FACTORS INFLUENCING BRANCH PRODUCTION
IN YOUNG APPLE TREES

by

Nopadol Jarassamrit

Bachelor of Science (Agriculture)

Kasetsart University

Thailand

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. To the best of my knowledge and belief it contains no copy or paraphrase of material previously published or written by another person, except where due reference is made in the text.

Nopadol Jarassamrit

University of Tasmania

Hobart, Tasmania,

Australia.

27 July 1989

Contents

SUMMARY

In commercial apple (*Malus domestica* Borkh.) orchards, early cropping is a very important economic consideration. Orchard turnover is now occurring more rapidly through the release of new varieties and this demands the minimisation of plant establishment costs. It has been reported that young trees with branches produce crops much earlier than those with no branches.

A series of experiments have been conducted to explore the factors involved in branch production, and to examine some methods of manipulating or inducing branches in nursery and one-year-old apple trees, particularly spur type 'Red Delicious'.

The results presented confirm that spur type Red Delicious apple nursery trees produce very few branches when compared with Golden Delicious and Red Fuji, on MM106 rootstocks. Chemical treatments, of Cytolin (BA+GA_{4+7}) at 800 ppm (single application) and four sequential applications of 200 ppm, induced lateral shoot formation on nursery trees; but the sequential applications produced narrow branch crotch angles. A more detailed study showed that BA is the main effective ingredient of the mixture, when applied as a single spray.

GA_{4+7} alone induced branching when applied in 4 sequential applications at 200 ppm, but the lateral shoots had narrow crotch angles. The GA_{4+7}-induced branch crotch angles became wider, while the branches were growing.

NAA at 10 ppm did not influence the Cytolin- or GA_{4+7}-induced branch crotch angle, when applied at different periods of growth.

Cytolin was also applied to one-year-old apple orchard

trees to induce lateral shoots, at lower concentrations than applied to the nursery trees. An optimum concentration range of Cytolin concentration of between 80 and 100 ppm is suggested. Concentrations of Cytolin were used up to 200 ppm without phytotoxicity symptoms. The higher concentrations resulted in excessive lateral shoot production but shoot length was reduced.

Other growth regulators i.e. M&B 25,105, thidiazuron, or paclobutrazol were also tested on nursery trees, but they produced unwanted side effects without any significantly increase in the number of lateral shoots.

Mechanical treatments i.e. the removal of young or mature leaves, lower lateral shoots or buds did not induce any increased lateral growth. The removal of leading shoot tips induced a cluster of lateral shoots, immediately below the apical node but these had narrow crotch angles.

The results are discussed in terms of the possible relationships between the plant hormones and their influence on lateral shoot induction. The practical considerations required to fully utilise the spur type apple varieties' natural advantages in early cropping are also discussed.

Acknowledgements

First of all, I would like to thank the Thai people, who sponsored me through a Thai Government Scholarship which gave me the opportunity to do a Master's degree at the University of Tasmania.

I express my profound gratitude to my supervisor Dr. R. C. Menary, Reader in Horticultural Science with the Faculty of Agricultural Science and my co-supervisors Mr. S. J. Wilson, Mr. K. M. Jones, and Mr. P. Jotic, Horticulturists of the Tasmanian Department of Agriculture, for their help and their encouragement and critical advice.

I would also like to express my gratitude to Mr. P. Andrews, Manager of the Grove Research Station, and his staff for their help in my field experiments. The assistance provided by Mr. M. Oakford, Miss Jane Croger, Miss Sally Shepherd, Mr. Clive Morris and other Technical Officers of the Tasmanian Department of Agriculture was also very much appreciated.

My thanks also go to Mr. T. B. Koen, Biometrician of the Tasmanian Department of Agriculture for his advice on planning my experiments and analysis of the data.

My thanks are also due to the teaching and technical staff and fellow post-graduates of Faculty of Agricultural Science, for providing facilities and assistance for this work, particularly Dr. J. J. Yates, Dr. M. Kerslake, Mr. J. Groot, and Mr. D. Bradford. The assistance provided by the staff of the Bio-Medical Library was very much appreciated.

I thank Mr. G. Adams and Mr. W. Hazell who allowed me to conduct my experiments on their property, Forest Home, and use their

vi

valuable apple nursery trees. I also thank Mr. S. C. Price, the manager of Rookwood, who let me conduct my experiment on his orchard trees.

Also acknowledged is the chemicals supplied by the manufacturers, particularly, Mr. N. E. Stone of Schering Pty. Ltd.

I wish to thank Mrs. Janet Ault who helped me overcome difficulties in English when I first arrived in Tasmania.

Lastly, I wish to express my gratitude to my voluntary English tutor Mr. Rex Beuganey for his supportive and useful advice.

1. Introduction

In the apple industry, apple cultivars which have high market demand are the ones required for new apple plantings. There are many other factors in successful modern apple production. Economic pressures now demand early, high and regular production, resulting in modern intensive planting systems which also increase the production efficiency of land.

