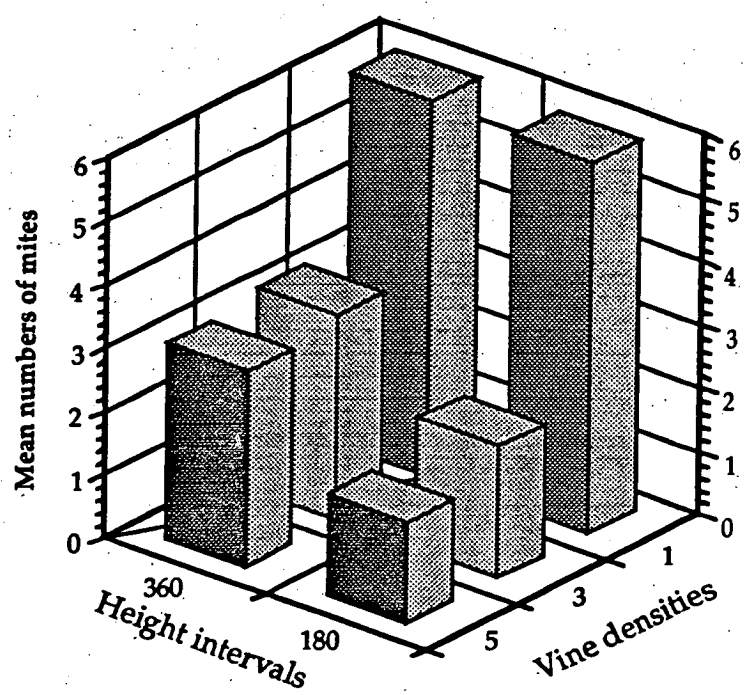


Fig. 8.11. Average numbers of predatory mites per leaf on the leaves at two height intervals for the two hop genotypes (A) and the three foliage densities (B) on February 24, 1993.

(A)



(B)



On the final sampling date (3 March), significant differences in average numbers of TSSM per leaf were detected again among the foliage densities used in these studies ($p < 0.05$), whereas the mite populations between the two hop genotypes did not differ significantly ($p \geq 0.05$; Table 8.9). For the predatory mite numbers per leaf, means differed significantly between the hop genotypes as well as among different foliage densities ($p < 0.05$; Table 8.10). Significantly more predatory mites were found on M26 than on M25 when averaged over hop genotypes. Meanwhile, the average number of predatory mites over the three foliage densities showed that hop plants at three and five vines per string had significantly fewer predatory mites than did those at one vine per string, even though they were not significantly different from each other.

Table 8.9. Average numbers of total mites per leaf on two genotypes of hops at three vine densities on March 3, 1993.

Genotype (p=0.3078ns)	Vine density (p=0.0318*)			Mean per leaf for each genotype
	1	3	5	
M25	40.750	19.917	21.750	27.472
M26	26.667	15.667	25.000	22.444
Mean per leaf for each vine density (PLSD = 11.967)	33.708	17.792	23.375	

Table 8.10. Average numbers of predatory mites per leaf on two genotypes of hops at three vine densities on March 3, 1993.

Genotype (p=0.0176*)	Vine density (p=0.0065**)			Mean per leaf for each genotype
	1	3	5	
M25	5.250	3.083	2.833	3.722
M26	12.750	5.750	3.667	7.389
Mean per leaf for each vine density (PLSD = 3.847)	9.000	4.417	3.250	

Furthermore, average numbers of TSSM and predatory mites per leaf at each height interval before harvesting are presented in Fig. 8.12 and 8.13, respectively. The populations of TSSM found on the 3.6-m leaves of both M25 and M26 were higher than those on the 1.8-m leaves (Fig. 8.12A). In terms of foliage densities, the numbers of TSSM at all stages varied from 14.25 to 43.167 individuals per leaf with 3.6-m leaves at one vine per string having the highest value (Fig. 8.12B). For the predatory mites, population densities at the height of 1.8 m ranged from 3.278 on M25 to 8.278 on M26, while those at the height of 3.6 m varied from 4.167 to 6.5 individuals per leaf on M25 and M26, respectively (Fig. 13A). It was also found that more than 50% of total predatory mite populations at both height intervals were detected on the hop plants with one vine per string (Fig. 13B).

Fig. 8.12. Average numbers of total mites per leaf on the leaves at two height intervals for the two hop genotypes (A) and the three foliage densities (B) on March 3, 1993.

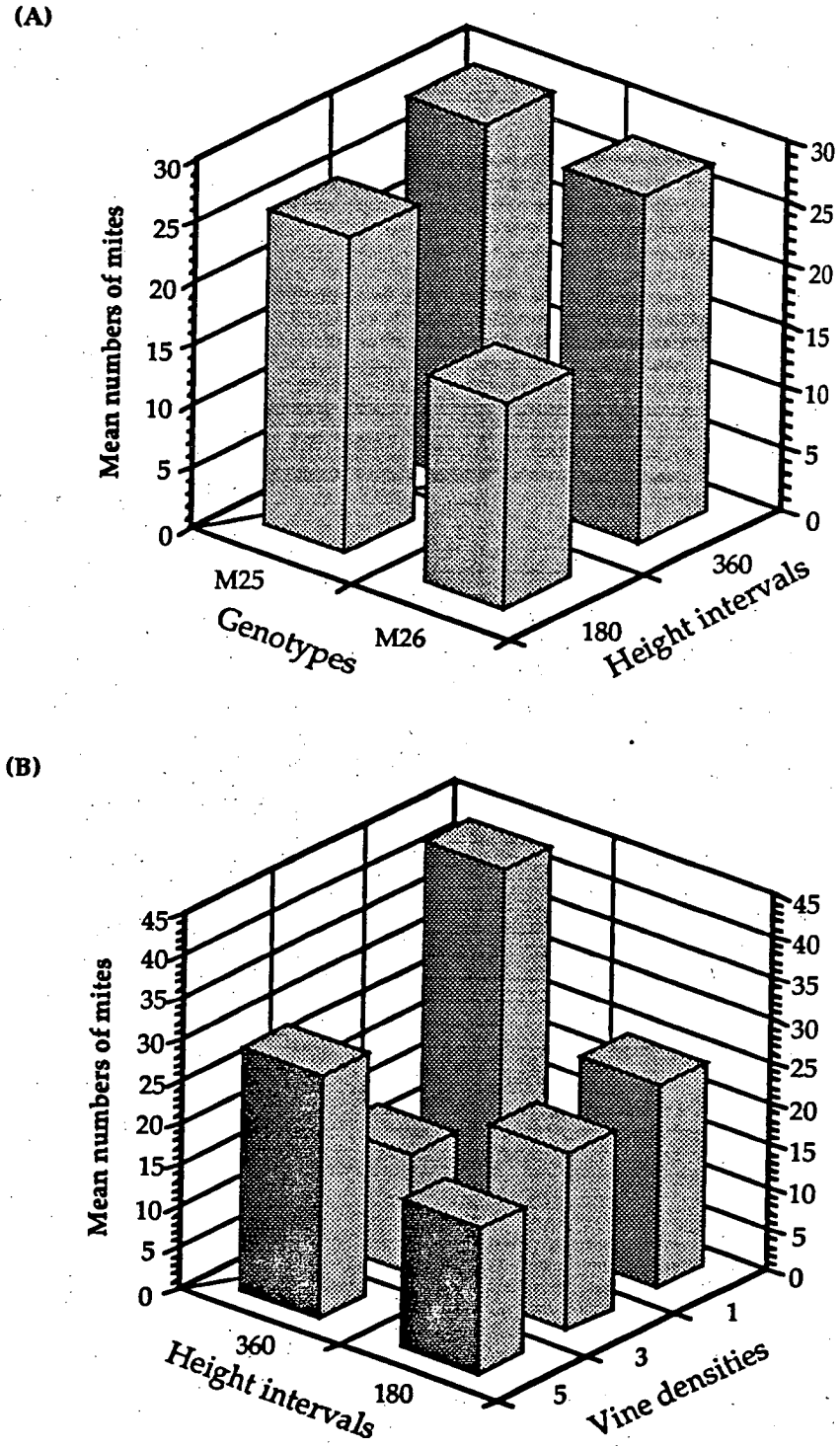
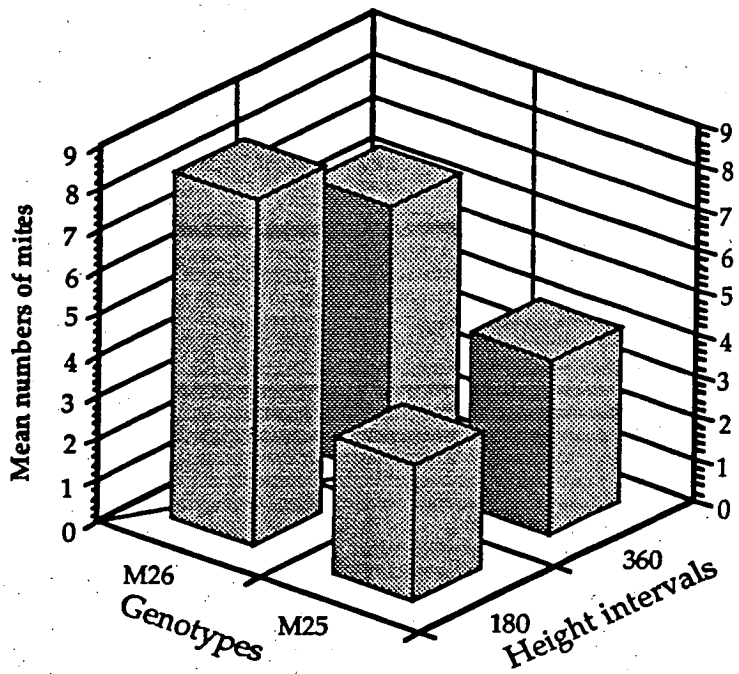
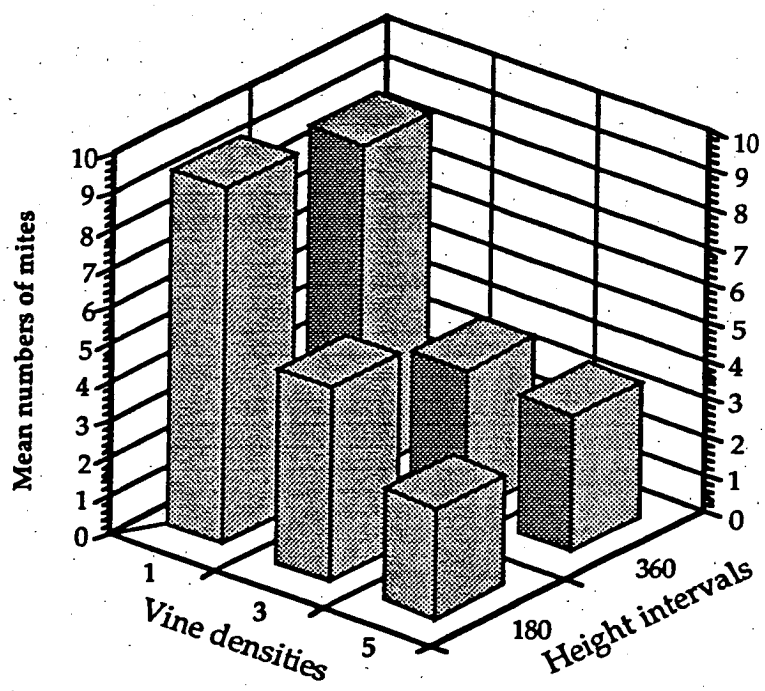


Fig. 8.13. Average numbers of predatory mites per leaf on the leaves at two height intervals for the two hop genotypes (A) and the three foliage densities (B) on March 3, 1993.

(A)



(B)



Means for the leaf surface areas of M25 and M26 on each sampling occasion are shown in Fig. 8.14. It was apparent that the leaves of M25 had greater surface areas than those of M26. In addition, the surface areas of leaves collected from hop plants at different foliage densities are presented in Fig. 8.15. From this figure, it can be seen that the leaves from three hop vines per string were larger than those from one and five hop vines per string.

Fig. 8.14. Leaf surface areas of M25 and M26.

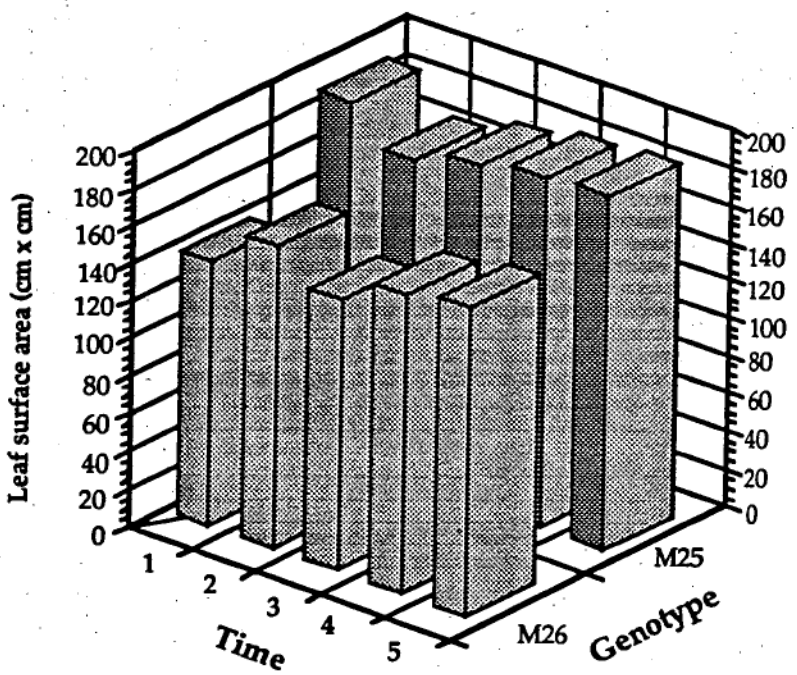
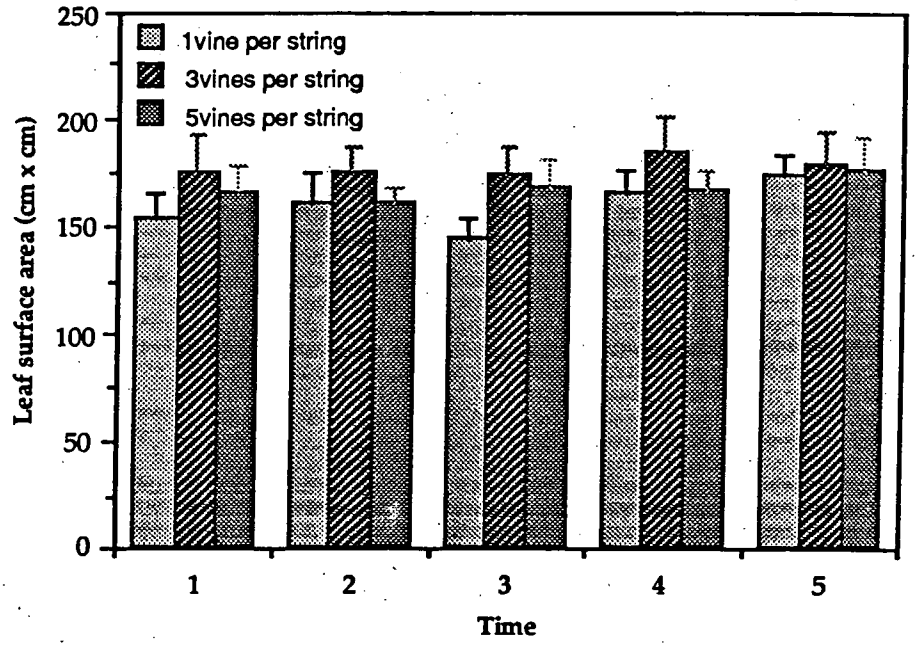


Fig. 8.15. Leaf surface areas of hop plants at different vine densities .



The average numbers of TSSM per cm^2 on M25 and M26 at each foliage density on 13 January, 10, 17, 24 February and 3 March 1993 are presented in Table 8.11, 8.12, 8.13, 8.14 and 8.15, respectively. Even though the above-mentioned density of mite populations was expressed as average numbers of mites per cm^2, similar results were also obtained.

Table 8.11. Average numbers of total mites per cm^2 on two genotypes of hops at three vine densities on January 13, 1993.

Genotype (p=0.0001**)	Vine density (p=0.0197*)			Mean per cm^2 for each genotype
	1	3	5	
M25	0.026	0.080	0.045	0.050
M26	1.513	0.672	0.240	0.808
Mean per cm^2 for each vine density (PLSD = 0.576)	0.769	0.376	0.143	

Table 8.12. Average numbers of total mites per cm^2 on two genotypes of hops at three vine densities on February 10, 1993.

Genotype (p=0.3468ns)	Vine density (p=0.4209ns)			Mean per cm^2 for each genotype
	1	3	5	
M25	0.022	0.005	0.001	0.009
M26	0.021	0.019	0.013	0.018
Mean per cm^2 for each vine density	0.021	0.012	0.007	

Table 8.13. Average numbers of total mites per cm^2 on two genotypes of hops at three vine densities on February 17, 1993.

Genotype (p=0.3871ns)	Vine density (p=0.2834ns)			Mean per cm^2 for each genotype
	1	3	5	
M25	0.035	0.038	0.017	0.030
M26	0.023	0.028	0.018	0.023
Mean per cm^2 for each vine density	0.029	0.033	0.018	

Table 8.14. Average numbers of total mites per cm^2 on two genotypes of hops at three vine densities on February 24, 1993.

Genotype (p=0.1587ns)	Vine density (p=0.0183*)			Mean per cm^2 for each genotype
	1	3	5	
M25	0.213	0.077	0.122	0.137
M26	0.248	0.163	0.145	0.185
Mean per cm^2 for each vine density (PLSD = 0.082)	0.230	0.120	0.133	

Table 8.15. Average numbers of total mites per cm^2 on two genotypes of hops at three vine densities on March 3, 1993.

Genotype (p=0.9953ns)	Vine density (p=0.0497*)			Mean per cm^2 for each genotype
	1	3	5	
M25	0.197	0.099	0.104	0.133
M26	0.152	0.097	0.151	0.134
Mean per cm^2 for each vine density (PLSD = 0.061)	0.175	0.098	0.128	

Average heights of the two hop genotypes at the various foliage densities during the growing season are shown in Table 8.16. There were no significant differences ($p \geq 0.05$) in hop heights among different treatments on the first occasion of measurement (18 November). Nevertheless, the variation in hop heights among the hop genotypes at different foliage densities was significant ($p < 0.05$) from the second occasion of measurement (12 December) until hop plants reached the top of trellis. It was found that M26 at five vines per string had the fastest growth rate, whereas M25 at one vine per string had the slowest.

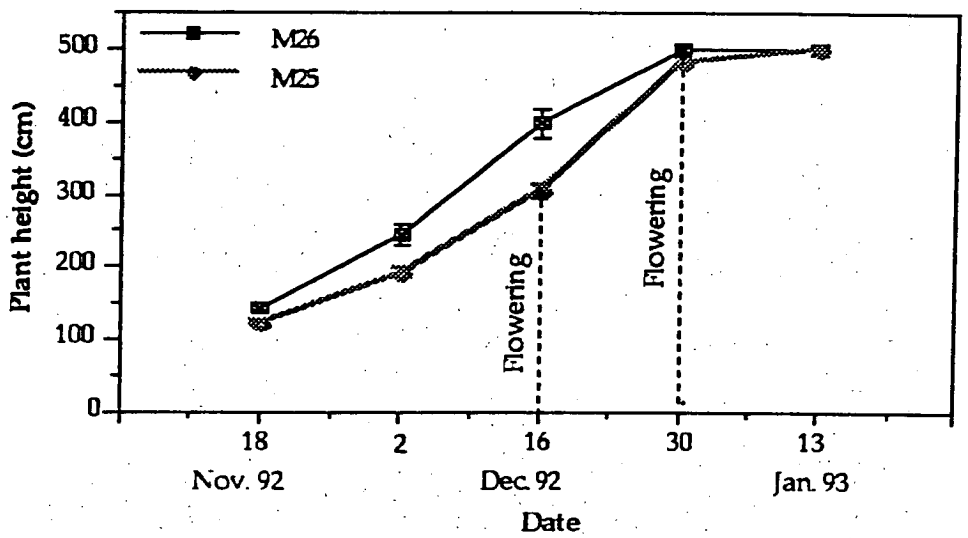
Table 8.16. Hop plant growth of M25 and M26 at different foliage densities.

Genotype (Vine density)	Average height of hop plants (cm) (S.E.)				
	18/11/92	2/12/92	16/12/92	30/12/92	13/1/93
M25 (1 vine)	115.33 (6.163)	178.00a (8.489)	283.33a (10.220)	470.00a (12.179)	500.00 (0.000)
M25 (3 vines)	128.33 (9.157)	204.33abc (9.229)	336.67ab (9.888)	496.67bc (3.333)	500.00 (0.000)
M25 (5 vines)	122.83 (3.24)	191.83ab (7.097)	293.33a (14.063)	481.67ab (7.601)	500.00 (0.000)
M26 (1 vine)	132.33 (10.055)	229.00abc (23.409)	385.00bc (38.449)	496.67bc (3.333)	500.00 (0.000)
M26 (3 vines)	148.00 (16.155)	246.00bc (31.394)	395.00bc (37.216)	500.00c (0.000)	500.00 (0.000)
M26 (5 vines)	148.33 (9.701)	256.83c (23.267)	413.33c (25.777)	500.00c (0.000)	500.00 (0.000)
p-value	0.1375ns	0.0476*	0.0031**	0.0070**	-

For each treatment, means within a column followed by same letter not significantly different ($p<0.05$).

A comparison of plant growth between M25 and M26 is illustrated in Fig. 8.16. Even though M26 grew faster than M25, the beginning of the flowering period of M26 was found to be slower than that of M25.

Fig. 8.16. Plant growth of M25 and M26 at Bushy Park during the 1992/93 growing season.



Mean relative humidity and temperature within plant canopy of the two hop genotypes at the three vine densities on March 3, 1993 are presented in Table 8.17 and 8.18, respectively. Both relative humidity and temperature within plant canopy among hop genotypes at different foliage densities did not vary significantly ($p \geq 0.05$). This may be due to cool, cloudy conditions which occurred on the day when temperature and relative humidity were measured.

Table 8.17. Average relative humidity (%) within plant canopy of two genotypes of hops at three vine densities on March 3, 1993.

Genotype (p=0.1241ns)	Vine density (p=0.9138ns)			Overall mean for each genotype
	1	3	5	
M25	52.389	52.706	52.244	52.446
M26	53.344	52.861	53.061	53.089
Overall mean for each vine density	52.867	52.783	52.653	

Table 8.18. Average temperature (°C) within plant canopy of two genotypes of hops at three vine densities on March 3, 1993.