There is considerable variation in the earliness of cropping of different cultivars. Fortunately, some of the important commercial cultivars, have mutants which have the potential to naturally crop early. Spur type strains of some major commercial cultivars are good examples of this. These spur types, although early flowering often show poor branch production at the early stages of growth, which may limit production efficiency in the mature orchard. Thus there is a need to produce branches at early stages of growth, to fully exploit the inherent production potential.

The present study is aimed at assessing the factors influencing or inducing, branch production in spur type 'Red Delicious'.

2. Literature Review

2.1. Apple tree morphogenesis

Definitions

Biologists and physiologists define morphogenesis as the origin of form. Morphogenesis also implies the process of growth and development of the form. As apple trees have different forms in time, space, and location, horticulturists define tree form, in general, as the above-ground parts. There are a lot of definitions of tree form which based on skeletal structure and on the canopy density of trees (Barlow, 1970). The skeletal structure of a tree is the outward and visible parts of the trees which could possibly be presented by the ratio of height to spread, the space occupied on ground (area of ground surface covered by the tree), the superficial volume where the fruit is borne, or the ratios of crop (numbers or weight) to some parameters of tree size. In young trees, the vertical growth is more dominant than the horizontal growth so the ratio of height to spread is high. As the trees grow older, the height to spread ratio is changed, as well as the ratio of height to the space occupied on the ground. Thus the tree form changes as the tree gets larger. The tree form would be more meaningful when defined as the ratio of height to superficial volume, where the best fruit is borne. This definition of form also refers to the position of the flowers and fruits. The tree form may change very quickly not only as the tree grows but also as the different varieties are compared (Barlow, 1970).

It is very useful to consider tree form in term of fruitfulness. There is another definition of tree form described in terms of the partition of energy captured by the tree into fruiting and non fruiting parts, using dry matter as a measure of energy captured. The fruitfulness

2

indices can be given from some ratios of crop (numbers or weight) to some parameters of tree size such as tree weight above the graft union, trunk cross-section, or area covered by the tree (Preston, 1967).

There are other definitions which are based on canopy density. The canopy density depends upon such factors as the opacity, shape and posture of the individual leaf, leaf arrangement such as leaf angle, the leaf number and size, and the total area of the foliage which covers the ground. As the total leaf area (leaf size x leaf number) might be useful in defining tree form; it has to be related to some other parameters of tree size e.g. Leaf Area Index (the measurement of leaf area per unit area of ground on any occasion) may be considered as the leaf area in relation to the ground covered by the tree (Jackson, 1970). Vyvyan (1957) suggested that Leaf Weight Ratio (the measurement of total leaf dry weight per total plant dry weight) should be more meaningful as it assesses the ratio of leaf weight to total increment rather than total plant weight. Avery (1969) suggested that time should be related to some definitions of tree form, as Leaf Area Duration (the area under the curve, if leaf area index is plotted against time, is a measure of the area and duration of leaves), because the growth rates, the production and duration of leaves and shoots are different from time to time.

Growth and development

Some definitions of tree form are related to the growth and development of trees. Growth is the term that is applied to quantitative changes occurring during development and is defined as irreversible changes in the size of a cell, an organ, or whole tree. Development involves both growth and differentiation, along certain axes between cells, tissues and organs, which can be studied by two major types of approach viz. the morphological, or the physiological and biochemical. Developmental morphology and anatomy are concerned with describing the visible changes occurring during development. The physiological and biological processes are also connected as they determine the rates of the morphological changes (Wareing and Phillips, 1981).

The gross external morphology of the tree (tree form) or the tree as a whole organisation can be considered on several different levels:

1. the structural organisation of the individual cell,

2. the organisation of cells to form tissues, and

3. the organisation of the tree body at a macroscopic level.

At cellular level, the enlargement and division of cells are directed by the increase in living materials. The relative elemental growth rates of cells along the x, y, and z coordinates play a direct role in influencing the final shape of a tree. The direction of cell expansion may influence the orientation of cell division. In primary meristematic regions, the direction of spindle orientation is commonly parallel to the long axis of cells. Because of the direction of the axis changes during mitosis, the direction of spindle orientation will also change. The final

result of such division is a solid three-dimensional structure. In addition, the long axis of the spindle tends to be parallel to the direction of the greatest active expansion, regardless of cell shape. Accordingly any factors which influence the rate or direction of cell expansion might indirectly influence the plane of cell division and expansion (Evans, 1984).

As a tree grows, not all the cells tend to grow equally but the main activities are limited to the meristems. There are two main types of meristematic tissues, apical and lateral. Apical meristems are located in the axial organs, the shoots and roots, which grow in length at the tip region when new tissues are being added. Lateral meristems including the cambium and phellogen (cork cambium), cause growth in thickness of the tree. These two types of meristem are capable of growth over a long period, and are described as "indeterminate" meristems. Other parts of the tree, particularly leaves, flowers, and fruits, have limited period of growth, where the whole organ reaches maturity and then proceeds to senescence. The growing regions of such organs may be described as "determinate" meristems. Indeterminate apical meristems with the capacity to form branches provide a precise and definitive tree form (Wareing and Phillips, 1981).

A bud is meristem from which shoots or flowers develop. An apple shoot develops from a vegetative bud which is located either terminally or laterally on last season's growth. A spur is a slow-growing shoot usually less than 2 cm. long. The vegetative bud contains leaf primordia around a central axis; the oldest primordia being located at its base and the youngest ones are near the apex. As the bud bursts, young leaves and internodes expand, and the extension of the main shoot, branches and leaves continues. In each leaf axil there is an axillary bud. Axillary buds are located spirally, counterclockwise around the shoot, and

5

is almost directly opposite (135°) from the one above or below it. Most apple varieties have a 3/8 spiral arrangement (phyllotaxy); i.e. 1 and 9, 2 and 10, 3 and 11, etc., buds will be directly above each other (Tukey, 1981).

The growth of a branch is influenced by its orientation. The vertical branches are the most vigorous; and the weakest growing are the most horizontal ones. A branch with an angle of 30° usually has vegetative growth of uniform vigour but near the top there will be the vertical and vigorous growth (Tukey, 1981). Flower bud formation is inhibited by vertical and stimulated by horizontal branching or a lower positioning in the tree (Tromp, 1987).

Apple flower buds are mixed buds, containing terminal flower primordia and subtended leaf and lateral bud primordia. A flower bud is a shortened axis bearing typically 21 leaf formations inserted in a spiral sequence. These consist of nine bud scales, three transition leaves, six true leaves, and three bracts. The axis is terminated by a flower primordium, the "king" flower and lateral flower primordia are formed in the axils of the three bracts and six true leaves. These are formed terminally on shoots and spurs, and occasionally they might be formed laterally. The leaf and lateral bud primordia are the future sites for new extension growth (Abbott, 1970; Tukey, 1981).

At the time of flower bud initiation, any fruits on the tree are developing rapidly. The apical meristems of the shoot or axillary buds begin to flatten out and primordia begin to arise to produce the various parts of the flower. The flower bud initiation can occur only after a given number of nodes in the bud meristem has been reached. This critical number of nodes varies with fruit and variety (Tukey, 1981). For example, for 'Cox's Orange Pipin' the critical number of nodes is 20 with 16 for 'Golden Delicious' (Tromp, 1976). A potential flower bud also needs a period of time to reach "ripeness to flower" which is defined in term of

number of nodes initiated in the bud meristem. Fruits and varieties which have a low critical number of nodes initiate flowers earlier than those which have a large critical number. The length of the period of time between the initiation of successive leaf primordia in the meristem, or plastochron, also varies (Tukey, 1981). Fulford (1966) considered that flower initiation is related to the length of the plastochron, and has shown that flowers do not form if this is longer than seven days. He observed that the length of the plastochron may be influenced by the inhibitory effect of successively older primordia

The roots play an important role in the growth and development of the tree. The function of the root is not only to support the tree and absorb water and nutrients from the soil, but also produce growth hormones which are transported to the shoot where they influence the physiological processes in the whole tree. The growth of the root, as well as the shoot, depends on cell division and enlargement at the tip (Tukey, 1981). Roots do not enter a period of rest as does the above-ground portion of the tree in the autumn. Root growth continues throughout the dormant period. The periods of root growth during the year are almost the opposite from that of shoot growth. In the spring, when the soil temperature rises, the root growth increases sharply and reaches a peak about the time of bud break. The rapid root growth may continue through the bloom period but declines rapidly when the shoot growth increases. Root growth declines very quickly when fruits are present on the tree and reaches a minimum 4-6 weeks after bloom. In mid summer after shoot growth has ceased, root growth commences again and continues during the autumn and throughout the winter, but declines with lower soil temperature (Head, 1966 and 1969; Tukey, 1981).

2.2. Factors influencing apple tree morphogenesis

Apple tree morphogenesis is the result of the growth and development of the tree. The tree growth and development can be considered in terms of either a whole-tree form, or separate components such as the type of shoot which is the result of this developmental sequence:

a). The absolute and relative amounts of cell division and enlargement in the shoot apex, lateral meristems, foliar and axillary buds, and

b). the orientation of cell division and enlargement in the shoot apex, lateral meristems, foliar and axillary buds;

c). the degree of apical dominance;

d). vascularization;

e). cambial activity.

These represent five primary form-builders which are affected by numerous factors (Barlow, 1970). The factors include endogenous morphogens, genetic characteristics of both scion and rootstock, and the cultural practices.

2.2.1.Morphogens

Morphogens (phytohormones, plant growth hormones or growth regulators) are defined as organic compounds other than nutrients produced by plants in low concentrations which regulate (promote or inhibit) or modify any plant physiological processes. Morphogens usually move within the plants from a site of production to a site of action (Weaver, 1972). Under this conceptual framework, the morphogen systems may be considered in terms of three primary components (Leopold and Noodén, 1984):

1). a site of synthesis or source of a morphogen,

2). movement from the source to the site of action and,

3). action by the morphogen upon the target site(s).