Genotype (p=0.6580ns)	Vine density (p=0.8305ns)			Overall mean for each genotype
	1	3	5	
M25	15.356	15.300	15.306	15.320
M26	15.417	15.289	15.428	15.378
Overall mean for each vine density	15.386	15.294	15.367	

After harvesting, statistical analyses of the data obtained from weighing dried hop cones indicated that there were highly significant differences ($p < 0.01$) between the two hop genotypes as well as among the foliage densities studied for both average dry weights of hop cones per string and those per vine (Table 8.19 and 8.20, respectively), whereas average cone weights did not differ significantly ($p \geq 0.05$; Table 8.21). It was apparent that M25 had significantly greater dry weights of hop cones per string than did M26. When yield per string was converted to yield per vine, the same differences between these hop genotypes were also detected. In addition, the average dry weight of hop cones per string increased for each increase in the number of vines per string, while the dry weight of hop cones per vine decreased.

Table 8.19. Average dry weights of hop cones per string (gm) from genotypes M25 and M26 at three vine densities.

Genotype (p=0.0001**)	Vine density (p=0.0001**)			Overall mean for each genotype
	1	3	5	
M25	232.83	362.83	395.17	330.28
M26	63.50	173.17	265.67	167.44
Overall mean for each vine density (PLSD = 90.44)	148.17	268.00	330.42	

Table 8.20. Average dry weights of hop cones per vine (gm) from genotypes M25 and M26 at three vine densities.

Genotype (p=0.0001**)	Vine density (p=0.0001**)			Overall mean for each genotype
	1	3	5	
M25	232.83	120.94	79.03	144.27
M26	63.50	57.72	53.13	58.12
Overall mean for each vine density (PLSD =48.82)	148.17	89.33	66.08	

Table 8.21. Average cone weights (mg) of genotypes M25 and M26 at three vine densities.

Genotype (p=0.3488ns)	Vine density (p=0.5497ns)			Overall mean for each genotype
	1	3	5	
M25	184.67	166.83	171.67	174.39
M26	139.33	159.00	185.50	161.28
Overall mean for each vine density	162.00	162.92	178.58	

Table 8.22 shows average percentage contents of alpha acid of hop cones havested from M25 and M26 at the three foliage densities during the 1992/93 growing season. According to a two-way analysis of variance, the variation in alpha acid percentage contents between the two hop genotypes was significant ($p < 0.05$), whereas the variation among different foliage densities was not significant ($p \geq 0.05$). It was found that M26 had significantly greater percentage contents of alpha acid than did M25.

Table 8.22. Average percentage content of alpha acid (%) from genotypes M25 and M26 at three vine densities.

Genotype (p=0.0001**)	Vine density (p=0.3358ns)			Overall mean for each genotype
	1	3	5	
M25	7.13	7.42	7.67	7.41
M26	10.67	11.27	11.53	11.16
Overall mean for each vine density	8.90	9.34	9.60	

8.3.2. Under glasshouse conditions

On the first occasion of sampling, average numbers of TSSM at all stages per leaf on hop plants of M7, M16, M17 and M24 at either one or three vines per string under glasshouse conditions are presented in Table 8.23. Significant differences in mean numbers of mites among the four hop genotypes were detected ($p < 0.05$), whereas means between different foliage densities did not vary significantly ($p \geq 0.05$). It was apparent that M16 had significantly more mite counts than did the other genotypes ($p < 0.05$). When the mite density was expressed as mean numbers of mites for all stages per cm^2, similar results were also obtained (Table 8.24). For the mite population at each stage studied, average numbers of adult females, adult males, immatures and eggs on each genotype at different foliage densities are illustrated in Fig. 8.17, 8.18, 8.19 and 8.20, respectively. It was found that M16 at one vine per string had the highest numbers of adult females, immatures and eggs compared with other treatments, while M7 at one vine per string and M17 at three vines per string had the highest adult male population.

Table 8.23. Average numbers of total mites per leaf on four genotypes of hops at two vine densities on the first occasion of sampling under glasshouse conditions.

Genotype (p=0.0023**)	Vine density (p=0.0930ns)		Mean per leaf for each genotype (PLSD = 14.8230)
	1	3	
M7	3.6667	8.0000	5.8333
M16	45.8333	5.3333	25.5833
M17	5.1667	6.0000	5.5833
M24	0.3333	5.5000	2.9167
Mean per leaf for each vine density	13.7500	6.2083	

Table 8.24. Average numbers of total mites per cm^2 on four genotypes of hops at two vine densities on the first occasion of sampling under glasshouse conditions.

Genotype (p=0.0024**)	Vine density (p=0.0596ns)		Mean per cm^2 for each genotype (PLSD = 0.3054)
	1	3	
M7	0.0707	0.1489	0.1098
M16	0.9530	0.0516	0.5023
M17	0.0957	0.1667	0.1312
M24	0.0059	0.0894	0.0477
Mean per cm^2 for each vine density	0.2813	0.1142	

Fig. 8.17. Average numbers of adult females per leaf on four genotypes of hops at two different foliage densities on the first occasion of sampling under glasshouse conditions.

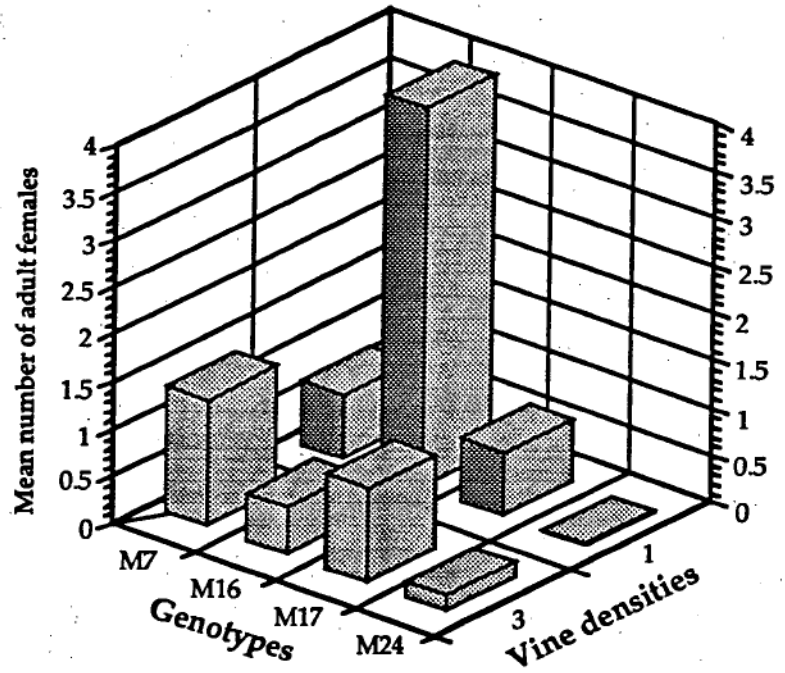


Fig. 8.18. Average numbers of adult males per leaf on four genotypes of hops at two different foliage densities on the first occasion of sampling under glasshouse conditions.

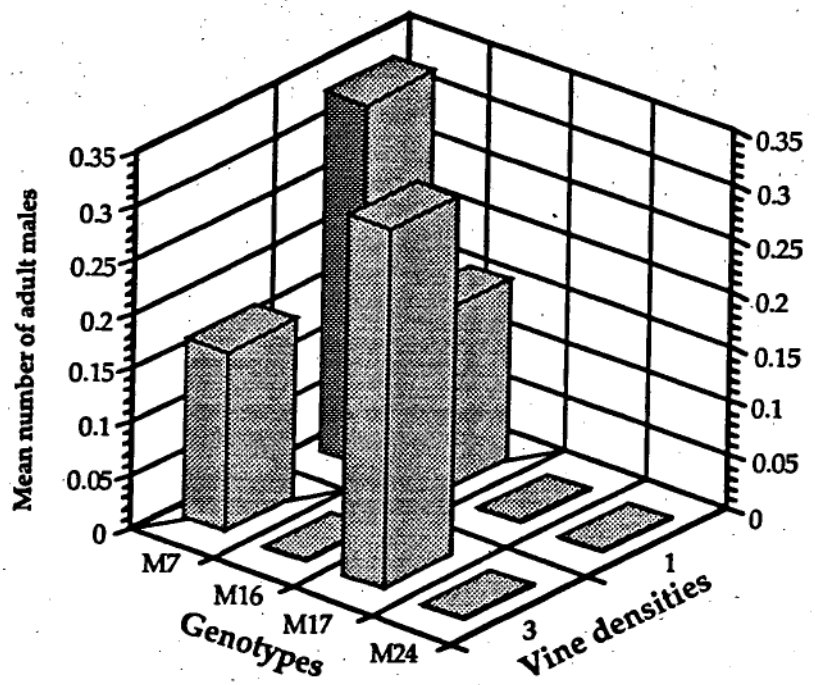


Fig. 8.19. Average numbers of immatures per leaf on four genotypes of hops at two different foliage densities on the first occasion of sampling under glasshouse conditions.

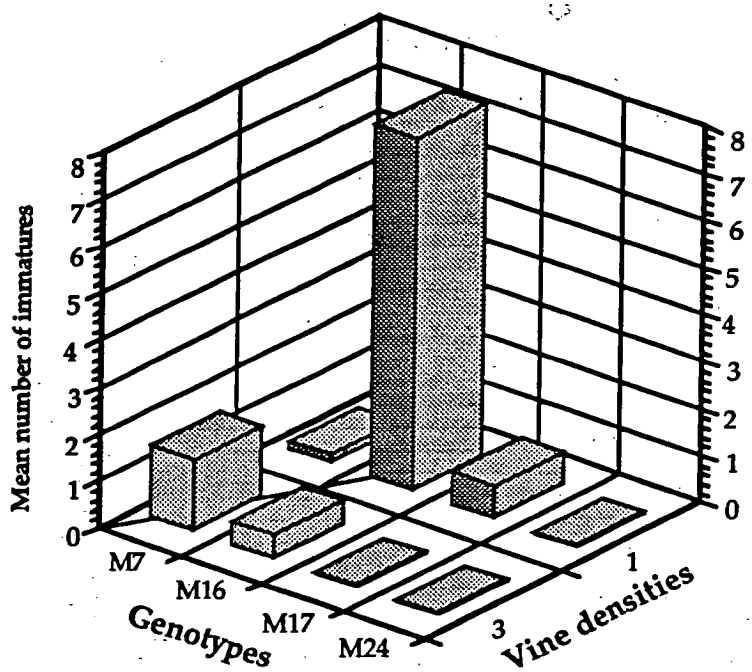
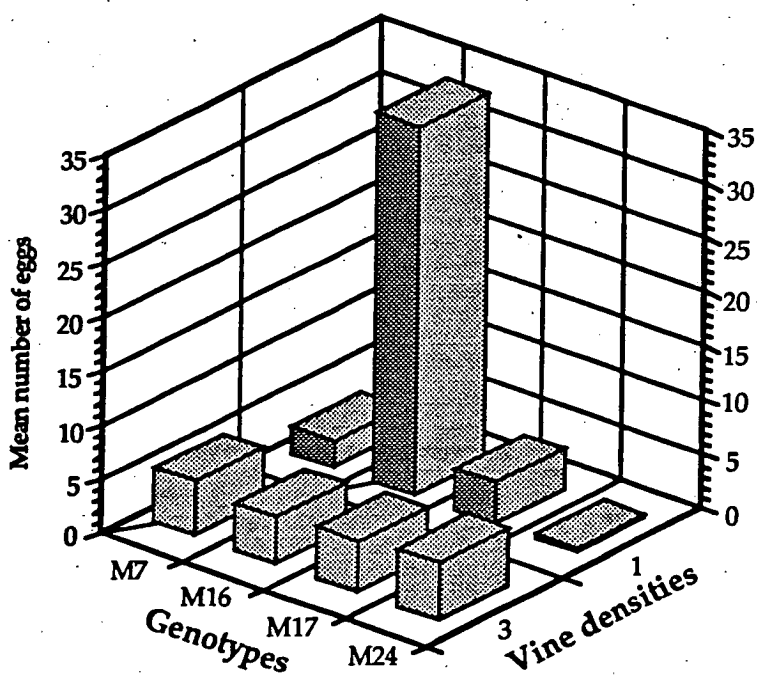


Fig. 8.20. Average numbers of eggs per leaf on four genotypes of hops at two different foliage densities on the first occasion of sampling under glasshouse conditions.



On the second sampling occasion, average numbers of mites at all stages per leaf on the four genotypes at the two foliage densities are shown in Table 8.25. Generally, the mite populations at this sampling occasion were found to be larger than those on the previous one. Significant differences in the mean mite populations were detected among the hop genotypes ($p < 0.05$), whereas the means between the two foliage densities did not differ significantly ($p \geq 0.05$). When the mite densities were expressed as mean numbers of mites at all stages per cm^2, there were significant differences in mite populations between these two foliage densities ($p < 0.05$; Table 8.26). Both mite densities were found to be highest on M16 at one vine per string. For the mite densities of individual stages, mean numbers of adult females, adult males, immatures and eggs on a leaf are illustrated in Fig. 8.21, 8.22, 8.23 and 8.24, respectively. The mean numbers of mites per leaf ranged from 0.000 to 2.833 for adult females, 0.000 to 1.667 for adult males, 0.333 to 51.833 for immatures and 0.667 to 69.667 for eggs. It was also found that the mite densities for all stages were highest on M16 at one vine per string.

Fig. 8.25 shows the linear regression relationship between all mite stages on a leaf and those caught using the adhesive tape. From this figure, it can be seen that the prediction of numbers of all mite stages on a leaf can be made from the number of all stages on the adhesive tape ($r^2 = 0.619$; Fig. 8.25A). When the raw data were transformed by log (x+1), the coefficient of determination (r^2) was increased to 0.858, indicating that the latter relationship was more reliable (Fig. 8.25B).

In addition, means for light intensity, relative humidity and temperature within plant canopy of the four hop genotypes at the two foliage densities are presented in Table 8.27, 8.28 and 8.29, respectively. These microenvironmental conditions between different foliage densities did not vary significantly ($p \geq 0.05$). Nevertheless, the light intensity of

plant canopy at three vines per string tended to be lower than that at one vine per string. On the other hand, the relative humidity tended to be higher at three vines per string than at one vine per string. In terms of the hop genotypes, the variation in light intensity was not significant ($p \geq 0.05$), whereas the variation in relative humidity and temperature were significant ($p < 0.05$).

Table 8.25. Average numbers of total mites per leaf on four genotypes of hops at two vine densities on the second occasion of sampling under glasshouse conditions.

Genotype (p=0.0001**)	Vine density (p=0.0677ns)		Mean per leaf for each genotype (PLSD = 34.7640)
	1	3	
M7	9.8333	40.0000	24.9167
M16	126.0000	22.0000	74.0000
M17	19.3333	17.8333	18.5833
M24	1.1667	5.1667	3.1667
Mean per leaf for each vine density	39.0833	21.2500	

Table 8.26. Average numbers of total mites per cm^2 on four genotypes of hops at two vine densities on the second occasion of sampling under glasshouse conditions.

Genotype (p=0.0001**)	Vine density (p=0.0087**)		Mean per cm^2 for each genotype (PLSD = 0.5875)
	1	3	
M7	0.2449	0.6321	0.4385
M16	2.3203	0.3288	1.3245
M17	0.4064	0.3398	0.3731
M24	0.0233	0.0968	0.0601
Mean per cm^2 for each vine density	0.7487	0.3494	

Fig. 8.21. Average numbers of adult females per leaf on four genotypes of hops at two different foliage densities on the second occasion of sampling under glasshouse conditions.

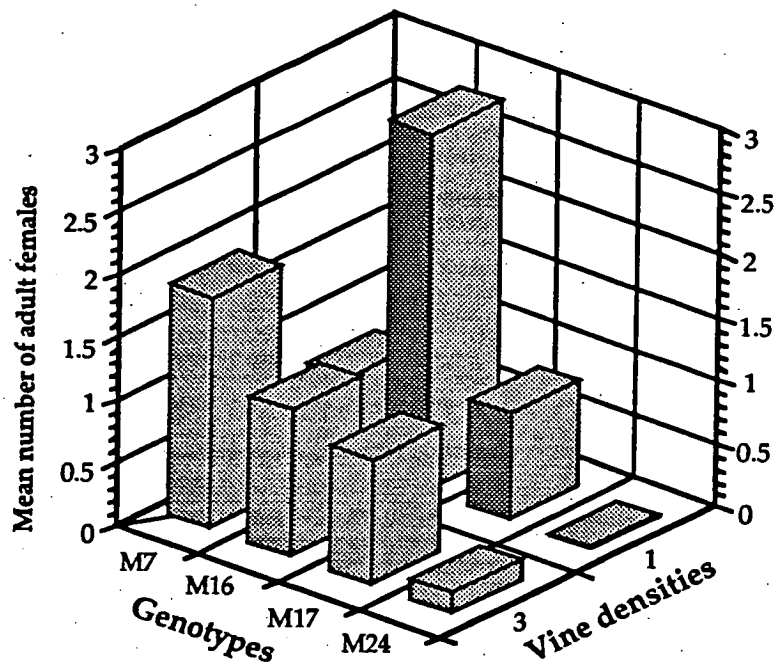


Fig. 8.22. Average numbers of adult males per leaf on four genotypes of hops at two different foliage densities on the second occasion of sampling under glasshouse conditions.

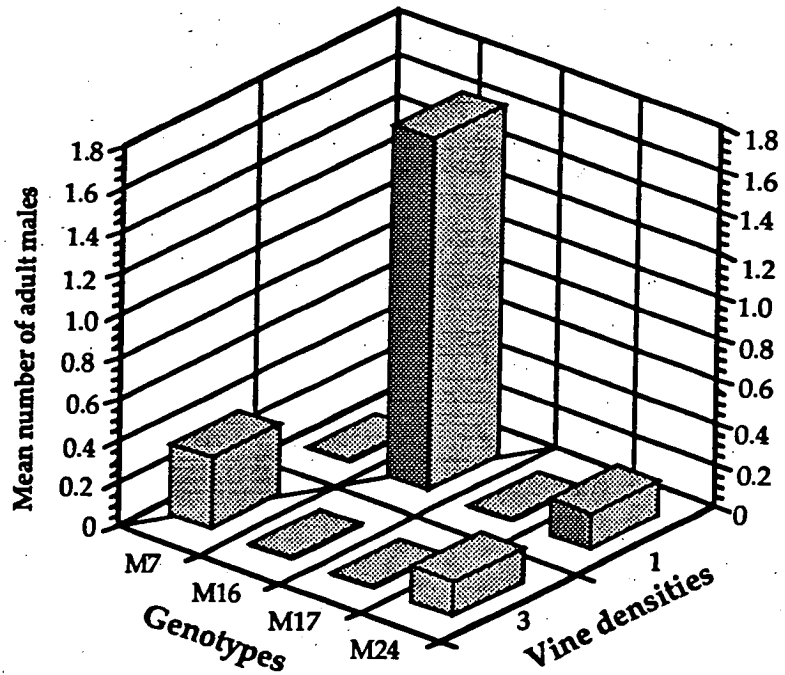


Fig. 8.23. Average numbers of immatures per leaf on four genotypes of hops at two different foliage densities on the second occasion of sampling under glasshouse conditions.

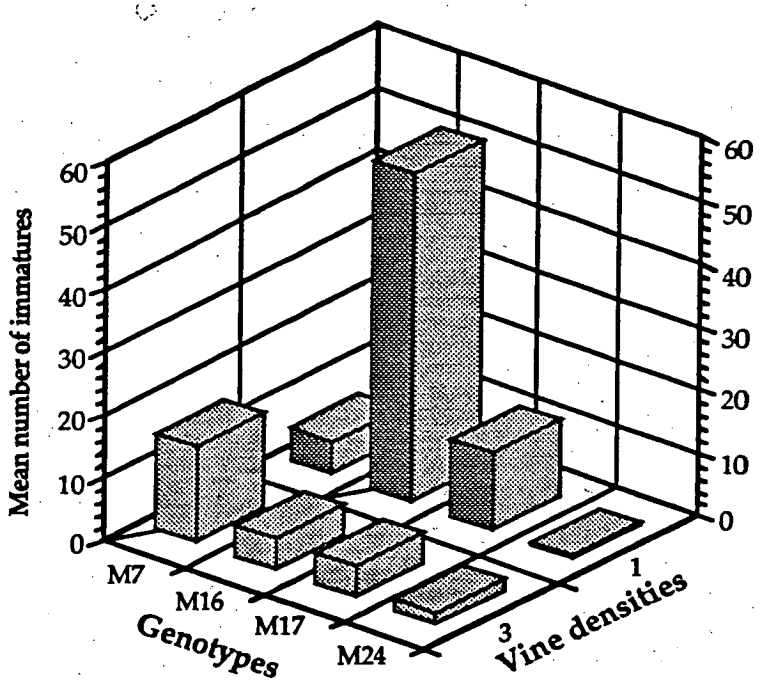


Fig. 8.24. Average numbers of eggs per leaf on four genotypes of hops at two different foliage densities on the second occasion of sampling under glasshouse conditions.

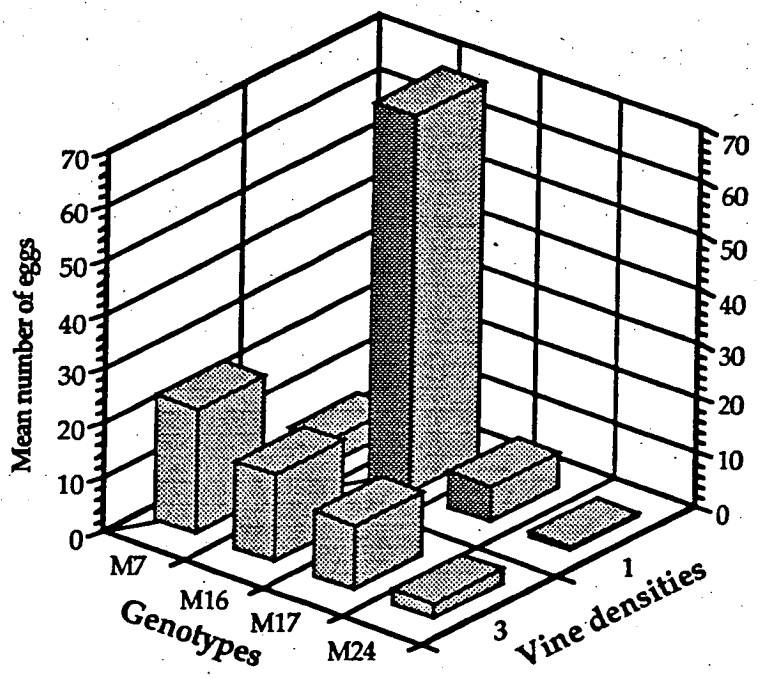
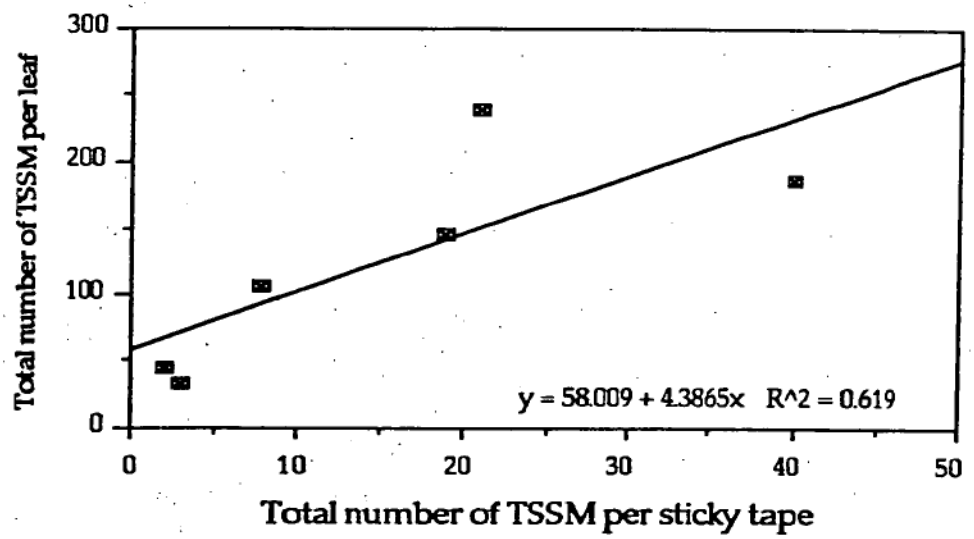


Fig. 8.25. Linear regression of total numbers of TSSM per leaf (Y) on total numbers of TSSM per adhesive tape (X).

A. for the original data



B. for the transformed data

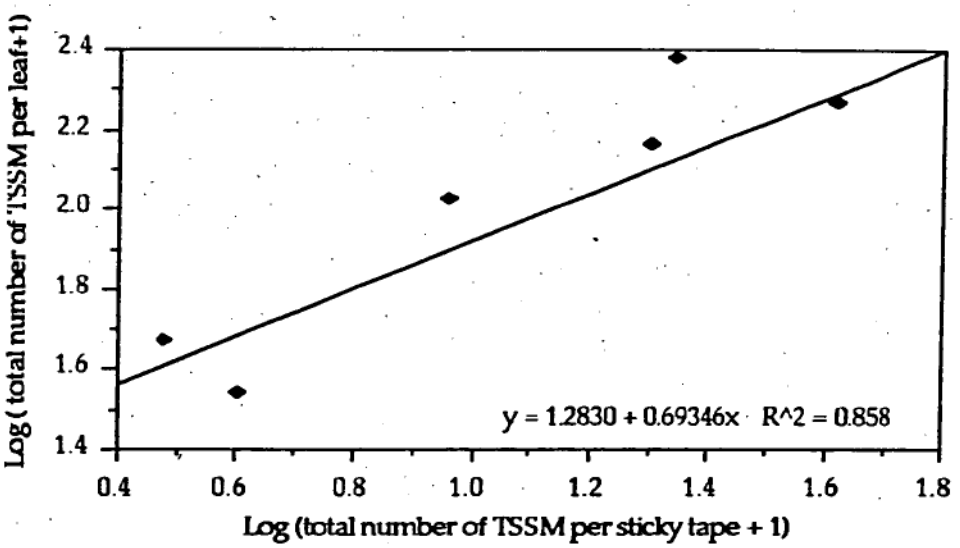


Table 8.27. Average light intensity (microEinsteins/m^2/sec) within the plant canopy of four hop genotypes at two foliage densities under glasshouse conditions.

Genotype (p=0.7975ns)	Vine density (p=0.1615ns)		Overall mean for each genotype
	1	3	
M7	610.00	496.67	553.33
M16	536.67	263.33	400.00
M17	656.67	483.33	570.00
M24	633.33	416.67	525.00
Overall mean for each vine density	609.17	415.00	

Table 8.28. Average relative humidity (%) within the plant canopy of four hop genotypes at two foliage densities under glasshouse conditions.

Genotype (p=0.0092**)	Vine density (p=0.1138ns)		Overall mean for each genotype (PLSD = 2.0914)
	1	3	
M7	39.967	40.300	40.133
M16	40.600	43.033	41.817
M17	43.800	44.167	43.983
M24	40.333	41.900	41.117
Overall mean for each vine density	41.175	42.350	

Table 8.29. Average temperature (°C) within the plant canopy of four hop genotypes at two foliage densities under glasshouse conditions.

Genotype (p=0.0318*)	Vine density		Overall mean for each genotype (PLSD = 0.1077)
	1	3	
M7	21.50	21.50	21.50
M16	21.53	21.53	21.53
M17	21.63	21.63	21.63
M24	21.67	21.67	21.67
Overall mean for each vine density	21.58	21.58	

8.4 DISCUSSION

8.4.1 Under field conditions

The results from the present study show that hop-canopy microenvironments can play an important role in seasonal population development of TSSM and that this role was amplified by hop susceptibility to the mites. For the two hop genotypes studied, naturally occurring populations of TSSM tended to increase more rapidly on sparsely leaved canopies than on densely leaved canopies. However, this is in contrast to the findings of Burdajewicz and Cone (1972) who reported that TSSM population increase was positively correlated with the numbers of hop vines per string. This difference in the buildup of mite populations may be due to the different hop genotypes used as host plants for comparing high with low foliage densities. In the present study, the effect of canopy microenvironments on TSSM population dynamics was found to be more adverse on the susceptible genotype used than on the resistant one.

Under natural conditions, several variables may have been responsible for the microenvironmental effect on mite populations. A few of these are relative humidity, temperature and host plant condition. During a growing season, the combined effect of all the three variables has been usually accepted to account for the variation in mite populations.

Because of transpiration from plant leaves, it is a common assumption that there is layering of water vapor near the leaf surfaces resulting in a gradient in humidity such that a high humidity is present in the region next to the leaf, where the mites live, even when ambient humidity is low. Nonetheless, the humidity of the air surrounding the leaves is influenced by plant cover (Nickel, 1960). Thus, the humidity at the leaf surface on a plant within a densely leaved canopy would tend to

be higher than that on a plant with a sparsely leaved canopy. Two possible mechanisms are suggested through which relative humidity may produce an adverse effect on mite populations: (1) the dense canopy may promote and sustain conditions of high relative humidity by a reduction in air movement and temperature. This would retard the metabolic processes of spider mites (Boudreaux, 1958); (2) the high relative humidity could provide optimal conditions for the spread and growth of fungal parasites of spider mites (Selhime and Muma, 1966). The former mechanism is demonstrated in the present study. In contrast, with sparse canopy relative humidity would at most times be equivalent to that of the general environment.

According to Simpson and Connell (1973), humidity conditions having the greatest influence are those in the actual habitat of the spider mites, i.e., the lower surface of the leaf, but this is an elusive factor to measure. Relative humidity is closely interrelated with temperature, and these two factors may be subject to considerable change within variable periods in this microhabitat. Both factors are influenced by the surrounding air temperature, as well as by the amount of available water in the soil, air currents, leaf type, angle and intensity of light to which the leaf is exposed, and other factors (Miller and Saunder, 1923). Two of these other factors comprise the exchange of infrared radiation between the leaf and other materials and the amount of water present in the atmosphere (Curtis, 1936). Gates et al. (1968) showed that leaf temperature frequently exceeded air temperature by as much as 10°C. Later, Simpson and Connell (1973) indicated that the microhabitat of spider mites on plant leaves attained higher maximum and lower minimum temperatures than those of the surrounding air. Luczynski et al. (1990) suggested that modifying the microclimate of leaf surface may affect mite oviposition indirectly. In the present study, it was found that TSSM and its predatory

mite were present at record low levels in the dense canopy and this may have been linked to adverse effects of microenvironmental conditions. However, the measurement of relative humidity and temperature influencing the microenvironment of the hop canopy were not sufficiently detailed to prove this.

In addition, the variation in mite abundance is also associated with host plant condition. Perring et al. (1986) suggested that the condition which results in plant stress can alter the microenvironment within the crop canopy. Toole et al. (1984), using a Banks grass mite population growth model, demonstrated that changed microenvironmental conditions caused rapid mite density increases on plants during moisture stress episodes. Perring et al. (1983) found that plant substances important in spider mite nutrition became more nearly optimal for spider mite density increase as plants aged and became water stressed. In the present study, mites were more abundant on the susceptible genotype (M26) which grew faster and had a longer vegetative period as compared with the resistant one (M25), indicating that it was not only hop phenology that influenced TSSM densities, but also conditions experienced by hop leaves during the vegetative period. Nevertheless, it was apparent that mite populations on young leaves in the upper part of the hop canopy were significantly greater than those on older lower leaves later in the season because of a reduction in the suitability of hop leaves to favour mite populations.

With regard to hop production, a positive correlation between the total dry weight of cones per string and the number of vines per string was noted. However, actual cone yield per vine decreased with increasing numbers of vines per string. A consistent percentage content of alpha acid was found among different foliage densities. Rybacek (1991) suggested that the reduction of light intensity resulting from shadowed

shoots reduces the numbers of flower buds, flowers and cones. It was also apparent that the resistant genotype (M25) had significantly higher cone production than did the susceptible genotype (M26) although the percent alpha acid of M25 was significantly less than that of M26.

In conclusion, the results of the analysis of the mite populations that show an inverse relationship between mite densities and the number of hop vines per string appear to conflict with the results of other investigators as mentioned earlier. However, the results of this study do provide a better understanding of previously published data on the microenvironments of hop canopy and TSSM performance.

8.4.2. Under glasshouse conditions

The results of this study tend to confirm the hypothesis that a sparsely leaved canopy is more prone to heavy mite infestation than the densely leaved one. Artificially mite infested plants had a greater density of mites per unit area on a canopy trained with one vine per string than on one with three vines per string under controlled conditions. Of the microenvironmental variables, light intensity and relative humidity declined slightly as the number of vines per string increased, while temperature did not vary between different foliage densities. In addition, the variation in mite populations appeared to be associated with the susceptibility of hop genotypes studied, whereas the single reading of relative humidity within plants suggested that humidity was not related to hop susceptibility. However, a continuous record of relative humidity within the canopies, which was not obtained because of the absence of appropriate equipment, could well have reflected the result obtained within the laboratory i.e. that high humidity suppressed population growth.

CHAPTER 9 PHYSIOLOGICAL AND CHEMICAL RESPONSES OF HOP PLANTS TO FEEDING OF TSSM

9.1. INTRODUCTION

It is generally accepted that physiological and chemical traits of many plant species change in response to herbivory. For spider mites, Sances et al. (1979b) found decreased stomatal opening at low levels of mite infestations to be a primary plant response to mite feeding. Similarly, transpiration and photosynthesis were affected at low infestation levels; both were also dependent on stomatal opening. Photosynthesis was further decreased with increased mite infestations, indicating additional cellular damage within plant leaves (Sances et al., 1979a). Mothes and Seitz (1982) reported that unpunctured cells adjacent to the punctured, collapsed cells show damage including degeneration of the chloroplasts and loss of chlorophyll. This damage to unattacked cells results in marked reductions in photosynthesis and other metabolic activities. Moreover, mite injury can influence the metabolism of secondary plant products (DeAngelis et al., 1983c). In the past, loss of chlorophyll and subsequent loss of photosynthetic activity due to mite damage has been observed for leaves of apples (Boulanger, 1958; Hall and Ferree, 1975); cassava (Bellotti and Byrnė, 1979); peppermint (DeAngelis et al., 1983b); beans (Mothes and Seitz, 1982); and soybeans (Carlson et al, 1979). However, adverse effects of mite feeding on physiological and chemical traits of hop foliage have not been investigated.

The objectives of the present work were to examine the changes in stomatal conductance and photosynthetic rate of hop leaves to TSSM injury for gaining a greater understanding of pest resistance mechanisms in plants and to determine what changes in secondary metabolites may have occurred in hops due to mite damage to leaves. This is because a

thorough knowledge of the mechanism of resistance is helpful for developing an effective breeding program (Kennedy, 1978).

9.2. MATERIALS AND METHODS

9.2.1. Physiological response

9.2.1.1. Under glasshouse conditions: The three genotypes of hops used to determine leaf photosynthesis and stomatal conductance were M4, M9 and M27. On 16 October 1992, these three genotypes were propagated from cuttings, except that M9 was planted with either cuttings or rootstocks. The cuttings were made of a stem and three pairs of leaves at the apex. All plants were maintained in 21-cm pots containing a mixture of sand and peat moss (60:20), and were grown in an unheated glasshouse under natural lighting conditions. The pots were arranged in a randomized complete block design with six replications on the floor of the glasshouse. After eight weeks, one leaf of the fifth pair below the apex was chosen from each plant for physiological measurements with a Leaf Chamber Analyzer No.2 (Analytical Development Co. Ltd., Hoddesdon, Herts., U.K.). These leaves were then paired with the opposite leaf as one kind of control. An adhesive barrier, composed of transparent plastic sheet (2 X 2 cm) smeared with lanolin, was placed on cotton wool encircling each leaf petiole to prevent movement of mites between leaves. In order to determine the effect of the barrier on leaf photosynthesis or stomatal conductance, the opposite leaf was not treated. One week later, physiological measurements were taken for each leaf with the Leaf Chamber Analyzer No.2 (LCA 2). Thereafter, the leaf with the barrier on each plant was artificially infested with a single density of TSSM taken from the culture mentioned in Chapter 6, by using an infestation level of 15 teneral females per leaf. In addition, the barrier was placed around the petiole of the opposite leaf which did not receive

any mites. Physiological measurements were taken at three days and two weeks following infestation. Photosynthesis and stomatal conductance were determined for each leaf with the LCA 2. Mite densities were also determined at the end of this study by removing the leaf and counting the number of motile stages under a binocular microscope (10X).

9.2.1.2. Under field conditions: Field observations were conducted on hop plants at the Horticultural Research Centre during the 1992/93 growing season. Because of the adverse effect of hot weather and strong wind on hop leaves in this season, the undamaged genotypes used, and the number of plants per genotype, were: 'M26' (3), 'M27' (2), 'M23' (1), 'M18' (1). These hop plants were distributed in a completely random pattern. On 15 January 1993, a leaf pair at the height of 1.8 m was chosen from each plant and the petiole of each leaf was encircled with the barrier described above. A single density of TSSM (15 teneral females) was transferred to one leaf of each pair. Twelve days after innoculation, photosynthesis and stomatal conductance were determined for each leaf with the LCA 2 mentioned above.

9.2.1.3. Statistical analyses: Analysis of variance was used to detect differences in physiological parameters among different hop genotypes. Mean comparisons were performed using PLSD at the 5% level. In addition, an unpaired t-test was also employed to distinguish between two treatment groups.

9.2.2. Chemical response

Preliminary studies on phenolic compounds and alkaloids in hop leaves were carried out during the 1992/93 growing season. The following genotypes grown at the Horticultural Research Centre were studied: M4, M9, M26 and M27. Fully expanded leaves of these four genotypes were collected and kept in a cold room at 4°C. For each genotype, five grams of the fresh leaves were homogenized for 5 min in

methanol (MeOH) and water (H_2O) (4:1) (10 X leaf weight). The mixture was then filtered through Whatman No.1 filter paper in a glass funnel. The filtrate was evaporated in a water bath (35°C) until 1/10 of the original volume remained. This filtrate was acidified with 2M H_2SO_4 and then extracted with chloroform ($CHCl_3$) (X 3). The $CHCl_3$ extract was dried by evaporation and redissolved with 1 ml methanol for spotting on 0.2 mm 20 X 20 cm pre-coated silica gel $60F_{254}$ TLC aluminium sheets (Merck) in order to detect phenolic compounds. After development in acetic acid (HOAc) and CH_3Cl_3 (1:9) solvent systems to a distance of 17 cm, the sheets were dried at room temperature and exposed to short wave UV light in order to detect the spots of moderately polar extracts. For the aqueous acid layer, the solution was basified to pH 10 with NH_4OH and then extracted with $CHCl_3$ - MeOH (3:1; twice) and $CHCl_3$ (once). Next, the $CHCl_3$ - MeOH extract was dried by evaporation and redissolved with 1 ml methanol for spotting on the TLC sheets to determine leaf alkaloids. The sheets were developed in MeOH - NH_4OH (200:3) solvent system to a distance of 17 cm and dried at room temperature. Subsequently, the dry sheets were exposed to short wave UV light to detect the spots of the basic extract (after Harborne, 1984). A total of five runs was performed for each genotype.

To determine the response of hop foliage to mite infestation, the following genotypes grown in a glasshouse were studied: M4 and M27.. When potted hop plants were eight weeks old, four fully-expanded leaves of each genotype were infested with teneral females obtained from the culture mentioned earlier, by using an infestation level of 15 mites per leaf. In addition, the adhesive barrier was also placed around the petiole of each leaf. One week later, the leaves were collected and all mite stages removed by a small camel's-hair brush. Then, these infested leaves were used for analysis of phenolic compounds as mentioned above. Because

leaves of a pair have similar chemical components, the leaf opposite each infested leaf was also collected as one kind of control.

9.2.3. Preliminary studies on damage caused by TSSM to the quality of hop leaves and hop cones

Two observations were conducted to investigate the effects of mite feeding on hop leaf volatiles. In the first observation, fresh uninfested leaves were collected from 9-wk-old field hop plants of M4 or M27 grown at the Horticultural Research Centre. Both immature and senescent leaves were avoided, and all the leaves studied were ca. the same age, size, colour and condition. The leaves were cut at the petiole-limb intersection. Approximately 20 grams of these leaves for each genotype were placed separately in 100 ml plastic containers, fitted with a tight fitting lid. There were two treatments for each genotype: mite-feeding and untreated control. For the mite-feeding treatment, the leaves in each container were artificially infested with 100 adult females for two hours at room temperature. Following this treatment, volatiles (5 ml) were collected from each container using a syringe. The volatiles were analyzed by gas chromatography (Hewlett Packard-5890 gas chromatograph) using a 24 meter X 0.32 mm X 0.17 µm film thickness HP 1 cross linked methyl-silica capillary column (SGE Pty. Ltd.). The gas chromatograph was programmed from 35° to 200°C at 6°C/minute and 200° to 290°C at 30°C/minute for 3 minutes using helium as carrier gas (70KPa and a flow rate of approximately 2 ml/minute).

In the second observation, only genotype M27 (Pride of Ringwood) was used to examine the effect of natural mite infestation of hop volatile. Fresh leaves and cones were collected from either infested or uninfested areas in Hop Yard No.3 at Bushy Park. Then, the volatiles of leaves and cones obtained from each area were analyzed via gas chromatography as described above.

A preliminary study was also conducted to determine foliage essential oils using analyses of fresh steam distillates. Again, fresh leaves of M27 collected from both infested hop and uninfested plants in Hop Yard No. 3 were used.

9.3. RESULTS

9.3.1. Physiological response to mite damage

A comparision of leaf gas exchange characteristics between different hop genotypes is presented in Fig. 9.1. Analysis of variance, showed significant differences ($p < 0.05$) in photosynthesis among the three genotypes studied (Fig. 9.1A). The photosynthesis of M4 and M27 was significantly higher than M9. For stomatal conductance, significant differences ($p < 0.05$) among the three genotypes were also detected (Fig. 9.1B). The leaves of M27 had the highest stomatal conductance, followed by those of M4 and M9.

Fig. 9.2 shows leaf gas exchange characteristics of hop plants propagated from different planting materials. According to unpaired t-tests, there were no significant differences in either photosynthesis or stomatal conductance between hop plants grown from cuttings and those planted from rootstocks ($p \geq 0.05$). Nevertheless, these two gas exchange characteristics of plants obtained from cuttings tended to be higher than those of the rootstock plants.

A comparison of the effect of sticky barriers on leaf photosynthesis and stomatal conductance for treated and control (uninfested) leaves is presented in Fig. 9.3. Since the sky was cloudy on the measuring date, only leaves on hop plants of M9 were used. An unpaired t-test showed no significant differences in photosynthesis as well as stomatal conductance between these two leaves ($p \geq 0.05$).

Fig. 9.1. Gas exchange characteristics of hop leaves collected from three genotypes: (A) photosynthesis; (B) stomatal conductance.

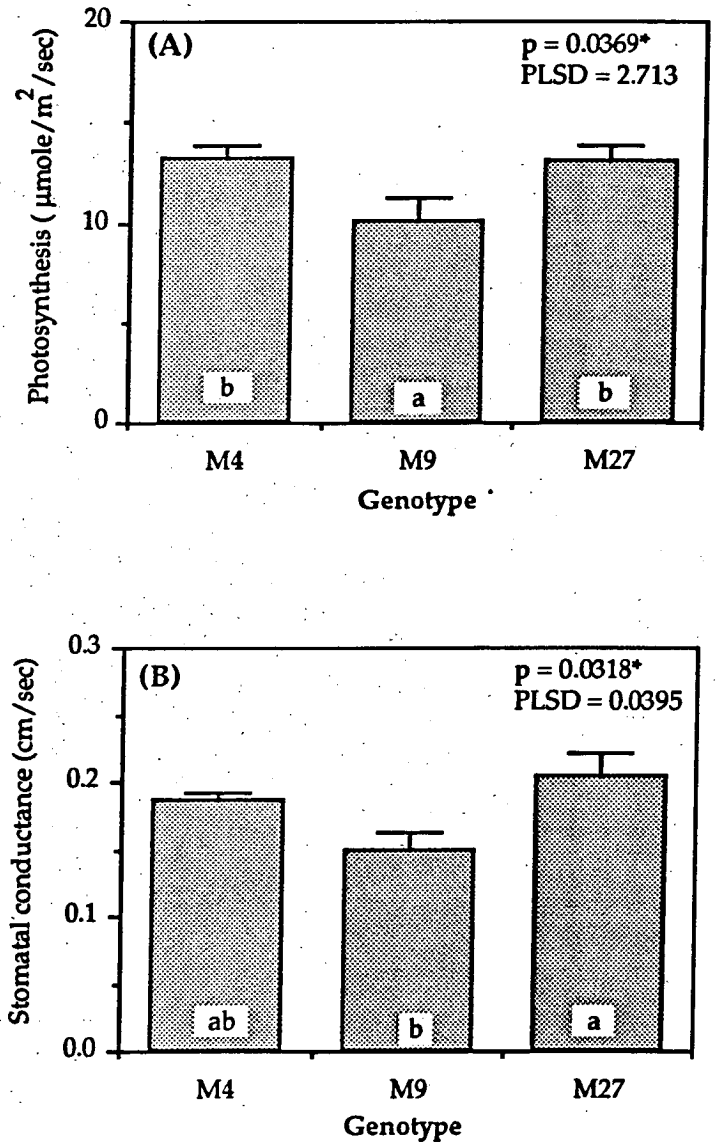
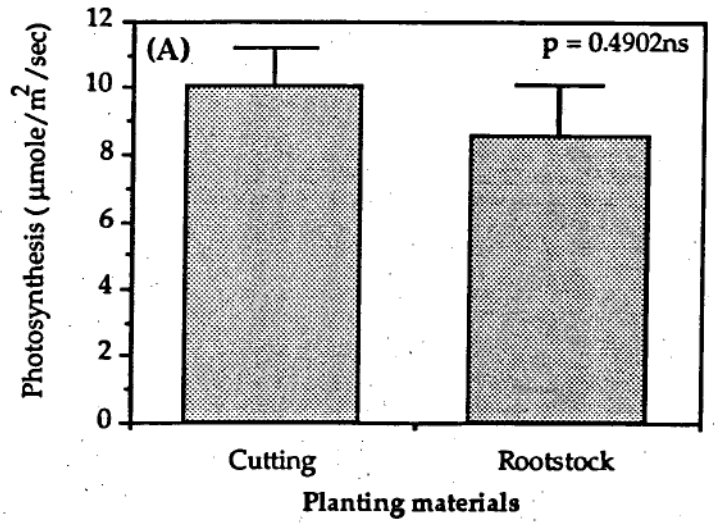


Fig. 9.2. Gas exchange characteristics of leaves on hop plants propagated from different planting materials: (A) photosynthesis; (B) stomatal conductance.