Morphogens appear to have a particular role in control at the intercellular level, serving to correlate growth in spatially distinct regions of the plant. Nevertheless, as a morphogen enters a cell it influences a number of biochemical activities which constitute part of the intracellular control mechanism. Also, many environmental effects on plants are apparently mediated through changes in internal morphogen levels and distribution. Both genetic and environmental control of growth and differentiation are, therefore, achieved by means which include the action of morphogens (Wareing and Phillips, 1981).

Each morphogen has its own role in the development of tree form; but most of its effect is the result of interaction with other morphogens. There are five main groups of morphogens: auxins, cytokinins, gibberellins, ethylene, and abscisic acid as shown in Figure 1. (Poovaiah, 1981).

9
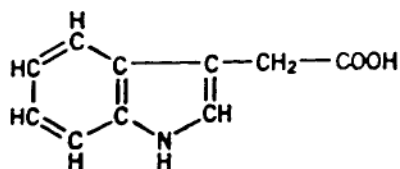
A. Indole acetic acid (IAA)
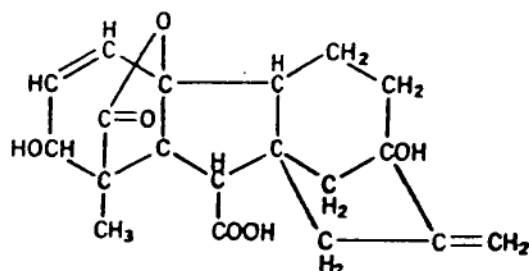
B. Gibberellic acid
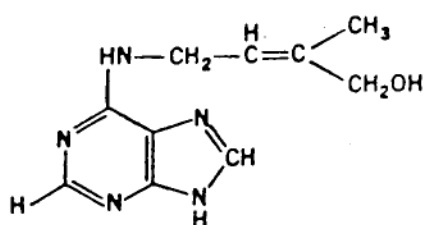
C. Zeatin
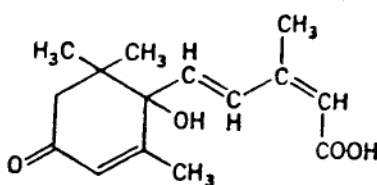
D. Abscisic acid
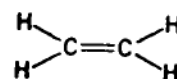
E. Ethylene

Figure 1. Naturally occurring plant hormones illustrated above are A. Indole acetic acid (IAA), the most common auxin; B. Gibberellic acid (GA$_3$), one of 72 known gibberellins; C. Zeatin, one of several cytokinins; D. Abscisic acid (ABA); and E. Ethylene, a gaseous growth regulator. (Poovaiah, 1981).

Auxins

Auxins are biosynthesized from L-tryptophan. IAA (Indole-3-acetic acid) is the most significant and common auxin present in plants (Bearder, 1980). The main sites of auxin synthesis are the meristematic tissues and young growing parts of the plant, the shoot apex, buds, developing seeds, and also mature leaves of a vegetative shoot system. The most active sites of IAA synthesis are the rapidly expanding leaves in the upper part of the shoot rather than the shoot tip tissues. (Sembdner et al.,1980).

Following exogenous application of auxin there is a "lag" or "latent" period before growth rate (as cell expansion) increases. The length of the latent period and processes within the period are the key to the role of auxin in inducing increased growth. However, the length of the period and the processes vary from tissue to tissue. Examples of the processes are stimulation of RNA synthesis, protein synthesis, cell wall synthesis and degradation, increased cell wall extensibility, respiration, and change in membrane potential. Sustaining growth requires continued RNA and protein synthesis, and auxin can stimulate the synthesis of RNA in elongating tissues. This requirement leads to the proposition of the so-called gene activation hypothesis which suggests that auxin derepresses certain genes, the expression of which was necessary for the extension process. In elongating tissues, enzymes are produced where the synthesis is promoted by auxin. This includes both those degrading and synthesizing components of the cell wall. (Zeroni and Hall, 1980). Dextran, one of the cell wall components, is broken down by dextranase which is sensitive to auxin. Dextran breakdown increases cell wall elasticity which is necessary for cell elongation. The auxin role in growth is affected by cell

wall-loosening process which is related to hydrogen ion release which in turn regulates cell extensibility and responses to turgor pressure. At the stage of cell enlargement, auxin promotes turnover of certain hemicelluloses involved in cell wall development (Lockard and Schneider, 1981).

Went (1928) discovered auxin and its polar basipetal transport. The polar basipetal auxin transport i.e., downward from the morphological apex to more basal regions, occurs in all organs of vegetative shoots and moves more rapidly than acropetally i.e., from basal to apical regions. The mechanism of an auxin polar transport hypothesis was proposed by Goldsmith (1977) as a chemiosmotic one; the mechanism requires metabolic energy from cells. It has been suggested that polar transport of auxin occurs only in association with cell elongation because the maturation processes in a tissue are associated with a gradual reduction of the polarity of auxin transport (Wareing and Phillips, 1981; Leopold and Kriedemann, 1975). During the meristematic state of a cell, the cell is retained indefinitely regardless of geotropic orientation of the tissue because in apples an inverted bark graft or intermediate stem piece may restrict auxin transport to the roots (Lockard and Scheider, 1981).