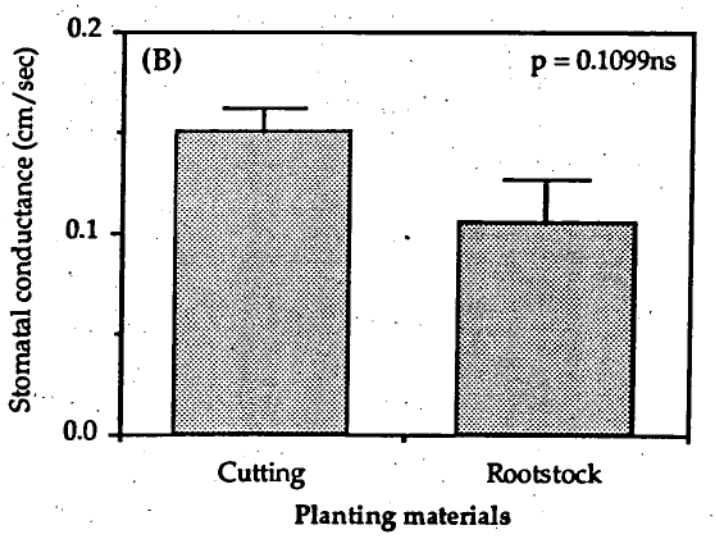
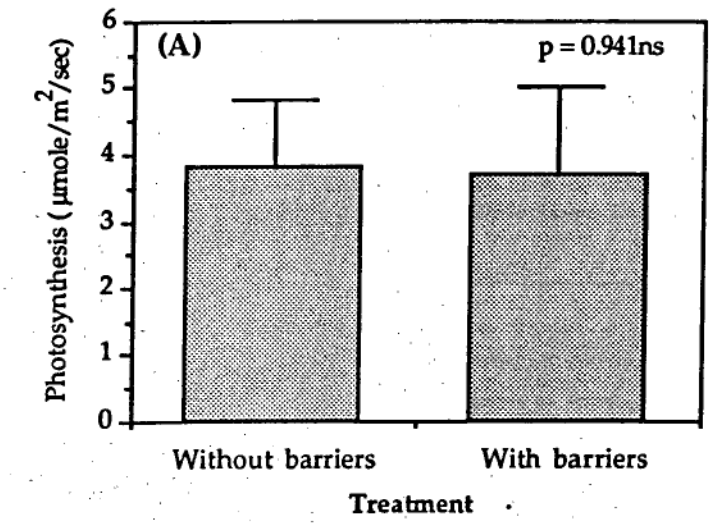
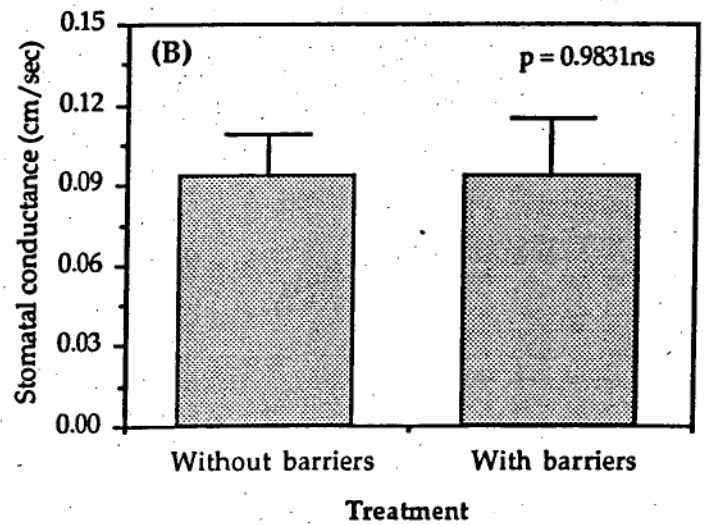


Fig. 9.3. Gas exchange characteristics of hop leaves affected by the sticky barrier: (A) photosynthesis; (B) stomatal conductance.



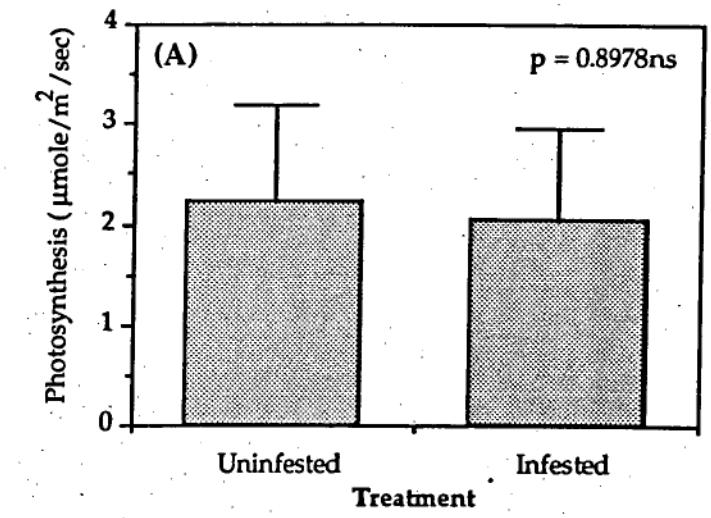


For TSSM feeding damage, the gas exchange characterstics of infested leaves of hop plants grown under glasshouse conditions at 3 and 14 days after inoculation in comparison with the uninfested ones are presented in Fig. 9.4 and 9.5, respectively. Due to the cloudy sky, the data for Fig. 9.4 were obtained from all the rootstock plants of M9, while those for Fig. 9.5 were obtained from only three rootstock plants of M9. No significant differences in photosynthesis or stomatal conductance were found between infested and uninfested leaves 3 or 14 days after inoculation. However, the average values of these two gas exchange characteristics tended to be higher on uninfested leaves than on infested ones 14 days after inoculation. It was apparent that photosynthesis was reduced by 8.05 and 60.76% and stomatal conductance by 13.23 and 57.14% at 45 mite-days per leaf (3 days after inoculation) and 1367.33 mite-days per leaf (14 days after inoculation), respectively.

The comparison of gas exchange characteristics between infested leaves and uninfested ones of hop plants grown under field conditions is shown in Fig. 9.6. Even though the values of photosynthesis or stomatal conductance between infested leaves and uninfested ones did not differ significantly ($p \geq 0.05$), these physiological parameters of uninfested leaves tended to be higher than those of infested ones. It was found that photosynthesis was reduced by 35.41% and stomatal conductance by 9.45% 12 days after inoculation.

In addition, a significant, positive, linear regression was observed between photosynthesis and stomatal conductance (Fig. 9.7). This regression was obtained by pooling data taken from all the studies mentioned above.

Fig. 9.4. Comparisons of gas exchange characteristics between uninfested and infested hop leaves 3 days after inoculation: (A) photosynthesis; (B) stomatal conductance.



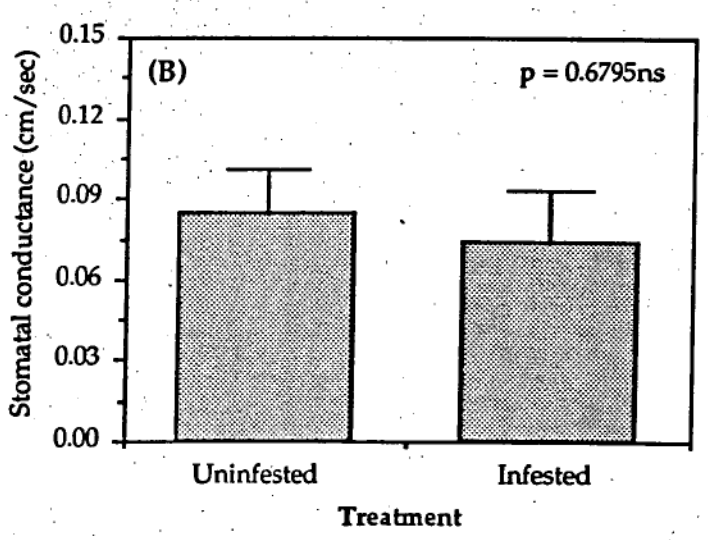


Fig. 9.5. Comparisons of gas exchange characteristics between uninfested and infested glasshouse hop leaves 2 weeks after inoculation: (A) photosynthesis; (B) stomatal conductance.

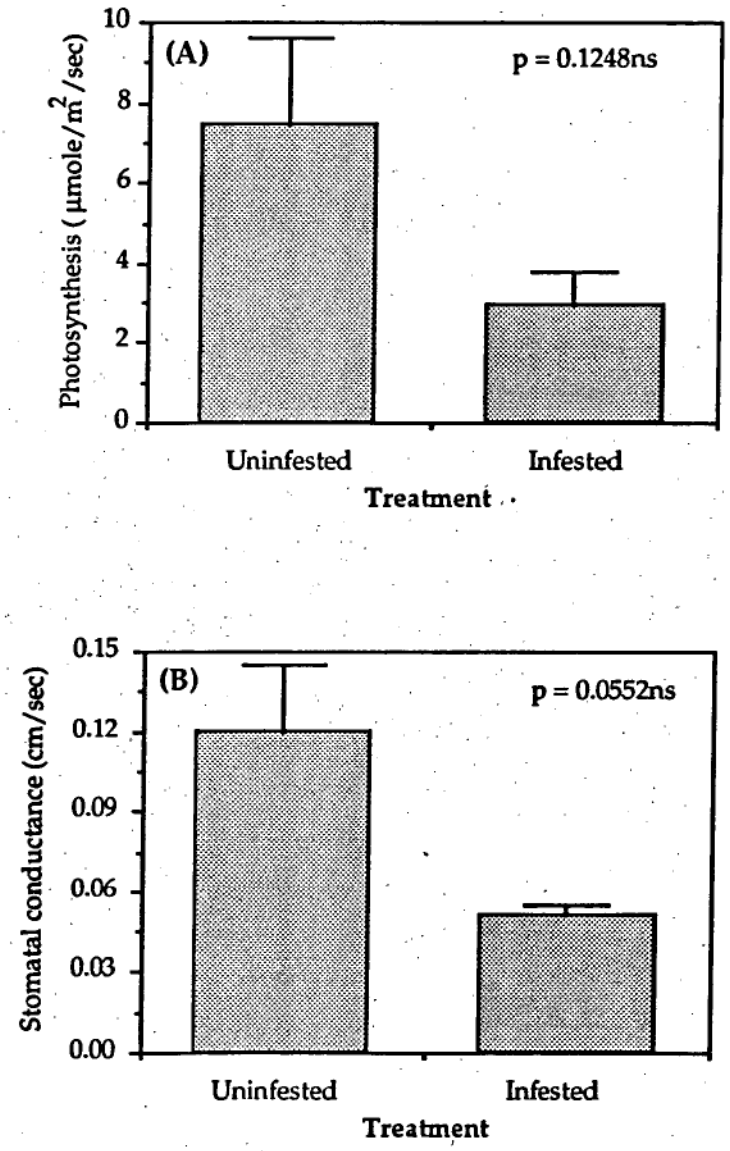
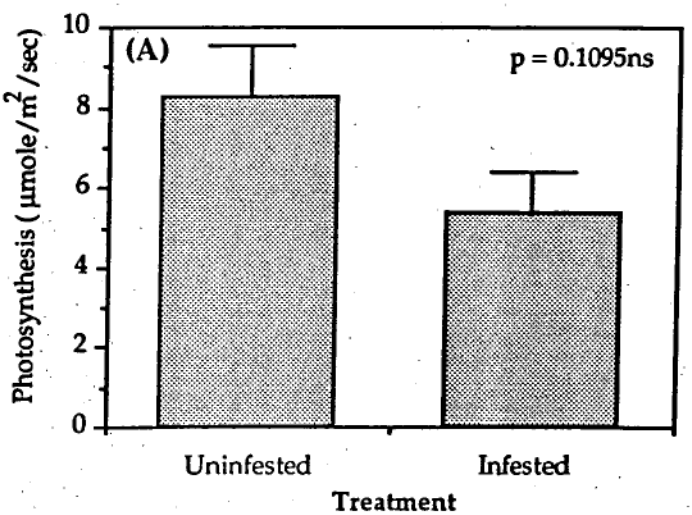


Fig. 9.6. Comparisons of gas exchange characteristics between uninfested and infested field hop leaves 10 days after inoculation: (A) photosynthesis; (B) stomatal conductance.



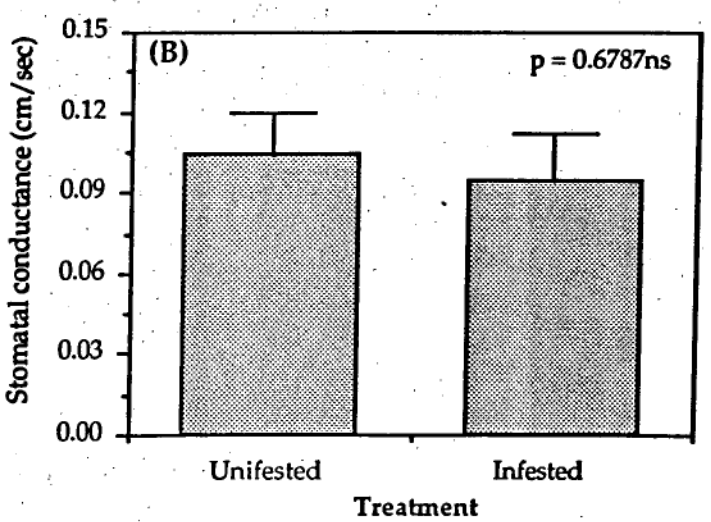
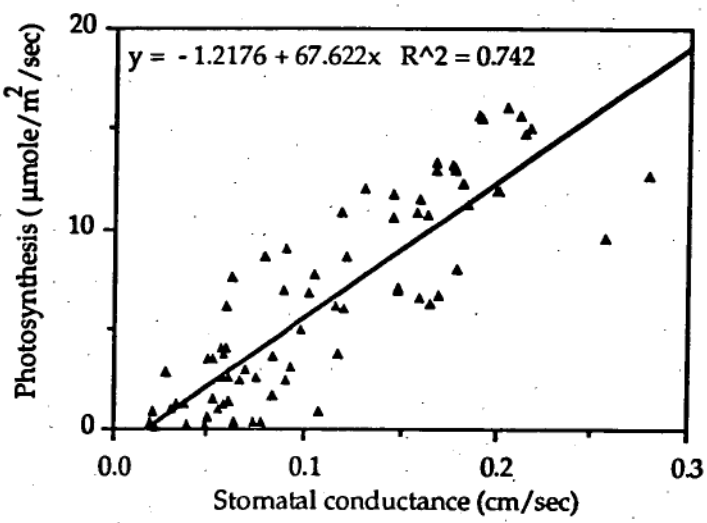


Fig. 9.7. Linear relationship between photosynthesis and stomatal conductance for combined data in the present study; n = 52.



9.3.2. Chemical response to mite damage

Some qualitative variation in chemical compounds of hop leaves were found. For phenolic compounds, TLC of moderately polar extracts of hop leaves collected from the four genotypes studied produced a similar series of spots (Table 9.1). Commonly, the R_f values for these extracts in solvent system HOAc-CH_3Cl_3 (1:9) were 0.50, 0.85, 0.95. In some extracts of hop genotypes M4 and M26, an unclear spot was also detected in the region of R_f 0.18. When alkaloids were separated, TLC of basic extracts of hop leaves collected from all the genotypes used produced only one spot at the R_f value of 0.78 in MeOH-NH_4OH (200:3) solvent system. A comparison of phenolic compounds and alkaloids between infested and uninfested leaves of both M4 and M27 showed no differences in the series of spots detected using this TLC technique.

Table 9.1. Rf values of moderately polar extracts in HOAc-CH_3Cl_3 (1:9) solvent system for four hop genotypes during five running occasions.

Genotype	Rf values				
	1	2	3	4	5
M4	0.50	0.18	0.50	0.50	0.50
	0.85	0.50	0.85	0.85	0.85
	0.95	0.85	0.95	0.95	0.95
		0.95			
M9	0.50	0.50	0.50	0.50	0.50
	0.85	0.85	0.85	0.85	0.85
	0.95	0.95		0.95	0.95
M26	0.18	0.18	0.50	0.85	0.50
	0.50	0.50	0.85	0.95	0.85
	0.85	0.85	0.95		0.95
	0.95	0.95			
M27	0.50	0.50	0.50	0.50	0.50
	0.85	0.85	0.85		0.85
	0.95		0.95		0.95

With regard to volatile compounds of hop foliage, the gas chromatography separations of these compounds are shown in Fig. 9.8, 9.9, 9.10 and 9.11 for uninfested M4 leaves, infested M4 leaves, uninfested M27 leaves and infested M27 leaves, respectively. It was noted that the chromatograms of the uninfested control and leaves infested with mites were similar for each hop genotype; however the quantity of volatile compounds in the chromatograms differed between the two genotypes. For hop cones, the chromatography separation of the volatile compounds obtained from uninfested and infested plants of M27 are shown in Fig. 9.12 and 9.13, respectively. No differences in these two chromatograms were observed. However, the abundance of myrcene in uninfested leaves was higher than that in infested ones.

Fig. 9.8. Chromatogram of volatile compounds of uninfested hop leaves collected from M4.

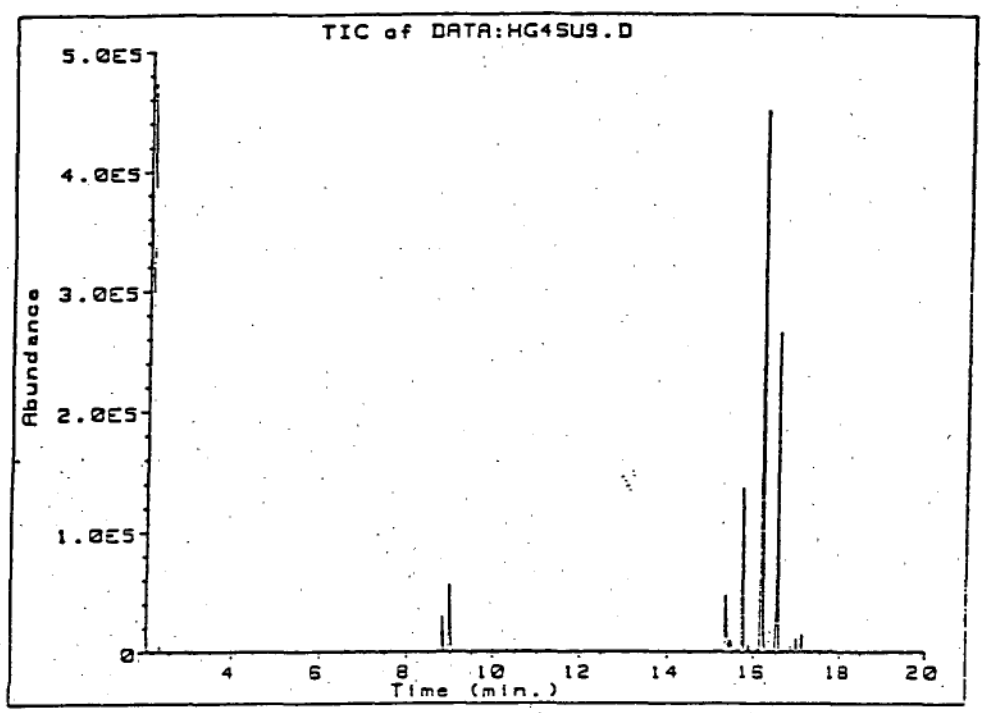


Fig. 9.9. Chromatogram of volatile compounds of infested hop leaves collected from M4.

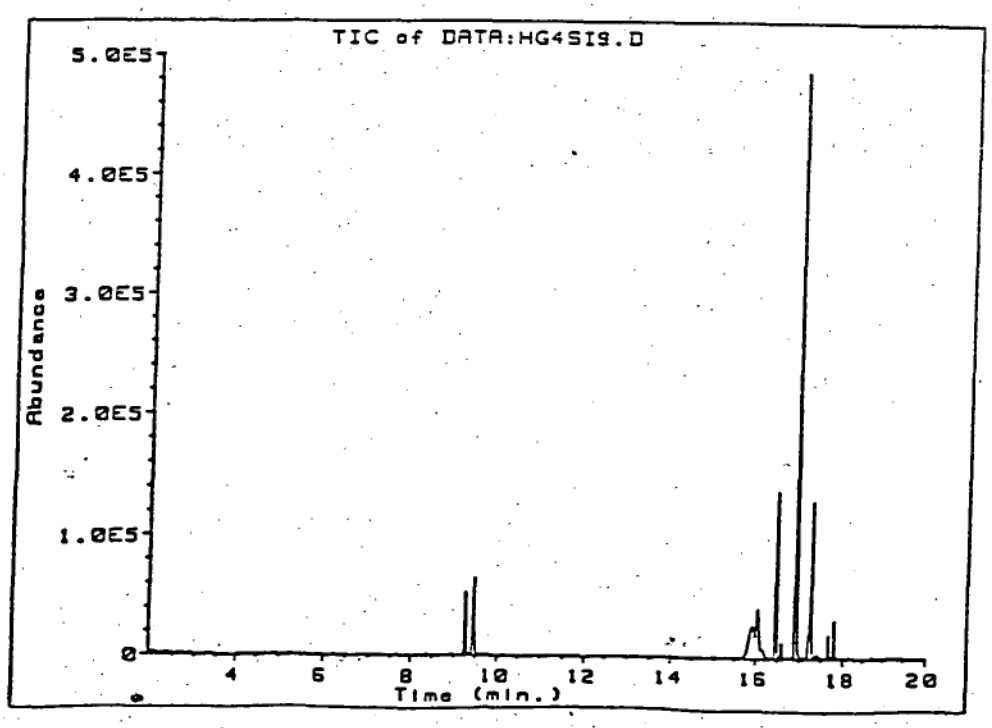


Fig. 9.10. Chromatogram of volatile compounds of uninfested hop leaves collected from M27.

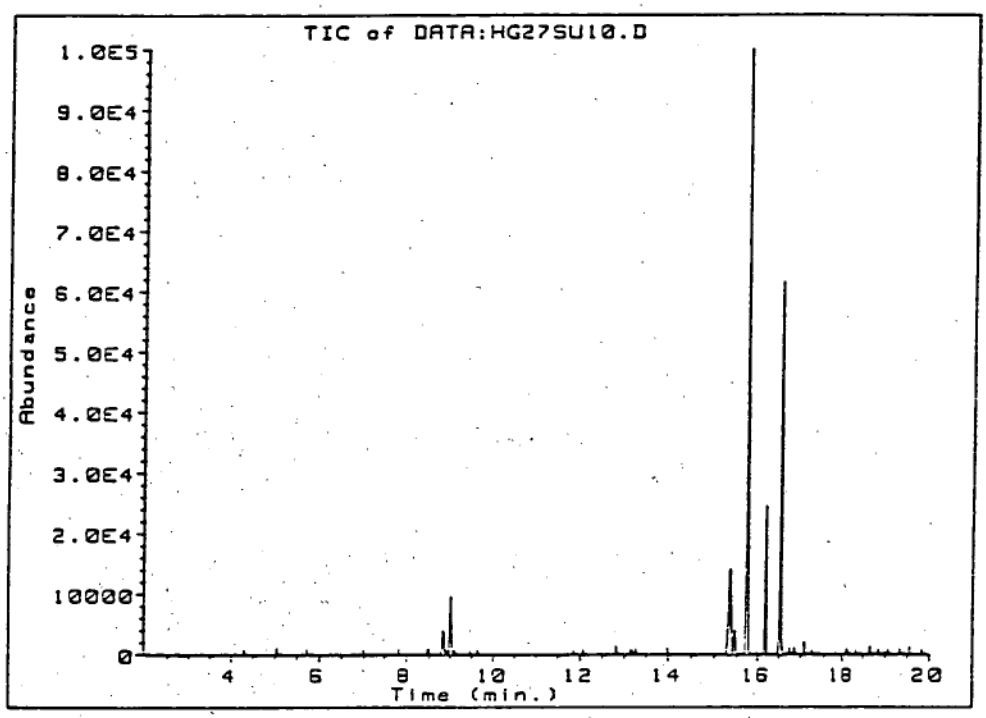


Fig. 9.11. Chromatogram of volatile compounds of infested hop leaves collected from M27.

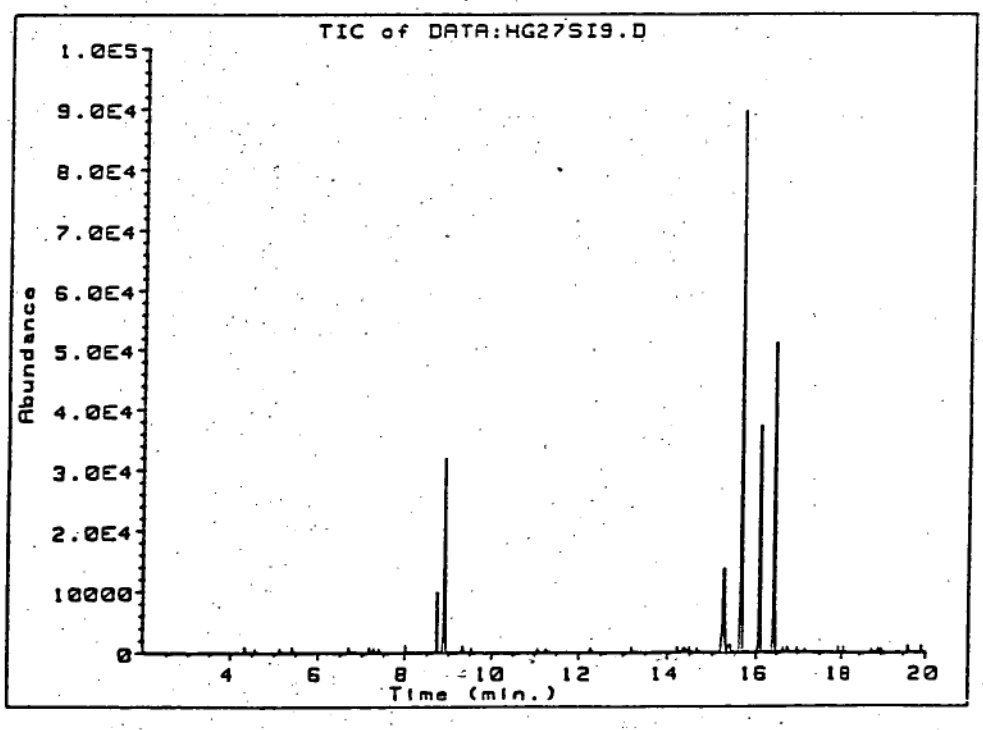


Fig. 9.12. Chromatogram of volatile compounds of hop cones collected from uninfested plants of M27.

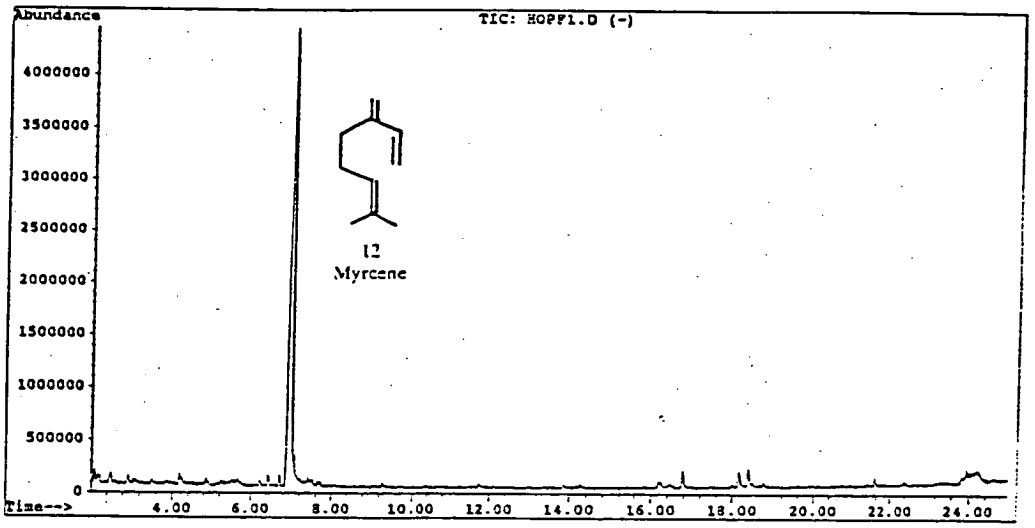
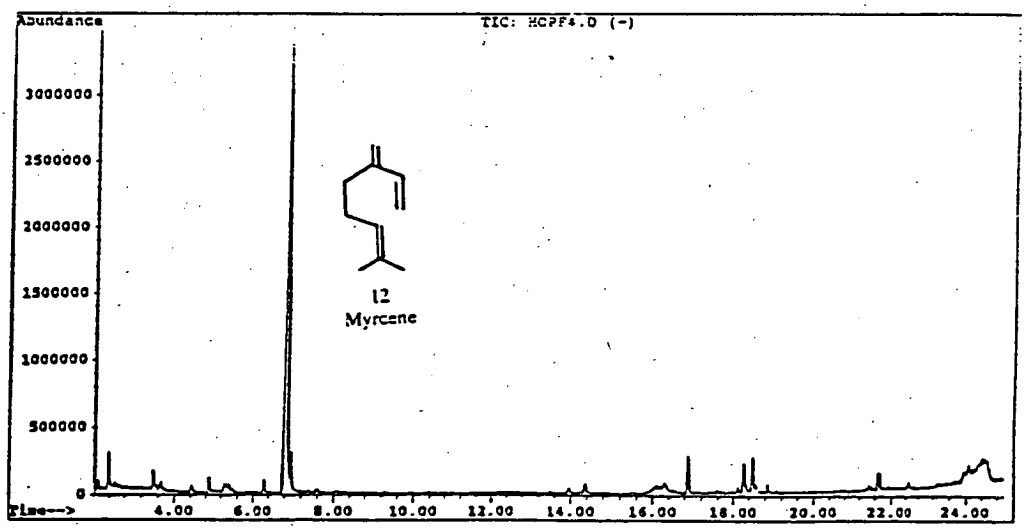


Fig. 9.13. Chromatogram of volatile compounds of hop cones collected from infested plants of M27.



The separation of volatile compounds achieved using the steam distillation technique, is shown in Fig. 9.14 and 9.15 for uninfested and infested leaves of M27, respectively. It was observed that there were no differences in chromatograms between these two foliage treatments due to the feeding damage of naturally occurring mite populations.

Fig. 9.14. Chromatogram of volatile compounds of uninfested hop leaves collected from M27 separated using the steam distillation technique.

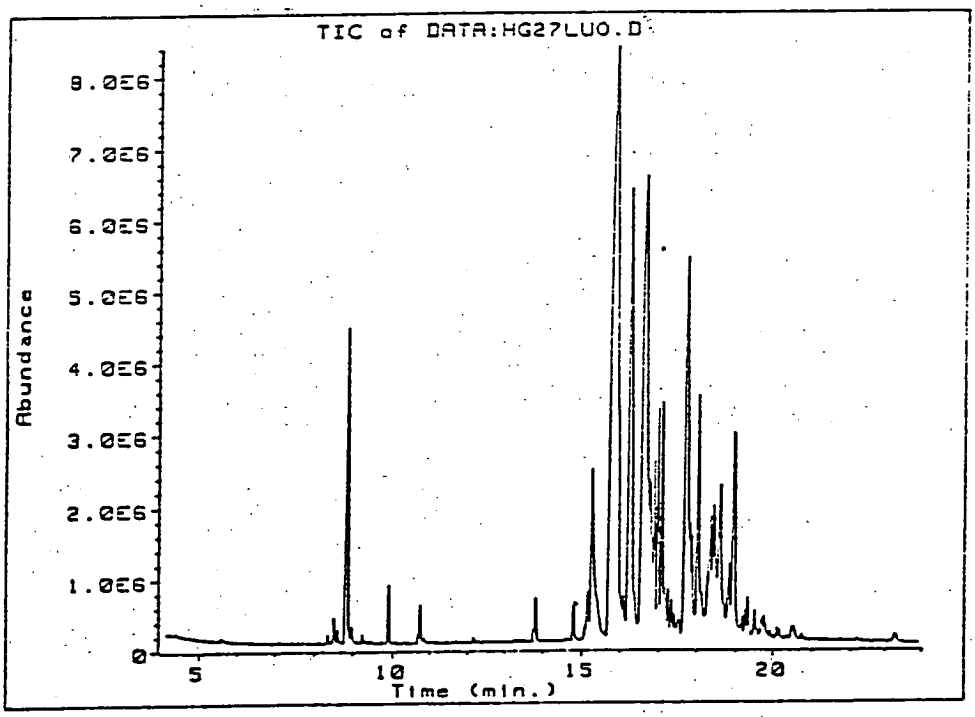
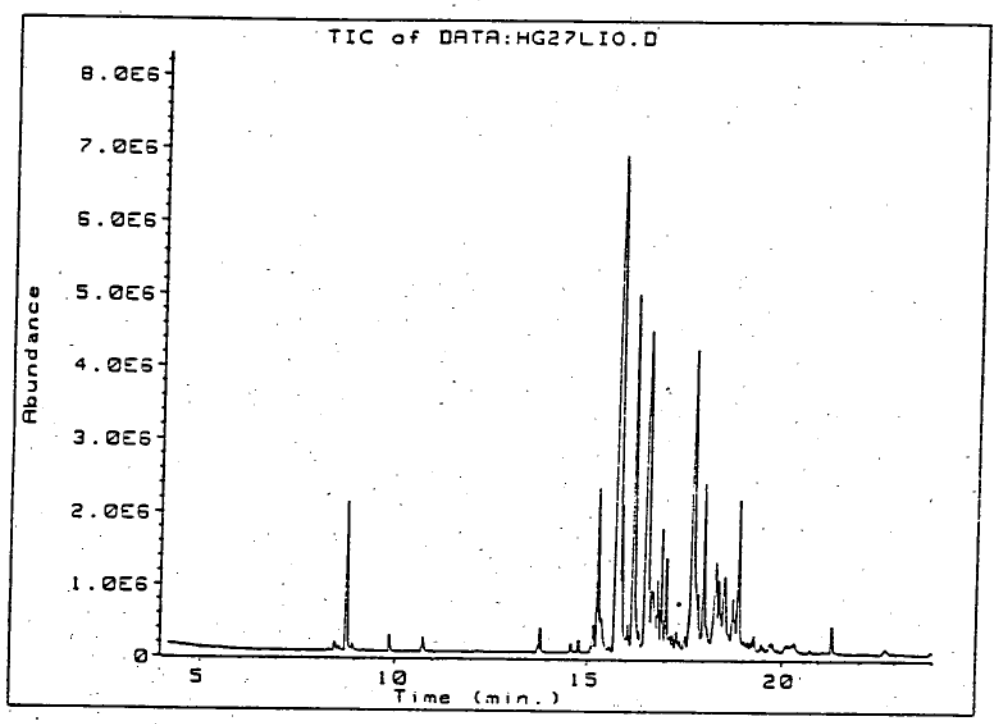


Fig. 9.15. Chromatogram of volatile compounds of infested hop leaves collected from M27 separated using the steam distillation technique.



9.4. DISCUSSION

9.4.1. Physiological response to mite damage

The results from the present study show that TSSM feeding damage in both the field and the glasshouse may lead to a decrease in gas exchange characteristics of hop leaves, including the rate of photosynthesis and stomatal conductance. This is in agreement with Welter et al. (1989) who reported that feeding injury by Pacific spider

mite, *T. pacificus* (McGregor), or Willamette mite, *Eotetranychus willametti* (McGregor), was shown to reduce grape leaf photosynthesis and stomatal conductance. Moreover, previous studies by Andrews and LaPre' (1979) and Youngman and Barnes (1986) also showed significant negative correlations beween mite damage and crop gas exchange parameters. However, Martens and Trumble (1987) indicated that undamaged leaves adjacent to leaves damaged by the leafminer, *Liriomyza trifolii* (Burgess), had increased photosynthetic rates.

Sances et al. (1981), working with TSSM on strawberry, showed that adverse effects of mite feeding on photosynthesis and transpiration of plants caused reductions in quality and quantity of harvestable fruit. Impaired carbon uptake of mite-infested leaves occurs as a result of stomatal closure and injury to chlorophyll containing mesophyll cells within leaf tissue (Sances et al., 1979a, b). Interference with CO_2 uptake and fixation reduce the availability of simple carbohydrates and other photosynthates required in the development of vegetative and reproductive plant structures. This sequence of events first contributes to a reduction in fruit size, and, subsequently, to significant decreases in total yield (Sances et al., 1981).

In addition, foliage and fruit expansion requires turgor from regulated water balance within healthy plants (Meidner and Sheriff, 1976). Improper functioning of stomata and the subsequent lack of internal tissue water balance stemming from a reduction in transpirational flux from heavily damaged foliage may act concomitantly with the restraint of available photosynthetic products to reduce growth and productivity (Sances et al., 1981).

The results in the present study also show that there were inherent differences in gas exchange characteristics among the hop genotypes studied. It was apparent that the gas exchange characteristics of M9 were

significantly higher than those of M4 and M27. This may be due to the variation in stomatal densities between these genotypes. As mentioned in Chapter 7, M4 had significantly lower numbers of stomata per unit area than M9 with the exception of M27. Stomatal transpiration may be associated with measurement of CO_2 assimilation by plants because the transpiration can result in an increase in water vapour concentration and a dilution of the mole fraction of all other gases, including CO_2 (Long and Hallgren, 1985).

Furthermore, a positive relationship between photosynthesis and stomatal conductance of hop leaves was noted in the present study. DeAngelis et al. (1983b), working with TSSM on peppermint, indicated that photosynthesis was strongly dependent on conductance at lower leaf conductance (high leaf resistance to gas exchange), whereas photosynthesis became nearly independent of gas exchange at higher conductance (low leaf resistance).

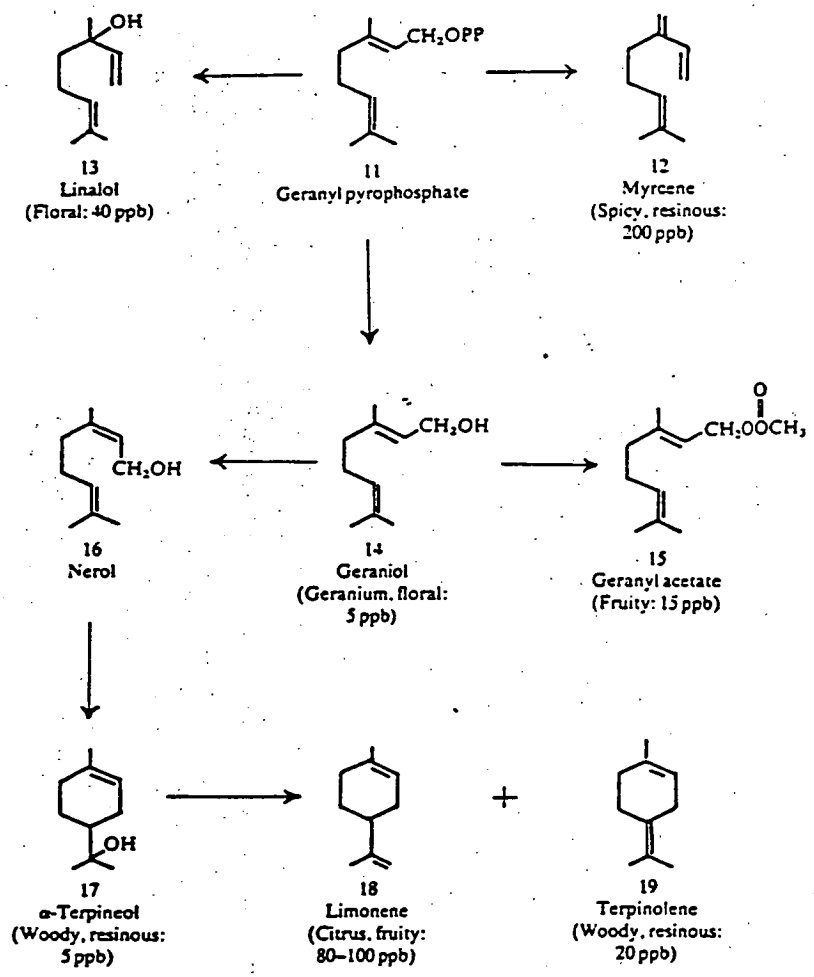
9.4.2. Chemical response to mite damage

This study, conducted in two different parts of hop plants, demonstrated the chemical responses of hops to TSSM injury. It was apparent that the volatile and leaf chemical compounds of the uninfested control and leaves infested with TSSM were similar for each genotype studied by using GC or TLC, however the abundance of volatile compounds in hop cones of infested plants tended to be lower than that of uninfested plants, especially for the monoterpene, myrcene. This compound is one of the most important hydrocarbon fractions in hop essential oils (Rybacek, 1991). In general, the essential oil is produced in lupulin glands which are denser on hop cones than on the leaves.

According to Neve (1991), recent biogenetic theory suggests that the terpene hydrocarbons are formed from oxygenated intermediates. The synthesis of myrcene appears to be the dominant pathway as the hop

ripens. Myrcene and other monoterpenoids are believed to be formed from geranyl pyrophosphate. Currently, many of these intermediates are thought to result in the hoppy flavour of beers. Fig. 9.16 presents the relationships of some of these compounds, the flavours produced and their concentrations in beers (Sharpe, 1988).

Fig. 9.16. Monoterpenoids in hop oil and beer (after Sharpe, 1988).



When the essential oils in uninfested and infested hop leaves were separated by using the steam distillation method, a similar set of volatile compounds occurring in similar amounts was observed in the present study. This would suggest that mites were not significantly affected, at least directly, by volatile leaf phytochemicals.

Theoretical considerations of herbivore-plant interactions assume that various chemical parameters of plants influence herbivore feeding, growth and survival (Marquis, 1984). Secondary metabolites such as phenolics and monoterpenes can reduce the palatability of plant tissue to herbivores and reduce herbivore growth rates, hence playing a major role in host plant resistance to pest (Rhoades and Cates, 1976; Mckey, 1979). These chemical compounds are not uniformly distributed throughout a plant; the capacity to synthesize and store them is dependent on tissue type and age (Mckey, 1979; Burbott and Loomis, 1969; DeAngelis et al., 1983c). Several phenolic compounds have been reported to be repellent to TSSM (Dabrowski and Rodriguez, 1972). Larson and Berry (1984) showed the impact of monoterpenes and phenolic compounds in different-aged peppermint leaves on TSSM fecundity, development and dispersal. In a more recent study, Luczynski et al. (1990), working with beach strawberry under glasshouse conditions, found that TSSM oviposition was negatively correlated with the concentration of total foliar phenolics. Nonetheless, Leszcynski et al. (1988), working with TSSM on hops, indicated that phenolic compounds were not major factors in the resistance of hops to TSSM, even though amounts of leaf phenols varied significantly among the hop cultivars studied. From the present study, it was also noted that both alkaloid and phenolic compounds were not important chemicals produced in hop leaves in response to TSSM infestations.

Additionally, earlier studies on chemical responses in plants caused by mite damage were investigated by several other researchers. In a comparison of resistance of two soybean varieties to TSSM, the cultivar with more constitutive resistance showed a stronger hypersensitive response to mite injury (Hildebrand et al., 1986). Similarly, the more resistant of two strawberry varieties showed a greater induced response to mite damage, measured in terms of mite-feeding preference (Kielkiewicz, 1988). In a study of lupins, Johnson et al. (1989) reported that leaves with the highest initial levels of alkaloids were the ones with the greatest induced increases relative to undamaged controls. Bell (1986) suggested that most of the compounds which are known to provide resistance in cotton against mites and other agents can also be induced by damage. Radioisotope incorporation studies of peppermint showed that monoterpene metabolism is extremely sensitive to the type and amount of metabolic substrate available from surrounding photosynthetic cells, and that gland cells may be deficient in oxidative metabolism (Burbott and Loomis, 1967, Croteau et a., 1972). Therefore, biosynthesis is highly dependent, both qualitatively and quantitatively, on the physiological state of surrounding photosynthetic tissue for supply of photosynthate, and thus is subject to the effects of mite-induced plant stress operating on these cells (DeAngelis et al., 1983c).

CHAPTER 10 SUMMARY

The primary objective of the present study was to gain a better understanding of mechanisms involved in the plant response to attacking mites in a system of cultivated hops. Five important aspects of this study were: (1) resistance-susceptibility of hop genotypes to TSSM infestations; (2) effects of environmental factors on the capacity of mite populations to increase; (3) morphological characteristics of hop leaves and their responses to TSSM infestations; (4) effects of hop leaf canopy on TSSM and its predatory mite and (5) physiological and chemical responses of hop foliage to damage caused by TSSM. An additional purpose of the study was to determine the seasonal abundance and the distribution of TSSM infesting commercial hops as well as the possibility of induced defence following reinfestation and this will be dealt with first.