By using ^{14}C-IAA Newman (1970) found that IAA is normally moved through the symplast not the apoplast because IAA could be maintained as a front moving with a constant speed behind which the concentration rose nearly linearly. Zajaczkowski et al. (1984) proposed a theory for auxin movement that polar basipetally transportation of auxin occurs in a wave-like pattern. The three-dimensional vector field which exists when auxin waves are propagated through stems can specify positional information to differentiating cambial derivatives. It has been observed that the increasing deviation of vectors of auxin waves occurs

from a cell's axis associated with the sequence of morphogenic events during axial tracheid differentiation. During organogenesis, in the cells of the meristematic regions, the auxin wave vectors are parallel with the axes of the cells. Organ polarity and the organ axis tend to parallel each other. Outside the meristematic regions, the process of cell differentiation and the gradual loss of polarity apparently contribute to the reduction of energy requirement, but the maintenance of undifferentiated tissue requires more energy. The result of the differences in the amounts of energy being used to compensate for the deviation of the vector of the auxin waves from the polar direction might provide positional information to control the developmental processes. In the shoot, gravity has some effects on cell and organ polarities, which is a requirement for attaining and maintaining the least energy state of the system. This concept can be used to explain the various types of branching that may be derived from different quantitative relationships between the parameters of the auxin waves moving along the organ axes. Dichotomous shoots may be produced by equal deviations of vectors in two interacting shoots. The domination of a main axis may completely inhibit propagation of auxin waves in lateral axes and result in suppression of lateral buds. A main stem which has been experimentally exposed to horizontal positioning would be expected to produce radial deviation of the vectors in response to gravity. For example, Mullins (1965 and 1967) found that placing young apple trees in horizontal positions caused a reduction in terminal extension growth and stimulation in lateral extension along the upper side, but did not reduce the total amount of growth compared with vertically growing trees. This would explain the differential growth of lateral axes (buds) on the opposite sides of the stem as is known to occur in the various cases of geotropism. (Zajaczkowski et al., 1984).

In leaf cells, auxin has both stimulatory and inhibitory effects on cell expansion. There is a correlation between increased auxin transport from the leaves and decreased cell division activity. Auxin promotes cell elongation in parenchyma, collenchyma and vascular tissues (Jacobs, 1984). Auxin also plays a very important role in a self-perpetuating vascular system. In the auxin synthesized regions, e.g. in stem tips, auxin is produced during xylem and phloem differentiation and promotes xylem and phloem formation (Sheldrake and Northcote, 1968). Patrick and Wareing (1972) suggested that the different in sucrose movement in IAA-treated and untreated plants was due to the fact that IAA prevents senescence of transporting tissues.

Gibberellins

Gibberellins (GAs) are biosynthesized in young leaves, roots, embryos, cotyledons, fruits, and seeds. GAs are also supplied by the apex, where the leaf primordia are the main source rather than the meristem itself. The leaf primordium appears to continue to produce GAs throughout the period of cell division (Leopold and Kriedemann, 1975). Of the 72 different known gibberellins, GA_3, GA_4, GA_7 (Poovaiah, 1981), GA_1, GA_{19}, and GA_{20} (Looney et al., 1988) have been found in apples.

Gibberellins are normally slowly degraded, after being formed, but they can be converted to inactive forms i.e. conjugates. These conjugates might be stored or translocated prior to release to function at the proper time and locations (Salisbury and Ross, 1985). GAs are able to move freely in all directions within trees. They move with equal facility in both basipetal and acropetal directions. It is considered that the movement of GAs within trees occurs through the normal circulatory system of the phloem and xylem vascular tissues, since they have been detected in both xylem and phloem sap. It has been suggested that GAs move in the same pattern as the carbohydrate translocation system (Leopold and Kriedemann, 1975; Wareing and Phillips, 1981). Crozier and Reid (1971) suggested that shoot-synthesized GA may be translocated to the roots where it is converted to another kind of GA and then recirculated to the shoot tip. The GA may then be active in shoot metabolism, but the root conversion may alter the effectiveness of the hormone.

Barlow (1970) suggested that GA should be regarded as a frame-building morphogen. GAs are involved in extension growth of plant tissues; stem extension by both cell division and cell elongation, and

stem thickening. They affect cell division in the subapical region. They may be more effective in initiating cell division than in accelerating division in cells already mitotically active (Evans, 1984). This can be seen in the internode extension without increase in the number of internodes formed (Sachs and Lang, 1961). GAs promote cell growth by increasing hydrolysis of starch into glucose and fructose. Cell wall plasticity can be increased by GAs which lead to cell elongation (Salisbury and Ross, 1985). GAs must be present continuously for the regulatory action to be produced and this may imply that they become attached to some site of action through a relatively simple attachment-detachment mechanism such as adsorption. GAs appear to involve an alteration of nucleic acid-directed protein synthesis in some longer term regulatory actions but also to involve some other types of activation phenomenon in short-term regulatory actions (Leopold and Kriedemann, 1975).