10.1. Seasonal abundance and distribution of TSSM infesting commercial hops

The results from field observations demonstrated a generalised pattern of fluctuations in naturally occurring mite populations infesting commercial hops at Bushy Park, Tasmania, during the three growing seasons 1990/91 to 1992/93. These hops were grown in either untreated or treated areas under sprinkler irrigation. In untreated areas, the normal pattern of population change showed that mites peaked after hops had formed the visible bases of inflorescences and that population fluctuated at peak number to decline in the autumn. The relationship between mite population size and the proportion of infested leaves indicated that all leaves sampled at a height of 1.8 m could be infested when the average number of mites per leaf was more than 100. For treated areas, the

normal pattern of infestation development was interrupted by the application of miticides. It was found that mites continued to infest hop plants and occurred at low levels after miticide applications.

Natural enemies did not appear at levels sufficient to give control. This may have been due to the effects of miticide applications in the previous season. The natural enemies found were *Stethorus* spp. and phytoseiid mites, ranging from 0.1 to 1.0 stages per leaf.

The variation in mite injury to hops was found to affect mite population reinfestations following spraying. Heavily injured plants became less suitable, while slightly damaged plants were more suitable for mite increase. This finding revealed a possible induction of resistance in hop plants following prior mite infestation.

In addition, it was noted that inclement weather was a potential factor in limiting mite population build-up. Abundant rainfall during some parts of the season appeared to be the possible cause in the retardation of some infestations. As pointed out by Linke (1953), rainfall physically dislodged the active stages of TSSM from hop leaves. It was also observed that mite populations developed more quickly during periods of little or no rainfall and high temperatures.

In terms of stage distribution, eggs were the dominant stages for most of the season and the stage-specific percent densities changed as the season progressed. At the peak density of mite populations in untreated areas during the 1990/91 season, the percentage of eggs, immatures, and adult mites averaged approximately 60%, 27% and 13%, respectively.

The results from the present study also showed that the spatial and vertical distribution of the mites for each stage varied with time. Following emergence from field litter during the early growing season and dispersal onto plants (Cao, 1989), populations of adult females were found to be uniformly distributed between hop plants and became

aggregated as the season progressed. For adult males, immatures and eggs, the dispersion was found to be aggregated throughout the study period. Populations of each life stage were found on the lower leaves early in the season but progressively moved up the plant as it grew. Approximately 66% of total mite populations occurring in early March before harvest were detected on the upper leaves, whereas only 12% of the total were found on lower leaves. The upward distribution of adult males and immatures was slower than that of adult females.

For feeding damage, the surface areas and dry weights of leaves in the area with high seasonal mite-day accumulations were significantly less than those in the areas with low seasonal mite-day accumulations. Relationships between total mite numbers and numbers of mites of each stage, in terms of both mite-days and transformed mite-days, indicated that the estimate of the actual mite-days of all stages of mites from only the mite-days of any particular stage results in a significant linear regression and that the numbers of adult female mite-days alone was the best indicator for the total population of all stages. Moreover, feeding damage may be predicted using the relationship between females at week t and total mites at week t+1 in terms of both the number of mite-days and the original number of mites and the best estimate of potential population trend was obtained seven days after female census.

10.2. Resistance-susceptibility of hop genotypes to TSSM infestations

Studies on the resistance-susceptibility of hop genotypes to artificial and natural infestations by TSSM revealed that all the genotypes tested expressed an intermediate or susceptible reaction to the mites, with M26 (Huller Bitterer) being the most susceptible. Despite no outstanding evidence of antibiosis, significant differences in susceptibility among the hop genotypes were detected in terms of tolerance, non-preference and

plant avoidance. It was also found that there were significant differences in mite densities between European and American hop cultivars. German Huller Bitterer (M26) had significantly greater TSSM densities than did American Aquila (M25). In these studies, M4 (EG-86-23) was shown to be the cultivar with the genotype most likely to provide mite resistant hops.

When the effects of different hop genotypes on developmental time, fecundity, survivorship and intrinsic rate of increase (r_m) of TSSM were evaluated using age-specific life table statistics, no significant differences in any of these parameters among genotypes were detected. Nevertheless, the effect of different hop genotypes on mite development was apparent during the first 12 days of the reproductive-oviposition period with the greatest differences in the cumulative number of eggs occurring on the fourth day of oviposition.

10.3. Effects of environmental factors on the capacity of mite populations to increase

Several environmental factors affected mite population growth rate. Thus, temperature, relative humidity, light intensity, plant age, source of leaves and leaf surface areas, singly or together, can determine the degree of variation in mite population build-up on plants.

It was found that growth rates of the mites were significantly greater at higher than at lower temperatures. That is, an increase in rate of development with increased temperature, within the favourable temperature range, contributes significantly to the realization of r_m. The lower thermal threshold for TSSM development, was estimated at 5.88°, 10.99° and 11.33°C for egg, female and male postembryonic stages, respectively. For survivorship and reproduction of TSSM, the present study confirmed that temperature influenced these two parameters.

Embryonic development, as well as the survival of postembryonic stages, was affected by relative humidity. There were significant differences in the duration of egg, total juvenile and pre-reproductive development between moderately humid conditions and water-saturated atmospheres. In addition, the sex ratio of immatures reaching adulthood was also influenced by humidity with a shift towards a higher female : male ratio at a humidity near saturation without the salt.

Light intensity was another environmental factor which had an influence on survival, development and reproduction of TSSM populations. Generation mortality of TSSM was found to be greater at low light intensities than at high light intensities. There were significant differences in total juvenile developmental and pre-reproductive periods of TSSM reared at different light intensities. The intrinsic rate of increase tended to be greater for TSSM reared at higher light intensities, while the mean generation time tended to be longer for mites reared at lower light intensities.

With regard to plant variables, the effects of leaf age and leaf regions on the biology of TSSM were examined using leaf discs. Very little difference occurred between survival, development and reproduction of mites on old and young leaf discs. This study also indicated that survival and reproduction of mites were not significantly affected by the size of leaf veins, but rate of development tended to be influenced by this variable.

The biological interaction of mites with their host plants appears to depend on a complex set of environmental factors that collectively influence the behaviour and physiology of mites. Modifications of any of these factors may influence the suitability of any plant as a host. For example, photosynthetic activity and related processes in plants can be highly regulated by environmental factors such as light and temperature.

10.4. Morphological characteristics and the responses of hop leaves to TSSM infestations

Morphological variation in external and internal characteristics of hop leaves occurs among the genotypes studied. Significant differences between cultivars were found in ventral gland size, trichome density, trichome size, length of trichomes, stomatal density, stomatal size and moisture content. Moreover, hop genotypes that were more tolerant had the highest density of ventral trichomes of the shortest average length, whereas susceptibility was highest on genotypes with a low density of trichomes of greatest average length.

The morphological characteristics of the hop leaves collected from the same genotype may vary significantly according to leaf age and growing conditions. When comparing the morphological characteristics of glasshouse versus field hop leaves, it was found that leaves collected from the glasshouse had denser ventrally occurring trichomes and glands than leaves collected from the field, while the thicknesses of the glasshouse leaves was less than those of field leaves. In the comparison of morphological characteristics of young and old leaves, numbers of ventral trichomes and glands per unit area were more sparse on old leaves than on young leaves, while the thickness of cellular layers, with the exception of the epidermal cells, was less in young leaves than in the old leaves. In young leaves the cuticle was thicker and this allowed for greater expansion of epidermal cells.

In addition, it was demonstrated that there was genetic variation in the morphological response of hop leaves to mite infestations and that this variation was related to the area of the leaf scarred and damaged by mite feeding and stomatal opening. It was found that the average number of yellow specks (ruptured cells) was significantly greater on the highly susceptible genotype M27 than on the slightly susceptible genotype

M4, whereas the the mean number of open stomata was significantly less on M27 than on M4.

10.5. Effects of hop leaf canopy on TSSM and *P. persimilis*

Evidence was obtained in the present study that hop-canopy microenvironments do play an important role in seasonal population development of TSSM. This role was amplified by hop susceptibility to the mites. For the hop genotypes studied, the populations of mites increased more rapidly on sparsely leaved canopies than on densely leaved canopies. In turn, the growth of *P. persimilis* populations was greater in sparse canopies. In addition, the effect of canopy microenvironments on TSSM population dynamics was found to be more adverse on the susceptible genotype used (M26) than on the resistant one (M25). Initially M26 grew faster than did M25. TSSM readily established and grew on M26, whereas population growth was slow on the slower growing cultivar M25.

Within a closed canopy, leaves are clustered to create conditions in which less air is circulated, light intensities and temperatures are reduced and relative humidities increased. In contrast, an open canopy has unrestricted air flow, high light intensities and elevated temperatures as well as humidities reduced to ambient levels. Furthermore, potentially confounding effects of temperature interacting with humidity or light intensity can affect mite population growth. High temperatures and light intensities with low relative humidities tend to increase intrinsic rates of increase and to decrease mean generation time, whereas low temperatures and light intensities with high relative humidities tend to decrease intrinsic rates of increase and to increase mean generation time.

The difference in the size and numbers of yellow specks between highly and lower susceptible genotypes which carried high and low TSSM

populations appear to reflect the water status of the respective plants. TSSM damage to hop cultivars reflects both mite numbers and the plants response to the feeding lesion. For susceptible cultivars mite numbers are usually higher resulting in greater feeding while the water stress induced by excessive feeding will under conditions of average temperatures and humidities result in water loss from the lession. This results in a large destructive speck. In contrast lower populations on more tolerant cultivars, which do not experience high stress because of the moderately effect of a dense canopy, have fewer and smaller specks because of the more hydrated leaf condition.

It is postulated that the difference between susceptible and more tolerant plants relate to the overall water status of individual plants/cultivars. That is TSSM damage results in direct water loss from the leaf surface. In actually growing plants with a high water demand the water deficit resulting from evaporation from the damaged surface leads to closure of stomata and reduced CO_2 uptake. The leaves are then exploited by TSSM.

In contrast slower growing plants do not experience a high water deficit with damage. For evaporative losses are adequately met resulting in small damage specks. These conditions are most often met when canopy structures are dense which in turn retard TSSM population growth.

10.6. Physiological and chemical responses of hop foliage to damage caused by TSSM

A preliminary study of the physiological and chemical responses of hop genotypes to mite feeding damage was conducted under field and the glasshouse conditions. It was noted that feeding damage of the mites tended to not only increase hop leaf resistance to CO_2 uptake but also

suppress photosynthetic rates in these experiments. Additionally, chromatographic analyses of chemicals extracted from hop leaves showed that phenolics and alkaloids as well as volatile compounds in infested leaves were qualitatively and quantitatively similar to those detected in undamaged control leaves. Nonetheless, the abundance of myrcene in hop cones of infested plants tended to be lower than that of uninfested plants. This was caused by reduction of active surface due to feeding damage.

On the basis of the results reported here it would appear that the mechanisms involved in hop resistance to TSSM infestations are best described in terms of either mite population variability or the reaction of the plant with both these phenomena being strongly influenced by environmental factors. For a more complete understanding of the possibilities of TSSM control by use of varietal resistance, further detailed information is required on genetic, cytological and biochemical aspects and intensive monitoring of the microhabitats in which the mites live.

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Appendix 3.1. Unpaired t-tests for mite densities in the middle region of treated and untreated hop plants in the early 1991/92 growing season.

Parameters	Sampling date	DF	Unpaired t values
No. of mites/leaf	14/11/91	78	-2.015*
	28/11/91	78	-2.164*
No. of mites/cm.^{2}	14/11/91	78	-2.029*
	28/11/91	78	-2.155*

Appendix 3.2. Unpaired t-tests for total numbers of TSSM (all stages) after re-infestation on 10/2/93 and 24/2/93.

Date	DF	Unpaired t values
10/2/93	-	-
24/2/93	12	1.2179ns

Appendix 3.3. One-factor ANOVA for surface areas of hop leaves at the height of 1.8 m. among different blocks during the 1990/91 growing season.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	8905.8593	2968.6198	67.5971**
Within groups	16	702.6619	43.9164	
Total	19	9608.5212		

Appendix 3.4. One-factor ANOVA for dry weights of hop leaves at the height of 1.8 m. among different blocks during the 1990/91 growing season.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	0.3776	0.1259	29.2432**
Within groups	16	0.0689	0.0043	
Total	19	0.4465		

Appendix 3.5. One-factor ANOVA for surface areas of hop leaves at the height of 1.8 m. among different blocks during the 1991/92 growing season.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	5580.9567	1860.3189	0.3367ns
Within groups	32	176786.6266	5524.5821	
Total	35	182367.5833		

Appendix 3.6. One-factor ANOVA for dry weights of hop leaves at the height of 1.8 m. among different blocks during the 1991/92 growing season.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	0.1745	0.0582	0.2350ns
Within groups	32	7.9208	0.2475	
Total	35	8.0953		

Appendix 3.7. One-factor ANOVA for surface areas of hop leaves at the fourth node among different blocks during the 1992/93 growing season.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	268.0871	89.3624	0.7547ns
Within groups	4	473.6353	118.4088	
Total	7	741.7224		

Appendix 3.8. One-factor ANOVA for dry weights of hop leaves at the fourth node among different blocks during the 1992/93 growing season.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	0.0035	0.0012	0.2129ns
Within groups	4	0.0219	0.0055	
Total	7	0.0255		

Appendix 3.9. One-factor ANOVA for surface areas of hop leaves at the height of 1.8 m. among different blocks during the 1992/93 growing season.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	3186.6750	1062.2250	0.1769ns
Within groups	32	192105.6614	6003.3019	
Total	35	195292.3365		

Appendix 3.10. One-factor ANOVA for dry weights of hop leaves at the height of 1.8 m. among different blocks during the 1992/93 growing season.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	0.0536	0.0179	0.0733ns
Within groups	32	7.7982	0.2437	
Total	35	7.8519		

Appendix 3.11. One-factor ANOVA for log (1+x) of adult female numbers per leaf among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	1.710	0.855	11.35**
Within groups	45	3.389	0.075	
Total	47	5.099		

Appendix 3.12. One-factor ANOVA for log (1+x) of adult male numbers per leaf among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	1.052	0.526	4.349*
Within groups	45	5.441	0.121	
Total	47	6.493		

Appendix 3.13. One-factor ANOVA for log (1+x) of immature numbers per leaf among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	4.254	2.127	11.668**
Within groups	45	8.203	0.182	
Total	47	12.456		

Appendix 3.14. One-factor ANOVA for log (1+x) of egg numbers per leaf among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	3.377	1.689	3.543*
Within groups	45	21.448	0.477	
Total	47	24.826		

Appendix 3.15. One-factor ANOVA for log (1+x) of total mite numbers per leaf among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	4.837	2.418	8.062**
Within groups	45	13.498	0.300	
Total	47	18.335		

Appendix 3.16. One-factor ANOVA for log (1+x) of Stethorus numbers per leaf among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	0.201	0.100	3.321*
Within groups	45	1.361	0.030	
Total	47	1.562		

Appendix 3.17. One-factor ANOVA for log (1+x) of predatory mite numbers per leaf among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	0.045	0.023	2.368ns
Within groups	45	0.430	0.010	
Total	47	0.476		

Appendix 3.18. One-factor ANOVA for log (1+x) of adult female numbers per $cm.^2$ among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	0.001	3.066E-4	6.418**
Within groups	45	0.002	4.776E-5	
Total	47	0.003		

Appendix 3.19. One-factor ANOVA for log (1+x) of adult male numbers per $cm.^2$ among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	0.001	0.001	2.862ns
Within groups	45	0.008	1.889E-4	
Total	47	0.010		

Appendix 3.20. One-factor ANOVA for log (1+x) of immature numbers per $cm.^2$ among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	0.034	0.017	5.045*
Within groups	45	0.151	0.003	
Total	47	0.184		

Appendix 3.21. One-factor ANOVA for log (1+x) of egg numbers per cm.^{2} among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	0.102	0.051	3.862*
Within groups	45	0.593	0.013	
Total	47	0.695		

Appendix 3.22. One-factor ANOVA for log (1+x) of total mite numbers per cm.^{2} among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	0.196	0.098	5.369**
Within groups	45	0.822	0.018	
Total	47	1.018		

Appendix 3.23. One-factor ANOVA for log (1+x) of Stethorus numbers per cm.^{2} among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	2.466E-5	1.233E-5	2.442ns
Within groups	45	2.272E-4	5.048E-6	
Total	47	2.518E-4		

Appendix 3.24. One-factor ANOVA for log (1+x) of predatory mite numbers per cm.^{2} among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	2.735E-6	1.368E-6	2.368ns
Within groups	45	2.598E-5	5.774E-7	
Total	47	2.872E-5		

Appendix 3.25. One-factor ANOVA for log (1+x) of adult female numbers per gm. among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	1.222	0.611	10.098**
Within groups	45	2.722	0.060	
Total	47	3.943		

Appendix 3.26. One-factor ANOVA for log (1+x) of adult male numbers per gm. among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	0.718	0.359	3.589*
Within groups	45	4.502	0.100	
Total	47	5.220		

Appendix 3.27. One-factor ANOVA for log (1+x) of immature numbers per gm. among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	3.215	1.607	9.290**
Within groups	45	7.787	0.173	
Total	47	11.002		

Appendix 3.28. One-factor ANOVA for log (1+x) of egg numbers per gm. among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	2.500	1.250	2.825ns
Within groups	45	19.912	0.442	
Total	47	22.412		

Appendix 3.29. One-factor ANOVA for log (1+x) of total mite numbers per gm. among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	3.719	1.860	6.376**
Within groups	45	13.125	0.292	
Total	47	16.844		

Appendix 3.30. One-factor ANOVA for log (1+x) of Stethorus numbers per gm. among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	0.138	0.069	3.018ns
Within groups	45	1.028	0.023	
Total	47	1.166		

Appendix 3.31. One-factor ANOVA for log (1+x) of predatory mite numbers per gm. among different foliage heights.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	0.029	0.014	2.464ns
Within groups	45	0.263	0.006	
Total	47	0.292		

Appendix 4.1. One-factor ANOVA for total numbers of mites per leaf among different genotypes infested artificially on the 1st. sampling occasion under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	346418.9615	13856.7585	1.4592ns
Within groups	78	740679.0	9495.8846	
Total	103	1087097.9615		

Appendix 4.2. One-factor ANOVA for log (1+x) of mite numbers per leaf among different genotypes infested artificially on the 1st. sampling occasion under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	14.1301	0.5652	2.1066**
Within groups	78	20.9271	0.2683	
Total	103	35.0572		

Appendix 4.3. One-factor ANOVA for total numbers of mites per leaf among different genotypes infested artificially on the 2nd. sampling occasion under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	725117.0865	29004.6835	3.3674**
Within groups	78	671847.7500	8613.4327	
Total	103	1396964.8365		

Appendix 4.4. One-factor ANOVA for log (1+x) of mite numbers per leaf among different genotypes infested artificially on the 2nd. sampling occasion under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	11.0022	0.4401	3.1879**
Within groups	78	10.7676	0.1381	
Total	103	21.7698		

Appendix 4.5. One-factor ANOVA for total numbers of mites per leaf among different genotypes infested artificially on the 3rd. sampling occasion under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	1030681.1154	41227.2446	1.4010ns
Within groups	78	2295259.0	29426.3974	
Total	103	3325940.1154		

Appendix 4.6. One-factor ANOVA for log (1+x) of mite numbers per leaf among different genotypes infested artificially on the 3rd. sampling occasion under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	8.3681	0.3347	1.5479ns
Within groups	78	16.8668	0.2162	
Total	103	25.2349		

Appendix 4.7. One-factor ANOVA for total numbers of mites per leaf among different genotypes infested artificially on the 4th. sampling occasion under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	1.20136E7	480545.9954	4.6993**
Within groups	78	7976183.5	102258.7628	
Total	103	1.99898E7		

Appendix 4.8. One-factor ANOVA for log (1+x) of mite numbers per leaf among different genotypes infested artificially on the 4th. sampling occasion under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	13.3496	0.5339	3.5644**
Within groups	78	11.6853	0.1498	
Total	103	25.0349		

Appendix 4.9. The mean size of eggs, adult males and adult females reared on 26 genotypes of hops under glasshouse conditions.

Genotype	Stages of TSSM (mm.)		
	Eggs	Adult males	Adult females
M1	0.14	0.36	0.45
M2	0.15	0.24	0.45
M3	0.15	0.30	0.54
M4	0.15	0.36	0.57
M5	0.15	0.30	0.54
M6	0.15	0.33	0.45
M7	0.15	0.30	0.48
M8	0.15	0.30	0.51
M9	0.15	0.30	0.48
M10	0.15	0.36	0.45
M11	0.15	0.33	0.48
M12	0.15	0.33	0.45
M13	0.15	0.33	0.48
M14	0.15	0.30	0.36
M15	0.15	0.36	0.45
M16	0.15	0.30	0.45
M17	0.15	0.30	0.48
M18	0.15	0.30	0.51
M19	0.15	0.33	0.48
M20	0.15	0.33	0.51
M21	0.15	0.33	0.51
M22	0.15	0.30	0.48
M23	0.15	0.33	0.48
M24	0.15	0.30	0.51
M25	0.15	0.30	0.45
M26	0.15	0.33	0.45

Appendix 4.10. One-factor ANOVA for total mite numbers per leaf among different genotypes in the first experiment of artificial infestations under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	2.78431E7	1113723.60615	7.37076**
Within groups	78	11785816.5	151100.21154	
Total	103	3.96289E7		

Appendix 4.11. One-factor ANOVA for numbers of mites among different genotypes in the second experiment of artificial infestations under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	703.0385	28.1215	0.7827ns
Within groups	78	2802.5000	35.9295	
Total	103	3505.5385		

Appendix 4.12. One-factor ANOVA for numbers of mites among different genotypes grown at the Horticultural Research Centre during 1991/92 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	11	10.5806	0.9619	3.0388**
Within groups	60	18.9921	0.3165	
Total	71	29.5727		

Appendix 4.13. One-factor ANOVA for numbers of mites among different genotypes grown at the Horticultural Research Centre during 1992/93 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	11	0.0313	0.0028	0.6644ns
Within groups	36	0.1541	0.0043	
Total	47	0.1854		

Appendix 4.14. One-factor ANOVA for numbers of mites per leaf among different genotypes infested naturally under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	23058.3397	922.3336	2.0118**
Within groups	130	59600.5000	458.4654	
Total	155	82658.8397		

Appendix 4.15. One-factor ANOVA for numbers of mites per cm.^{2} among different genotypes infested naturally under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	1604.4820	64.1793	2.5513**
Within groups	130	3270.2575	25.1558	
Total	155	4874.7395		

Appendix 4.16. One-factor ANOVA for log (x+1) of mite numbers per cm.^{2} among 24 genotypes of hops infested naturally in Hop Yard No. 1 on February 6, 1992.