Gibberellins rarely show supra-optimal (high concentration) inhibition of elongation. Even very high concentrations of exogenous gibberellic acid (GA_3) can bring about a maximum growth response (Wareing and Phillips, 1981). In apple, an application of exogenous GAs can also break lateral bud dormancy (Jones and Lacey, 1968). Wareing et al. (1964) have shown that gibberellins can stimulate cambium division, the production of unlignified xylem parenchyma, and a strong growth promotion of phloem. An increase in apical dominance can also occur after an application of exogenous gibberellins to an intact plant (Wareing and Phillips, 1981).

The regulatory roles of GA in plant development include nearly a complete range of the plant development functions. GAs promote germination of seeds, growth of buds, control of flowering, fruit setting and growth rate, stimulation of the mobilisation of nutrients in

seeds, and delay of senescence in leaves (Salisbury and Ross, 1985).

Cytokinins

Cytokinins are N^6-substituted adenine derivatives compounds such as kinetin or zeatin. Cytokinins promote cell division (cytokinesis) and organ formation, and regulate nucleic acids (DNA and RNA), apical dominance, branching, and bud initiation. They influence transport of nutrients and metabolites, prevent abscission and senescence of flowers, leaves and fruits, and inhibit root initiation (Westwood, 1978), and increase nutrient sink activities (Salisbury and Ross, 1985). Cytokinins are required for both initiation and continuation of cell division, and the regulation of differentiation in excised tissues. They probably act at the molecular or gene level by incorporation into nucleic acids (Weaver, 1972).

Sheldrake and Northcote (1968) suggest that cytokinins are produced in regions of cell maturation, especially associated with the autolysis of nucleic acid rich cells, such as sieve tubes, perhaps by direct release of purine bases with kinin activity present in tRNA (Barlow, 1970). Cytokinins provide an essential requirement, by influencing the synthesis or activation of protein, collecting the products of dying cells, or inducing new cell formation and anti-senescence (Barlow, 1970; Wareing and Phillips, 1981).

Cytokinins are transported in the sap stream not as free purines but in conjugated forms, such as ribosides or glucosides in both xylem and phloem sap, to the regions of undifferentiated cell (Barlow, 1970; Wareing and Phillips, 1981). It also has been suggested that the main site of synthesis is the root (Evans, 1984). In xylem sap, the common cytokinins to be found are zeatin and its nucleoside and nucleotide

17

(Lockard and Schneider, 1981; Looney et al., 1988). On the way into these vascularized regions they may induce phloem development and this facilitates the subsequent movement of other growth factors, particularly photosynthates (Barlow, 1970). In the xylem sap of trees, the upward flow of cytokinins reaches a peak in spring about the time of full bloom, declines to a low level in late summer and remains low throughout the winter (Westwood, 1978).

At the cellar level, cytokinins seem most likely to play a direct role in the regulation of cell division as an essential leading up to mitosis by increasing the rate of protein synthesis (Salisbury and Ross, 1985). In meristematic tissues, because supra-optimal levels of cytokinins are inhibitory to cell division, it has been suggested that the quiescent center is the site of cytokinin production and that the high level of cytokinin diffusing into the surrounding meristematic cell maintains active division there. Cytokinins also enhance expansion in leaf cells with little enhancement of cell division. (Evans, 1984). Cytokinins also play an important role in apical dominance. The application of cytokinins to axillary buds of apple overcomes apical dominance because one of the factors which control the growth and development of buds is cytokinins (Williams and Stahly, 1968).

Abscisic acid

Abscisic acid (ABA) has a primary site of biosynthesis in chloroplast (Walton, 1980); and also in other plastids (Salisbury and Ross, 1985) ABA has also been found in root caps and shows basipetally transport toward the elongation zone in the root. (Evans, 1984). ABA translocation occurs in both xylem, phloem and in parenchyma cells outside vascular bundles (Salisbury and Ross, 1985).

A major function of ABA in plants is to cause stomates to close as water stress takes place or when elevated CO_2 levels occur in guard cells (Salisbury and Ross, 1985). ABA is a natural growth inhibitor which plays a role in bud dormancy and inhibits the growth of shoots. The levels of ABA increased considerably in leaves and buds when bud dormancy occurs in short days of late summer (Salisbury and Ross, 1985). The regulatory role of ABA in resting buds appears linked to the changing level of GA and other promotors which rise sharply when chilling is completed and the rest period is broken. (Westwood, 1978). A higher ABA level in stems has been found in some apple dwarfing rootstocks compared with the more vigorous ones (Lockard and Schneider, 1981).

ABA inhibitory action against the influences of auxin, GA, and cytokinin appears to be nonspecific in many situations. At cellular level, ABA causes depression or inhibition of RNA and protein synthesis, particularly acting on RNA synthesis. (Zeroni and Hall, 1980), and protein translocation (Salisbury and Ross, 1985). In some cases, it blocks GA induced enzyme production and stimulates fruit and leaf abscission and senescence (Westwood, 1978). In leaf abscission, ABA acts synergistically with kinetin to stimulate callus formation in the leaf abscission zone (Evans, 1984).

19

Ethylene

Ethylene (C_2H_4) is a simple, small unsaturated hydrocarbon, the only known gaseous plant growth regulator (Stoddart and Venis, 1980; Wareing and Phillips, 1981). There are many substances which have been proposed as ethylene precursors such as methionine, ethanol, sucose, glucose, etc. Among them, methionine has been given ~~prominance~~ prominance as a physiological precursor in ethylene biosynthesis. Ethylene biosynthesis has been proved to occur in all plant parts. Rates of the ethylene biosynthesis vary from organ to organ and in the same organ these rates also vary from tissue to tissue and are dependent on the growth and development processes. (Sembdner et al., 1980)

Ethylene is moderately water-soluble, one volume dissolving in four volumes of water at 0°c and in nine volumes at 25°c. These properties allow it to pass rapidly between tissues with the minimum of obstruction in either the gaseous or liquid phase. (Sembdner et. al., 1980). Ethylene moves in plant parts through tissues or air spaces where movement related to tissue porosity. The small molecule and its solubility in water and even greater solubility in lipophilic systems permits easy movement through membranes throughout plants. It appears that ethylene is not translocated between different parts of the plant to a physiologically significant extent, but its changing levels in one part of a plant can influence those in another. Thus, an increase in ethylene levels in the roots can also induce increased levels in the shoot apex. (Leopold and Kriedemann, 1975; Wareing and Phillips, 1981).

The regulatory roles for ethylene are best demonstrated through the inhibitory effects on growth and development. Ethylene

inhibits the growth of shoots, roots and leaves, induces premature abscission of leaves, young fruits, and other organs (Weaver, 1972). At the cellular level, ethylene inhibits cell division in meristems which is accompanied by inhibition of DNA synthesis and a premature switch from a mitotic to a nonmitotic state in meristematic regions. (Evans, 1984). When elongation of the stem and root is inhibited by ethylene, the cell shape is altered and thickened caused by a more longitudinal orientation of cellulose microfibrils being deposited in the cell walls, preventing expansion parallel to these microfibrils but allowing expansion perpendicular to them (Salisbury and Ross, 1985). These effects of ethylene are similar to those which can be induced by supra-optimal concentrations of auxins. It is possible that auxins are not themselves inhibitors of stem elongation, but rather that at high concentrations they stimulate the synthesis of ethylene in plant tissues (Wareing and Phillips, 1981). Weaver (1972) suggested a hypothesis that ethylene regulated growth by altering the transport or metabolism of auxin, and ethylene stimulated important enzyme systems associated with cell membranes. These effects could occur because ethylene may play a role in the transcription and translocation of the genetic code from DNA to RNA to protein (Weaver, 1972).

2.2.2. Interaction of morphogens

Plant hormones regulate the plant at a variety of levels ranging from responses to cellular growth, differentiation and biochemical modulation to maturation and physiological homeostasis with the external environment. There are very few processes which are regulated by a single hormone. The synergistic and antagonistic action of two or more hormones generally provide multiple influences but also the balanced responses to a variety of internal and external factors (Matthysse and Scott, 1984).

Leopold and Noodén (1984) described four general types of hormone interaction:

1). A balance or ratio between hormones. Digby and Wareing (1966) showed that the interaction of auxin (IAA) and gibberellin (GA) in *Populus* had some effects on vascular tissue in terms of a balanced interaction. Fully differentiated xylem was produced when IAA was applied alone, but when GA was applied alone the cambial products on the xylem side did not differentiate into mature xylem. In contrast, no phloem differentiation took place with IAA applied alone, but GA alone promoted it considerably.

2). Opposing effects between hormones. Hall (1952) suggested that ethylene stimulates leaf abscission but auxin inhibits it.

3). Alteration of the effective concentration of one hormone by another. The effects of one hormone on another can include alteration of hormone biosynthesis, translocation or inactivation. Gibberellin seems to mediate the synthesis of tryptophan, a precursor of auxin (Westwood, 1978). The increasing of auxin transport, caused by GA or cytokinin, was correlated with the increased formation of xylem. The

addition of abscisic acid could cause a decrease in xylem area which affects the decrease in IAA transport (Jacobs, 1984). Harrison and Kaufman (1984) showed that IAA promoted cytokinin breakdown.

4). Sequential regulation by several hormones. The growth regulation of oat coleoptiles has been shown to pass through a stage in which growth was stimulated by gibberellin, followed by a stage of cytokinin stimulation and then the final growth phase controlled by auxin (Leopold and Noodén, 1984).