Source	DF	Sum of square	Mean square	F-test
Between groups	23	0.47468	0.02064	1.77736*
Within groups	96	1.11472	0.01161	
Total	119	1.58940		

Appendix 4.17. One-factor ANOVA for log (x+1) of mite numbers per cm.^{2} among 24 genotypes of hops infested naturally in Hop Yard No. 1 on February 20, 1992.

Source	DF	Sum of square	Mean square	F-test
Between groups	23	0.54950	0.02389	2.7121**
Within groups	96	0.84569	0.00881	
Total	119	1.39519		

Appendix 4.18. One-factor ANOVA for log (x+1) of mite numbers per cm.^{2} among 24 genotypes of hops infested naturally in Hop Yard No. 1 on March 5, 1992.

Source	DF	Sum of square	Mean square	F-test
Between groups	23	1.49748	0.06511	3.6336**
Within groups	96	1.72013	0.01792	
Total	119	3.21761		

Appendix 4.19. One-factor ANOVA for log (x+1) of total mite numbers per cm.^{2} among 24 genotypes of hops infested naturally in Hop Yard No. 1 during 1991/92 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	23	2.94658	0.12811	6.5940**
Within groups	96	1.86514	0.01943	
Total	119	4.81173		

Appendix 4.20. One-factor ANOVA for mite numbers per cm.^{2} among 24 genotypes of hops infested naturally in Hop Yard No. 1 on November 4, 1992.

Source	DF	Sum of square	Mean square	F-test
Between groups	23	0.08788	0.00382	2.2028**
Within groups	72	0.12489	0.00173	
Total	95	0.21276		

Appendix 4.21. One-factor ANOVA for mite numbers per cm.^{2} among 24 genotypes of hops infested naturally in Hop Yard No. 1 on November 18, 1992.

Source	DF	Sum of square	Mean square	F-test
Between groups	23	16.21937	0.70519	9.2644**
Within groups	72	5.48054	0.07612	
Total	95	21.69991		

Appendix 4.22. One-factor ANOVA for total mite numbers per $cm.^2$ among 24 genotypes of hops infested naturally in Hop Yard No. 1 during 1992/93 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	23	18.34757	0.79772	10.8862**
Within groups	72	5.27602	0.07328	
Total	95	23.62359		

Appendix 4.23. One-factor ANOVA for damage ratings among 26 hop genotypes following the infestations under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	31.49038	1.25962	2.6465**
Within groups	78	37.12500	0.47596	
Total	103	68.61538		

Appendix 4.24. Kruskal-Wallis test for mean ranks of cumulative mite-days among 24 hop genotypes grown in Hop Yard No. 1 during three growing seasons.

Parameters	DF	#Groups	# Cases	H values
Adult females	23	24	72	25.3091ns
Adult males	23	24	72	17.9342ns
Immatures	23	24	72	27.1780ns
Eggs	23	24	72	27.3881ns
Motiles	23	24	72	27.1854ns
All stages	23	24	72	29.0282ns

Appendix 4.25. Mann-Whitney U test for mean ranks of cumulative mite-days between two hop genotypes grown in Hop Yard No. 2 during three growing seasons.

Parameters	U	U-prime	Z values
Adult females	0	9	-1.9640*
Adult males	0	9	-1.9926*
Immatures	0	9	-1.9640*
Eggs	0	9	-1.9640*
Motiles	0	9	-1.9640*
All stages	0	9	-1.9640*

Appendix 4.26. One-factor ANOVA for internode lengths among 26 hop genotypes grown under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	269.57325	10.78293	1.3473ns
Within groups	78	624.27057	8.00347	
Total	103	893.84382		

Appendix 4.27. One-factor ANOVA for surface areas of hop leaves among 26 genotypes grown under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	126.33583	5.05343	2.9099**
Within groups	494	857.91292	1.73667	
Total	519	984.24875		

Appendix 4.28. One-factor ANOVA for numbers of leaves among 26 hop genotypes grown under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	39226.00962	1569.04038	2.0337**
Within groups	78	60179.75000	771.53526	
Total	103	99405.75962		

Appendix 4.29. One-factor ANOVA for numbers of tillers among 26 hop genotypes grown under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	441.16346	17.64654	3.3757**
Within groups	78	407.75000	5.22756	
Total	103	848.91346		

Appendix 4.30. One-factor ANOVA for plant heights among 26 hop genotypes grown under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	106528.38462	4261.13538	8.500
Within groups	52	26067.33333	501.29487	
Total	77	132595.71795		

Appendix 4.31. One-factor ANOVA for surface areas of hop leaves among 26 genotypes grown under field conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	403602.94705	16144.11788	7.7926**
Within groups	208	430920.43931	2071.73288	
Total	233	834523.38636		

Appendix 4.32. One-factor ANOVA for dry weights of hop leaves among 26 genotypes grown under field conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	25	22.97234	0.91889	15.0110**
Within groups	208	12.73264	0.06121	
Total	233	35.70498		

Appendix 4.33. One-factor ANOVA for numbers of cones per vine among 26 hop genotypes grown at the Horticultural Research Centre during the 1991/92 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	11	2646305.77778	240573.25253	3.0119**
Within groups	60	4792438.66667	79873.97778	
Total	71	7438744.44444		

Appendix 4.34. One-factor ANOVA for dry weight per cone among 26 hop genotypes grown at the Horticultural Research Centre during the 1991/92 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	11	0.23689	0.02154	3.6873**
Within groups	60	0.35043	0.00584	
Total	71	0.58732		

Appendix 4.35. One-factor ANOVA for dry weights of cones per vine among 26 hop genotypes grown at the Horticultural Research Centre during the 1991/92 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	11	36077.73486	3279.79408	2.9314**
Within groups	60	67130.92500	1118.84875	
Total	71	103208.65986		

Appendix 4.36. One-factor ANOVA for numbers of cones per vine among 26 hop genotypes grown at the Horticultural Research Centre during the 1992/93 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	11	4821664.13338	438333.10303	5.1344**
Within groups	60	5122343.34356	85372.38906	
Total	71	9944007.47694		

Appendix 4.37. One-factor ANOVA for dry weight per cone among 26 hop genotypes grown at the Horticultural Research Centre during the 1992/93 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	11	0.26484	0.02408	11.0395**
Within groups	60	0.13086	0.00218	
Total	71	0.39570		

Appendix 4.38. One-factor ANOVA for dry weights of cones per vine among 26 hop genotypes grown at the Horticultural Research Centre during the 1992/93 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	11	208372.89651	18942.99059	6.4843**
Within groups	60	175281.94693	2921.36578	
Total	71	383654.84344		

Appendix 4.39. One-factor ANOVA for dry weights of cones per vine among between different blocks of hops grown at the Horticultural Research Centre during the 1992/93 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	14853.33129	7426.66564	1.3895ns
Within groups	69	368801.51216	5344.94945	
Total	71	383654.84344		

Appendix 4.40. One-factor ANOVA for dry weight per cone among between different blocks of hops grown at the Horticultural Research Centre during the 1992/93 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	0.00229	0.00114	0.2006ns
Within groups	69	0.39341	0.00570	
Total	71	0.39570		

Appendix 4.41. One-factor ANOVA for the number of cones per vine among between different blocks of hops grown at the Horticultural Research Centre during the 1992/93 season.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	207563.3774	103781.6887	0.7355ns
Within groups	69	9736444.0995	141107.8855	
Total	71	9944007.4769		

Appendix 5.1. One-factor ANOVA for hatchability of TSSM among four genotypes of hops in Experiment 1.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	0.03202	0.01067	0.7247ns
Within groups	8	0.11784	0.01473	
Total	11	0.14986		

Appendix 5.2. One-factor ANOVA for survival of TSSM immatures among four genotypes of hops in Experiment 1.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	0.11811	0.03937	2.5474ns
Within groups	8	0.12364	0.01545	
Total	11	0.24175		

Appendix 5.3. One-factor ANOVA for sex ratio (F/M) of TSSM among four genotypes of hops in Experiment 1.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	1.74854	0.58285	0.4331ns
Within groups	8	10.76493	1.34562	
Total	11	12.51347		

Appendix 5.4. One-factor ANOVA for longevity of TSSM among four genotypes of hops in Experiment 1.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	145.09534	48.36511	1.0949ns
Within groups	54	2385.31845	44.17256	
Total	57	2530.41379		

Appendix 5.5. One-factor ANOVA for the cumulative number of eggs laid by TSSM among four genotypes of hops during the first fourth days of ovipositon in Experiment 1.

Source	DF	Sum of square	Mean square	F-test
Between groups	3	3215.3555	1071.78517	5.2536**
Within groups	54	11016.5238	204.00970	
Total	57	14231.8793		

Appendix 5.6. Daily record of the numbers of TSSM females and their eggs on four genotypes of hops in Experiment 1.

Date	Genotype							
	M4		M9		M26		M27	
	Females	Eggs	Females	Eggs	Females	Eggs	Females	Eggs
0-11	16	7	16	13	14	30	12	41
12	16	69	16	99	14	107	12	119
13	14	119	16	170	11	178	12	160
14	14	121	16	140	11	115	12	171
15	14	111	15	115	11	126	12	152
16	14	115	13	80	11	116	12	141
17	14	112	13	65	10	111	11	156
18	12	79	12	56	7	71	11	111
19	11	87	9	92	6	81	11	106
20	10	76	9	77	6	78	11	81
21	9	59	9	69	6	37	9	55
22	9	54	9	60	6	32	9	46
23	9	81	7	65	5	31	7	41
24	8	67	7	45	3	17	6	22
25	8	56	7	28	3	14	5	12
26	8	45	6	29	2	20	5	13
27	6	46	6	39	1	6	5	14
28	6	44	4	15	1	5	3	6
29	5	28	3	6	1	0	2	0
30	4	18	2	0	1	0	2	1
31	4	15	0	0	1	0	2	0
32	3	8			1	0	0	0
33	2	6			1	0		
34	2	4			1	0		
35	2	2			1	0		
36	0	0			1	0		
37					1	0		
38					1	0		
39					1	0		
40					1	0		
41					0	0		

Appendix 5.7. Life-fecundity table for TSSM on four genotypes of hops in Experiment 1.

	Genotype											
	M4			M9			M26			M27		
x	l_x	m_x[a]	l_xm_x	l_x	m_x	l_xm_x	l_x	m_x	l_xm_x	l_x	m_x	l_xm_x
0-11	1.000	0.219	0.219	1.000	0.406	0.406	1.000	1.071	1.071	1.000	1.708	1.708
12	1.000	2.156	2.156	1.000	3.094	3.094	1.000	3.821	3.821	1.000	4.958	4.958
13	0.875	4.250	3.719	1.000	5.313	5.313	0.786	8.091	6.357	1.000	6.667	6.667
14	0.875	4.321	3.781	1.000	4.375	4.375	0.786	5.227	4.107	1.000	7.125	7.125
15	0.875	3.964	3.469	0.938	3.833	3.594	0.786	5.727	4.500	1.000	6.333	6.333
16	0.875	4.107	3.594	0.813	3.077	2.500	0.786	5.273	4.143	1.000	5.875	5.875
17	0.875	4.000	3.500	0.813	2.500	2.031	0.714	5.550	3.964	0.917	7.091	6.500
18	0.750	3.292	2.469	0.750	2.333	1.750	0.500	5.071	2.536	0.917	5.046	4.625
19	0.688	3.954	2.719	0.563	5.111	2.875	0.429	6.750	2.893	0.917	4.818	4.417
20	0.625	3.800	2.375	0.563	4.278	2.406	0.429	6.500	2.786	0.917	3.682	3.375
21	0.563	3.278	1.843	0.563	3.833	2.156	0.429	3.083	1.321	0.750	3.056	2.292
22	0.563	3.000	1.688	0.563	3.333	1.875	0.429	2.667	1.143	0.750	2.556	1.917
23	0.563	4.500	2.531	0.438	4.643	2.031	0.357	3.100	1.107	0.583	2.929	1.708
24	0.500	4.188	2.094	0.438	3.214	1.406	0.214	2.833	0.607	0.500	1.833	0.917
25	0.500	3.500	1.750	0.438	2.000	0.875	0.214	2.333	0.500	0.417	1.200	0.500
26	0.500	2.813	1.406	0.375	2.417	0.906	0.143	5.000	0.714	0.417	1.300	0.542
27	0.375	3.833	1.438	0.375	3.250	1.219	0.714	3.000	0.214	0.417	1.400	0.583
28	0.375	3.667	1.375	0.250	1.875	0.469	0.071	2.500	0.179	0.250	1.000	0.250
29	0.313	2.800	0.875	0.188	1.000	0.188	0.071	0.000	0.000	0.167	0.000	0.000
30	0.250	2.250	0.563	0.125	0.000	0.000	0.071	0.000	0.000	0.167	0.250	0.042
31	0.250	1.875	0.469	0.000	0.000	0.000	0.071	0.000	0.000	0.167	0.000	0.000
32	0.188	1.333	0.250				0.071	0.000	0.000	0.000	0.000	0.000
33	0.125	1.500	0.188				0.071	0.000	0.000			
34	0.125	1.000	0.125				0.071	0.000	0.000			
35	0.125	0.500	0.063				0.071	0.000	0.000			
36	0.000	0.000	0.000				0.071	0.000	0.000			
37							0.071	0.000	0.000			
38							0.071	0.000	0.000			
39							0.071	0.000	0.000			
40							0.071	0.000	0.000			
41							0.000	0.000	0.000			

[a]The proportion of the offsprings that were females was assumed to be 0.5.

Appendix 5.8. Reproductive parameters of TSSM on 27 hop genotypes in Test 1 of Experiment 2.

Genotypes	Reproductive Parameters									
	Pre-reproductive period	rm (Birch)	rm (Wyatt and White)	Ro	T	rc	Tc	Finite rate for increase	Doubling time	Natality
M1	9.375	0.2952	0.3052	48.750	13.166	0.2491	15.605	1.3434	2.3476	4.1071
M2	9.000	0.3103	0.3172	39.300	11.831	0.2853	12.868	1.3638	2.2333	5.3541
M3	8.110	0.3342	0.3631	41.111	11.120	0.2933	12.669	1.3968	2.0736	5.2923
M4	10.429	0.2426	0.2454	44.786	15.671	0.1967	19.329	1.2746	2.8567	1.9248
M5	8.077	0.3424	0.3515	51.962	11.538	0.2507	15.759	1.4083	2.0239	5.3655
M6	8.857	0.3024	0.3153	51.286	13.021	0.2232	17.644	1.3531	2.2917	3.0902
M7	8.750	0.3223	0.3541	56.875	12.538	0.2613	15.463	1.3803	2.1502	4.1802
M8	8.000	0.3443	0.3428	50.071	11.366	0.2662	14.703	1.4110	2.0128	5.3363
M9	8.429	0.3072	0.3305	32.571	11.339	0.2792	12.478	1.3596	2.2559	3.6657
M10	7.833	0.3335	0.3415	38.917	10.979	0.2892	12.659	1.3958	2.0780	4.8437
M11	8.000	0.3673	0.3846	47.250	10.497	0.3456	11.156	1.4438	1.8867	7.3221
M12	8.000	0.3686	0.3779	54.375	10.841	0.3172	12.598	1.4457	1.8801	6.8483
M13	8.000	0.3372	0.3352	42.813	11.141	0.2843	13.216	1.4010	2.0552	4.6960
M14	8.833	0.3308	0.3452	56.833	12.213	0.2699	14.969	1.3921	2.0949	4.1624
M15	8.800	0.3172	0.3303	49.300	12.289	0.2505	15.558	1.3733	2.1847	3.7535
M16	8.286	0.3545	0.3589	69.357	11.958	0.2979	14.232	1.4255	1.9549	5.1877
M17	9.444	0.2939	0.2913	50.889	13.371	0.2370	16.582	1.3416	2.3579	3.8069
M18	8.857	0.3315	0.3397	61.357	12.418	0.2815	14.622	1.3931	2.0905	4.0152
M19	8.750	0.3276	0.3418	64.125	12.701	0.2692	15.454	1.3876	2.1154	3.8471
M20	8.857	0.3222	0.3351	40.929	11.520	0.2927	12.681	1.3802	2.1508	3.8592
M21	10.250	0.2794	0.2699	49.875	13.993	0.2427	16.110	1.3223	2.4803	4.0043
M22	10.600	0.2663	0.2644	78.000	16.360	0.1933	22.541	1.3051	2.6023	3.3542
M23	8.000	0.3307	0.3218	46.773	11.628	0.2700	14.244	1.3919	2.0956	4.1772
M24	7.889	0.3761	0.3648	71.556	11.355	0.2817	15.158	1.4566	1.8426	6.6767
M25	9.833	0.2372	0.2748	37.278	15.255	0.1836	19.712	1.2677	2.9216	2.5711
M26	10.000	0.2764	0.2703	52.600	14.337	0.2167	18.288	1.3184	2.5072	4.1617
M27	8.857	0.3453	0.3491	75.786	12.534	0.2660	16.270	1.4124	2.0070	4.6530

Appendix 5.9. Reproductive parameters of TSSM on 27 hop genotypes in Test 2 of Experiment 2.

Genotypes	Reproductive Parameters									
	Pre-reproductive period	rm (Birch)	rm (Wyatt and White)	Ro	T	rc	Tc	Finite rate for increase	Doubling time	Natality
M1	16.250	0.1457	0.1650	21.875	21.176	0.1378	22.386	1.1568	4.7563	1.9392
M2	16.000	0.1805	0.2047	32.000	19.201	0.1636	21.181	1.1978	3.8393	2.6876
M3	17.000	0.1436	0.1735	22.167	21.578	0.1378	22.489	1.1544	4.8259	2.9816
M4	17.000	0.1401	0.1799	20.167	21.442	0.1333	22.529	1.1504	4.9465	2.6304
M5	16.667	0.1659	0.1794	54.500	24.100	0.1403	28.492	1.1805	4.1772	2.6447
M6	17.000	0.1673	0.1736	38.250	21.782	0.1601	22.768	1.1821	4.1423	3.3507
M7	16.500	0.1814	0.1917	82.000	24.293	0.1575	27.973	1.1989	3.8203	3.1720
M8	17.000	0.1710	0.1898	49.563	22.826	0.1584	24.638	1.1865	4.0526	2.8264
M9	16.500	0.1505	0.1861	42.143	24.858	0.1349	27.737	1.1624	4.6047	2.4707
M10	16.167	0.1672	0.1857	42.333	22.402	0.1519	24.663	1.1820	4.1447	2.2731
M11[a]	-	-	-	-	-	-	-	-	-	-
M12	16.625	0.1470	0.1758	26.944	22.407	0.1286	25.604	1.1584	4.7143	2.3247
M13	17.600	0.1590	0.1686	55.400	25.249	0.1429	28.098	1.1723	4.3585	1.9325
M14	15.833	0.1644	0.1952	36.000	21.798	0.1450	24.708	1.1787	4.2153	2.3316
M15	16.000	0.1579	0.1873	31.188	21.786	0.1420	24.220	1.1710	4.3889	2.7060
M16	16.333	0.1790	0.1814	61.333	22.996	0.1620	25.413	1.1960	3.8715	2.9281
M17	17.500	0.1420	0.1687	27.400	23.613	0.1244	26.604	1.1505	4.9429	2.4162
M18	17.000	0.1675	0.1832	53.250	23.731	0.1503	26.446	1.1823	4.1373	3.3010
M19	16.670	0.1317	0.1703	16.500	21.286	0.1216	23.057	1.1408	5.2620	1.7891
M20	16.000	0.1808	0.1828	52.000	21.854	0.1732	22.808	1.1982	3.8330	3.0852
M21	16.670	0.1352	0.1482	14.500	19.779	0.1319	20.270	1.1448	5.1257	1.9279
M22	17.000	0.1582	0.1871	45.000	24.062	0.1453	26.206	1.1714	4.3805	3.8981
M23	16.750	0.1509	0.1449	19.500	19.685	0.1492	19.910	1.1629	4.5924	2.1386
M24	17.500	0.1457	0.1522	27.375	22.715	0.1381	23.973	1.1568	4.7563	1.9463
M25[b]	16.000	-	-	-	-	-	-	-	-	-
M26[b]	16.667	-	-	-	-	-	-	-	-	-
M27[b]	16.333	-	-	-	-	-	-	-	-	-

a = All immatures reaching adults were males.
b = Some chemical residues were found on field hop leaves late in the season.

Appendix 5.10. Reproductive parameters of TSSM on 27 hop genotypes in Test 3 of Experiment 2.

Genotypes	Reproductive Parameters									
	Pre-reproductive period	rm (Birch)	rm (Wyatt and White)	Ro	T	rc	Tc	Finite rate for increase	Doubling time	Natality
M1	12.200	0.1614	0.1574	11.833	15.309	0.1583	15.606	1.1752	4.2937	1.7891
M2	12.000	0.2364	0.2392	41.929	15.804	0.2123	17.595	1.2667	2.9315	3.0852
M3	12.167	0.2215	0.2379	28.125	15.064	0.2122	15.724	1.2479	3.1287	1.9279
M4	12.000	0.1927	0.1884	16.750	14.626	0.1883	14.970	1.2125	3.5963	3.8981
M5	12.500	0.2231	0.2315	46.375	17.198	0.2045	18.763	1.2499	3.1062	2.1386
M6	12.000	0.2089	0.2231	32.250	16.628	0.1751	19.835	1.2323	3.3174	1.9453
M7	11.714	0.2238	0.2537	32.750	15.589	0.2086	16.725	1.2508	3.0965	1.3303
M8	11.800	0.2395	0.2453	43.500	15.753	0.2082	18.119	1.2706	2.8935	4.2753
M9	11.571	0.2287	0.2377	26.700	14.363	0.2216	14.824	1.2570	3.0302	2.7291
M10	11.571	0.2081	0.2406	19.400	14.249	0.2016	14.706	1.2313	3.3301	2.4592
M11	11.625	0.2532	0.2672	68.583	16.699	0.2179	19.407	1.2881	2.7370	3.1053
M12	10.000	0.2411	0.2678	43.500	15.648	0.2115	17.835	1.2726	2.8743	3.1447
M13	11.250	0.2445	0.2495	43.667	15.446	0.2069	18.256	1.2770	2.8344	3.0386
M14	11.600	0.2577	0.2646	34.667	13.759	0.2472	14.341	1.2940	2.6892	3.1902
M15	12.000	0.1912	0.1897	13.333	13.547	0.1886	13.738	1.2107	3.6245	3.2481
M16	12.000	0.2432	0.2414	41.250	15.295	0.2148	17.318	1.2753	2.8495	2.7384
M17	11.330	0.2399	0.2521	40.214	15.399	0.2141	17.254	1.2711	2.8887	3.8074
M18	11.800	0.2542	0.2557	57.250	15.922	0.2276	17.782	1.2894	2.7262	3.7087
M19	11.750	0.1978	0.2230	16.750	14.249	0.1925	14.642	1.2187	3.5035	3.6740
M20	11.830	0.2113	0.2278	25.750	15.374	0.1973	16.466	1.2353	3.2797	5.3686
M21	12.000	0.1415	0.1440	6.625	13.363	0.1406	13.453	1.1520	4.8975	2.9559
M22	12.250	0.2130	0.2106	34.583	16.636	0.1693	20.935	1.2374	3.2535	4.9092
M23	12.000	0.2215	0.2081	29.000	15.202	0.2172	15.500	1.2479	3.1287	3.5500
M24[a]	12.000	0.2171	0.2486	33.500	16.175	0.1988	17.664	1.2425	3.1921	3.7920
M25[a]	-	-	-	-	-	-	-	-	-	-
M26	-	-	-	-	-	-	-	-	-	-
M27	13.000	0.2163	0.2089	63.250	19.173	0.1753	23.660	1.2415	3.2039	4.0988

a = Some chemical residues were found on field hop leaves.

Appendix 5.11. Reproductive parameters of TSSM on 27 hop genotypes in Test 4 of Experiment 2.

Genotypes	Reproductive Parameters									
	Pre-reproductive period	rm (Birch)	rm (Wyatt and White)	Ro	T	rc	Tc	Finite rate for increase	Doubling time	Natality
M1	11.000	0.2548	0.2604	76.000	16.997	0.2102	20.602	1.2902	2.7198	3.7095
M2	10.857	0.2647	0.2880	50.500	14.817	0.2419	16.215	1.3030	2.6181	3.5835
M3	11.000	0.2427	0.2814	44.500	15.639	0.2158	17.588	1.2747	2.8554	4.2457
M4	11.800	0.2415	0.2451	54.000	16.518	0.2188	18.232	1.2732	2.8696	4.2906
M5	11.000	0.2896	0.2956	113.500	16.339	0.2468	19.176	1.3359	2.3930	6.1245
M6	13.200	0.2122	0.2124	74.000	20.283	0.1744	24.679	1.2364	3.2658	3.0665
M7	11.200	0.2737	0.2735	71.500	15.600	0.2368	18.032	1.3148	2.5320	4.9304
M8	10.330	0.2696	0.2788	57.250	15.013	0.2287	17.699	1.3094	2.5705	3.6651
M9	11.000	0.2597	0.2702	50.500	15.102	0.2348	16.703	1.2965	2.6685	3.1184
M10	11.250	0.2652	0.2583	42.500	14.138	0.2553	14.688	1.3037	2.6131	4.9944
M11	12.000	0.2548	0.2550	87.500	17.550	0.2081	21.486	1.2902	2.7198	4.7885
M12	10.833	0.1279	0.1012	4.500	11.760	0.1277	11.778	1.1364	5.4183	2.1729
M13	11.500	0.2455	0.2482	72.000	17.420	0.2169	19.715	1.2783	2.8228	4.1579
M14	11.250	0.2872	0.2900	113.000	16.460	0.2323	20.354	1.3327	2.4130	5.8825
M15	11.000	0.2767	0.2800	69.750	15.341	0.2551	16.638	1.3188	2.5045	5.1841
M16	11.000	0.2647	0.2708	46.750	14.525	0.2505	15.348	1.3030	2.6181	4.7798
M17	12.110	0.2021	0.2168	40.400	18.302	0.1823	20.290	1.2240	3.4290	1.7231
M18	11.000	0.2735	0.2498	41.000	13.578	0.2671	13.902	1.3146	2.5338	6.0106
M19	12.000	0.2685	0.2684	82.000	16.412	0.2121	20.781	1.3080	2.5810	4.5130
M20[a]	-	-	-	-	-	-	-	-	-	-
M21	11.000	0.2267	0.2611	30.750	15.112	0.2081	16.463	1.2545	3.0569	3.6264
M22	11.000	0.2651	0.2661	58.250	15.333	0.2293	17.725	1.3036	2.6141	4.6709
M23	11.000	0.2716	0.2795	62.250	15.211	0.2554	16.177	1.3121	2.5515	4.9916
M24	11.000	0.2754	0.2625	53.500	14.451	0.2595	15.336	1.3171	2.5163	5.3142
M25	13.000	0.2218	0.2204	96.500	20.602	0.1768	25.850	1.2483	3.1244	3.5588
M26	13.000	0.2052	0.2071	115.500	23.145	0.1561	30.424	1.2278	3.3772	2.6724
M27	12.000	0.2055	0.2103	54.773	19.480	0.1588	25.203	1.2281	3.3723	3.1871

a = All immatures reaching adults were males.

Appendix 5.12. Reproductive parameters of TSSM reared on three different surface areas of leaf discs cut from 24 hop genotypes.

Reproductive parameters	Surface areas of leaf discs		
	Large	Medium	Small
Field hop leaf discs			
Intrinsic rate of increase (Wyatt)	0.2707	0.2448	0.2408
Intrinsic rate of increase (Birch)	0.2604	0.2322	0.2228
Gross reproductive rate	120.645	73.429	52.046
Net reproductive rate	80.813	38.688	36.563
Capacity for increase	0.2109	0.2051	0.2006
Mean generation time	16.867	15.743	16.154
Cohort generation time	20.830	17.824	17.939
Pre-reproductive period	11.630	11.670	11.750
Finite rate of increase	1.2970	1.2610	1.2500
Doubling time	2.6610	2.9840	3.1100
Natality	4.2918	3.1102	2.6231
Mortality	4.0314	2.8780	2.4003
Total number of eggs	161.625	77.375	73.125
Longevity (days)	32.000	22.875	23.958
Glasshouse hop leaf discs			
Intrinsic rate of increase (Wyatt)	0.3013	0.2854	0.2659
Intrinsic rate of increase (Birch)	0.2754	0.2613	0.2362
Gross reproductive rate	117.860	88.379	56.548
Net reproductive rate	86.031	69.127	36.663
Capacity for increase	0.2290	0.2206	0.2146
Mean generation time	16.175	16.211	15.249
Cohort generation time	19.449	19.201	16.784
Pre-reproductive period	11.000	11.090	11.350
Finite rate of increase	1.3170	1.2990	1.2660
Doubling time	2.5160	2.6520	2.9340
Natality	3.9758	3.3051	2.5708
Mortality	3.7004	3.0438	2.3347
Total number of eggs	172.060	138.254	73.326
Longevity (days)	31.040	31.208	23.500

Appendix 6.1. Daily record of numbers of TSSM reaching each stage on M4 and M27 at 76%RH and three temperatures with a light intensity of 171 lux; E. = egg, L. = larva, PC. = Protochrysalis, PN. = Protonymph, DC. = Deutochrysalis, DN. = Deutonymph, TC. = Teleiochrysalis, MA. = Male adult, FA. = Female adult.

TSSM on M4 at 20°C

	Mite stages								
Date	E.	L.	PC.	PN.	DC.	DN.	TC.	MA.	FA.
0-6	20	-	-	-	-	-	-	-	-
7	10	10	-	-	-	-	-	-	-
8		14	4	-	-	-	-	-	-
9		7	9	2	-	-	-	-	-
10		1	9	6	2	-	-	-	-
11			4	7	7	-	-	-	-
12				7	7	4	-	-	-
13				1	7	10	-	-	-
14					6	7	4	-	-
15					3	6	5	2	1
16						6	6	3	2
17	1					6	5	3	3
18	2					3	5	4	5
19	6						5	3	6
20	5							3	10
21	13							3	10
22	12							2	10
23	12							2	9
24	8							2	9
25	9							2	9
26	14							1	9
27	20							1	9
28	16							1	9
29	11							1	8
30	6							1	8
31	8							1	7
32	4							1	7
33	4							1	6
34	3							1	6
35	0							1	6
36	1							1	6
37	1							1	6
38	2							1	4
39	1							0	3
40	0								2
41	1								2

TSSM on M27 at 20°C

	Mite stages								
Date	E.	L.	PC.	PN.	DC.	DN.	TC.	FA.	MA.
0-6	20	-	-	-	-	-	-	-	-

7	10	10	-	-	-	-	-	-	-
8		11	3	-	-	-	-	-	-
9		10	10	-	-	-	-	-	-
10		2	9	7	-	-	-	-	-
11		1	5	5	7	-	-	-	-
12			1	6	8	3	-	-	-
13			1	2	7	8	-	-	-
14				1	5	4	8	-	-
15					1	5	10	2	-
16					1	3	5	3	6
17	5					1	5	5	7
18	25					1	3	4	10
19	34						1	4	13
20	51							4	13
21	53							4	13
22	42							2	13
23	33							2	13
24	33							2	13
25	14							2	13
26	32							2	13
27	46							2	12
28	54							2	12
29	46							2	12
30	29							2	11
31	25							2	10
32	8							2	8
33	8							2	7
34	11							2	7
35	7							2	7
36	5							2	7
37	2							2	6
38	2							2	5
39	5							2	5
40	1							2	5
41	0							2	5

TSSM on M4 at 25°C

	Mite stages								
Date	E.	L.	PC.	PN.	DC.	DN.	TC.	FA.	MA.
0-4	25	-	-	-	-	-	-	-	-
5	10	15	-	-	-	-	-	-	-
6	3	1	21	-	-	-	-	-	-
7		4	7	14	-	-	-	-	-
8				1	17	7	-	-	-
9					3	15	7	-	-
10						7	11	2	5
11	3					4	4	3	14
12	14						4	6	15
13	9							6	19
14	7							3	19
15	18							2	18
16	49							1	18
17	60							1	18

TSSM on M27 at 25°C

	Mite stages								
Date	E.	L.	PC.	PN.	DC.	DN.	TC.	FA.	MA.
0-4	25	-	-	-	-	-	-	-	-
5	13	12	-	-	-	-	-	-	-
6	4	12	9	-	-	-	-	-	-
7		1	12	12	-	-	-	-	-
8				12	12	1	-	-	-
9					3	11	11	-	-
10					2	8	11	2	2
11	2					2	8	5	10
12	9					1	3	6	13
13	25						2	6	14
14	37						1	7	14
15	55						1	4	14
16	81						1	4	13
17	79							4	12

TSSM on M4 at 30°C

	Mite stages								
Date	E.	L.	PC.	PN.	DC.	DN.	TC.	FA.	MA.
0-3	65	-	-	-	-	-	-	-	-
4	27	36	2	-	-	-	-	-	-
5	11	8	27	19	1	-	-	-	-
6		4	2	24	9	14	7	-	-
7				3	11	20	14	2	5
8	7				4	8	20	10	11
9	68					4	11	14	22
10	128					2		16	31
11	113					2		15	30
12	176					2		10	25
13	207							8	25
14	117							8	22
15	67							5	20
16	41							5	18
17	25							1	16
18	9							1	15
19	6							1	10
20	13								8
21	10								5
22	14								4
23	9								4
24	0								2
25	2								2
26	0								1

TSSM on M27at 30°C

Date	Mite stages E.	L.	PC.	PN.	DC.	DN.	TC.	FA.	MA.
0-3	65	-	-	-	-	-	-	-	-
4	36	29	-	-	-	-	-	-	-
5		19	22	13	-	-	-	-	-
6		2	2	18	6	15	8	-	-
7				4	4	16	15	4	4
8	9			1	3	5	19	12	6
9	74					4	9	13	19
10	157						6	13	22
11	177							15	26
12	143							10	23
13	253							10	20
14	230							7	20
15	189							5	19
16	108							5	17
17	65							5	15
18	52							3	12
19	42							3	8
20	61							1	7
21	35							1	7
22	23							1	7
23	28							1	6
24	12							1	4
25	8							1	3
26	1							1	2

Appendix 6.2. One-factor ANOVA for developmental period from eggs to adults of TSSM on M4 at 76%RH and a light intensity of 171 lux among different temperatures.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	686.6413	343.3207	227.0035**
Within groups	58	87.7194	1.5124	
Total	60	774.3607		

Appendix 6.3. One-factor ANOVA for developmental period from eggs to adults of TSSM on M27 at 76%RH and a light intensity of 171 lux among different temperatures.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	584.8265	292.4132	222.7864**
Within groups	50	65.6264	1.3125	
Total	52	650.4528		

Appendix 7.1. One-factor ANOVA for the number of ventral glands among 27 genotypes of hops.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	182.03798	7.00146	1.1635ns
Within groups	189	1137.36847	6.01782	
Total	215	1319.40645		

Appendix 7.2. One-factor ANOVA for the number of trichomes among 27 genotypes of hops.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	359.36297	13.82165	2.8781**
Within groups	189	907.63893	4.80232	
Total	215	1267.00190		

Appendix 7.3. One-factor ANOVA for the diameters of ventral glands among 27 genotypes of hops.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	25528.90852	981.8811	4.2899**
Within groups	189	43258.91067	228.8831	
Total	215	68787.81919		

Appendix 7.4. One-factor ANOVA for the basal diameters of trichomes among 27 genotypes of hops.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	10436.05497	401.38673	1.8749*
Within groups	135	28901.17918	214.08281	
Total	161	39337.23416		

Appendix 7.5. One-factor ANOVA for the length of trichomes among 27 genotypes of hops.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	558643.33778	21486.28222	1.5933*
Within groups	135	1820502.22667	13485.20168	
Total	161	2379145.56444		

Appendix 7.6. One-factor ANOVA for the number of stomata per mm^2 among 27 genotypes of hops.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	1.38227E10	5.31644E8	2.3875**
Within groups	189	4.20869E10	2.22682E8	
Total	215	5.59096E10		

Appendix 7.7. One-factor ANOVA for stomatal length among 27 genotypes of hops.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	546.08214	21.00316	2.3263**
Within groups	189	1706.38985	9.02852	
Total	215	2252.47199		

Appendix 7.8. One-factor ANOVA for stomatal width among 27 genotypes of hops.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	72.58409	2.7917	2.7330**
Within groups	189	193.05797	1.0215	
Total	215	265.64206		

Appendix 7.9. One-factor ANOVA for the thickness of leaves among 27 genotypes of hops.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	2211.8842	85.07247	0.9333ns
Within groups	135	12305.1250	91.14907	
Total	161	14517.0092		

Appendix 7.10. One-factor ANOVA for thickness of leaf veins among 27 genotypes of hops.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	0.56293	0.02165	0.2114ns
Within groups	135	13.82373	0.10240	
Total	161	14.38665		

Appendix 7.11. One-factor ANOVA for cuticle thickness of leaves among 27 genotypes.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	12.35478	0.47518	0.66795ns
Within groups	135	96.04000	0.71141	
Total	161	108.39478		

Appendix 7.12. One-factor ANOVA for percent dry weight of leaves among 27 genotypes.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	273.82540	10.53175	2.9452**
Within groups	135	482.75092	3.57593	
Total	161	756.57632		

Appendix 7.13. One-factor ANOVA for upper epidermis of leaves among 27 genotypes.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	245.32884	9.43572	0.72677ns
Within groups	135	1752.73000	12.98319	
Total	161	1998.05884		

Appendix 7.14. One-factor ANOVA for lower epidermis of leaves among 27 genotypes.

Source	DF	Sum of square	Mean square	F-test
Between groups	26	28.59858	1.09995	1.02877ns
Within groups	135	144.34012	1.06919	
Total	161	172.93869		

Appendix 8.1. Two-factor ANOVA for the number of adult females per leaf between two hop genotypes at three foliage densities under field conditions on December 30, 1992.

Source	DF	Sum of square	Mean square	F-test
Genotypes (A)	1	13.44444	13.44444	13.4444**
Foliage densities (B)	2	0.50000	0.25000	0.2500ns
AB	2	0.05556	0.02778	0.0278ns
Error	30	30.00000		

Appendix 8.2. Two-factor ANOVA for the total number of mites per leaf between two hop genotypes at three foliage densities under field conditions on January 13, 1993.

Source	DF	Sum of square	Mean square	F-test
Genotypes (A)	1	64685.4444	64685.4444	28.3364**
Foliage densities (B)	2	26343.0556	13171.5278	5.7699**
AB	2	29651.3889	14825.6944	6.4946**
Error	30	68483.0000	2282.7667	

Appendix 8.3. Two-factor ANOVA for the total number of mites per adhesive tape between two hop genotypes at three foliage densities under field conditions on January 27, 1993.

Source	DF	Sum of square	Mean square	F-test
Genotypes (A)	1	96.69444	96.69444	3.28955ns
Foliage densities (B)	2	10.88889	5.44444	0.18522ns
AB	2	20.22222	10.11111	0.34398ns
Error	30	881.83333	29.39444	

Appendix 8.4. Two-factor ANOVA for the total number of mites per leaf between two hop genotypes at three foliage densities under field conditions on February 10, 1993.

Source	DF	Sum of square	Mean square	F-test
Genotypes (A)	1	16.0000	16.0000	0.88889ns
Foliage densities (B)	2	37.5556	18.7778	1.04321ns
AB	2	8.6667	4.3333	0.24074ns
Error	30	540.0000	18.0000	

Appendix 8.5. Two-factor ANOVA for the total number of mites per leaf between two hop genotypes at three foliage densities under field conditions on February 17, 1993.

Source	DF	Sum of square	Mean square	F-test
Genotypes (A)	1	91.1250	91.1250	1.21732ns
Foliage densities (B)	2	158.0278	79.0139	1.05553ns
AB	2	56.2500	28.1250	0.37571ns
Error	66	4940.5833	74.8573	

Appendix 8.6. Two-factor ANOVA for the total number of mites per leaf between two hop genotypes at three foliage densities under field conditions on February 24, 1993.

Source	DF	Sum of square	Mean square	F-test
Genotypes (A)	1	50.00000	50.00000	0.08049ns
Foliage densities (B)	2	5277.52778	2638.76389	4.24765*
AB	2	817.75000	408.87500	0.65817ns
Error	66	41001.16667	621.22980	

Appendix 8.7. Two-factor ANOVA for the total number of mites per leaf between two hop genotypes at three foliage densities under field conditions on March 3, 1993.

Source	DF	Sum of square	Mean square	F-test
Genotypes (A)	1	455.01389	455.01389	1.05636ns
Foliage densities (B)	2	3130.33333	1565.16667	3.63368*
AB	2	906.77778	453.38889	1.05258ns
Error	66	28428.75000	430.73864	

Appendix 8.8. Two-factor ANOVA for the total number of predatory mites per leaf between two hop genotypes at three foliage densities under field conditions on February 17, 1993.

Source	DF	Sum of square	Mean square	F-test
Genotypes (A)	1	45.1250	45.1250	8.048**
Foliage densities (B)	2	23.4444	11.7222	2.091ns
AB	2	2.3333	1.1667	0.208ns
Error	66	370.0830	5.6073	

Appendix 8.9. Two-factor ANOVA for the total number of predatory mites per leaf between two hop genotypes at three foliage densities under field conditions on February 24, 1993.

Source	DF	Sum of square	Mean square	F-test
Genotypes (A)	1	120.125	120.125	7.606**
Foliage densities (B)	2	183.583	91.792	5.812**
AB	2	22.750	11.375	0.720ns
Error	66	1042.417	15.794	

Appendix 8.10. Two-factor ANOVA for the total number of predatory mites per leaf between two hop genotypes at three foliage densities under field conditions on March 3, 1993.

Source	DF	Sum of square	Mean square	F-test
Genotypes (A)	1	242.00000	242.00000	5.929*
Foliage densities (B)	2	443.44444	221.72200	5.432**
AB	2	142.33333	71.16700	1.744ns
Error	66	2694.00000	40.81800	

Appendix 8.11. Two-factor ANOVA for the total number of mites per leaf among four hop genotypes at two foliage densities on the first sampling occasion under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Genotypes (A)	3	3958.562	1319.521	5.725**
Foliage densities (B)	1	682.521	682.521	2.961ns
AB	3	4376.729	1458.91	6.33**
Error	40	9219.167	230.479	

Appendix 8.12. Two-factor ANOVA for the total number of mites per leaf among four hop genotypes at two foliage densities on the second sampling occasion under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Genotypes (A)	3	33745.167	11248.389	10.39**
Foliage densities (B)	1	3816.333	3816.333	3.525ns
AB	3	31416.500	10472.167	9.673**
Error	40	43302.667	1082.567	

Appendix 9.1. One-factor ANOVA for the photosynthesis rate of hop leaves among three genotypes.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	40.268	20.134	4.144*
Within groups	15	72.881	4.859	
Total	17	113.149		

Appendix 9.2. One-factor ANOVA for the stomatal conductance of hop leaves among three genotypes.

Source	DF	Sum of square	Mean square	F-test
Between groups	2	0.009	0.005	4.379*
Within groups	15	0.015	0.001	
Total	17	0.025		

Appendix 9.3. One-factor ANOVA for the photosynthesis rate of hop leaves between cutting and rootstock plants.

Source	DF	Sum of square	Mean square	F-test
Between groups	1	6.313	6.313	0.513ns
Within groups	10	123.074	12.307	
Total	11	129.387		

Appendix 9.4. One-factor ANOVA for the stomatal conductance of hop leaves between cutting and rootstock plants.

Source	DF	Sum of square	Mean square	F-test
Between groups	1	0.006	0.006	3.077ns
Within groups	10	0.020	0.002	
Total	11	0.026		

Appendix 9.5. One-factor ANOVA for the photosynthesis rate of hop leaves between plastic treated and untreated plants.

Source	DF	Sum of square	Mean square	F-test
Between groups	1	0.096	0.096	0.006ns
Within groups	22	378.245	17.193	
Total	23	378.341		

Appendix 9.6. One-factor ANOVA for the stomatal conductance of hop leaves between plastic treated and untreated plants.

Source	DF	Sum of square	Mean square	F-test
Between groups	1	2.042E-6	2.042E-6	4.571E-4ns
Within groups	22	0.098	0.004	
Total	23	0.098		

Appendix 9.7. One-factor ANOVA for the photosynthesis rate of hop leaves between TSSM infested and uninfested plants for the first measurement under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	1	0.095	0.095	0.017ns
Within groups	10	55.008	5.501	
Total	11	55.104		

Appendix 9.8. One-factor ANOVA for the stomatal conductance of hop leaves between TSSM infested and uninfested plants for the first measurement under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	1	3.741E-4	3.741E-4	0.181ns
Within groups	10	0.021	0.002	
Total	11	0.021		

Appendix 9.9. One-factor ANOVA for the photosynthesis rate of hop leaves between TSSM infested and uninfested plants for the second measurement under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	1	30.600	30.600	3.752ns
Within groups	4	32.621	8.155	
Total	5	63.222		

Appendix 9.10. One-factor ANOVA for the stomatal conductance of hop leaves between TSSM infested and uninfested plants for the second measurement under glasshouse conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	1	0.007	0.007	7.189ns
Within groups	4	0.004	0.001	
Total	5	0.011		

Appendix 9.11. One-factor ANOVA for the photosynthesis rate of hop leaves between TSSM infested and uninfested plants under field conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	1	29.872	29.872	2.988ns
Within groups	12	119.973	9.998	
Total	13	149.844		

Appendix 9.12. One-factor ANOVA for the stomatal conductance of hop leaves between TSSM infested and uninfested plants under field conditions.

Source	DF	Sum of square	Mean square	F-test
Between groups	1	3.401E-4	3.401E-4	0.18ns
Within groups	12	0.023	0.002	
Total	13	0.023		