Figure 2. indicates one possible way in which the morphogens control shoot growth. From the stem apex, auxin is the major factor involved in the mobilization of the metabolites which make possible continued differentiation of leaves at the apex. The production of auxin by the apex is assumed to be stimulated by gibberellin from the young leaves; and gibberellin possibly accompanied with auxin, also stimulates the elongation of the internodes. There are some limiting factors which cause the approximately constant rate of growth observed in apple shoots throughout the growing season. The limiting factor may be the rate at which nutrient materials can be moved through the vascular system to the growing points. On the other hand, it could be the accumulation of inhibitors from the mature leaves or the reduction of the cytokinins supply from the root system, which IAA can influence (Luckwill, 1970).

old leaves → ABSCISIC ACID → Counteracts effect of gibberellin

young leaves → GIBBERELLIN → Internode extension

stem apex → AUXIN → Mobilization of nutrients

Protein synthesis

CYTOKININ

root
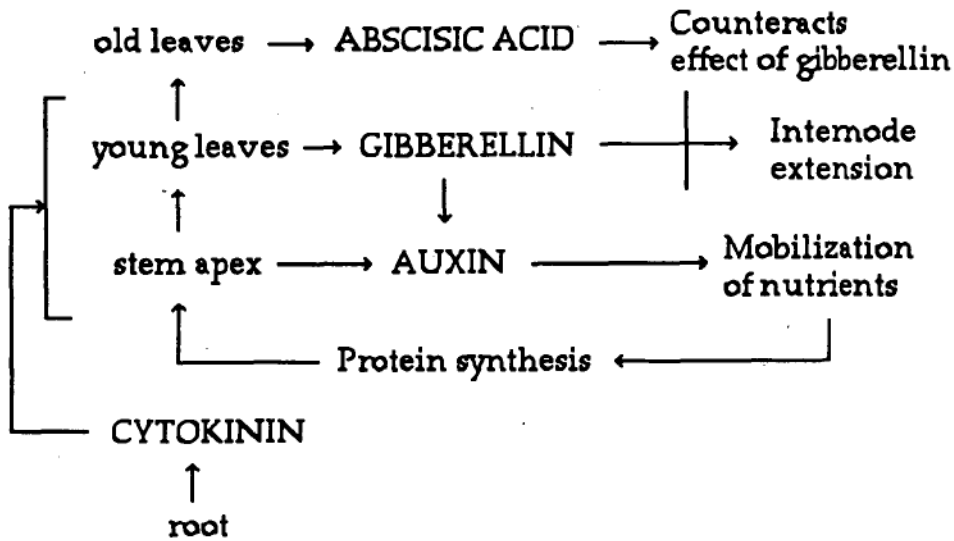
Figure 2. Diagram of possible interactions of types of endogenous hormones in control of shoot growth. (Modified from Luckwill, 1970).

Auxin and cytokinin each stimulate cambial activity in the portion of the plant in which they are synthesized. The formation and action of ethylene in some cases is linked to the continuous presence of IAA. An example is the inhibition of elongating growth by high concentrations of auxin, which result in the production of ethylene. (Matthysse and Scott, 1984).

The interaction of hormones integrates the growth and differentiation of the plant as a whole. It is necessary that the root and shoot meristems communicate with one another and communicate their status to presumptive lateral meristems. Auxin plays a major role in carrying information from the shoot apex to regulate the growth of shoot, lateral branches and lateral roots. Cytokinin carries information from the root apex as it regulates the growth of lateral roots and in addition to lateral branches of the shoot. In some cases, the regulation of synthesis and transport of one hormone by another may involve communication

24

and integration. An example of this is the increase in auxin synthesis in responses to low levels of abscisic acid (Matthysse and Scott, 1984).

Several different seasonal physiological phases can be identified during tree growth. Rapid growth in spring, summer rest, break of rest by low temperatures, and winter dormancy are all thought to be under hormonal control. The major period of growth occurs in spring, particularly following pollination. Cytokinins, gibberellins and auxin all reach a maximum level in spring. However, in winter their production and levels are low. Abscisic acid level is highest during the beginning of rest and reaches a lower levels thereafter. The hormone balance is altered by increasing day length in spring and shortening days in late summer. Growth inhibitors such as ABA, tend to increase while growth promotors (and respiration rate) decrease when buds go into rest or winter dormancy. (Poovaiah, 1981).

During the early stages of tree development, there are a small number of growing points as the sources and the targets of morphogens, when the influence of some morphogens would be more dominant than the others. In addition, at these early stages vegetative growth is dominant. The features of the main branch system are determined in the early stages by three components determining the branching pattern i.e., the degree of apical dominance, the frequency of lateral shoots, and the branch angle. Marked apical dominance can be seen in young stages of development, but there is a gradual loss of apical dominance. As the tree ages, the growing points, the sources and the targets of morphogens, are increased as well as be influenced by some other processes such as, maturation and reproduction. The complexity of the effects of morphogens increases as the tree ages because of differences in the production and interaction of morphogens and the responses of the tree at differing stages of growth and development (Wareing, 1970).

Apical dominance

Apical dominance is a correlative phenomenon. This is because it in general, refers to the correlative inhibition of lateral buds by the terminal buds or growing apex of the shoot. Luckwill (1968) described the term apical dominance, in the woody plant, with reference to the stronger growth made by the upper or leading shoot on a branch, in comparison with the weaker growth of the lateral shoots. The degree of apical dominance of the different plant parts also varies from species to species. In herbaceous plants, the correlative inhibition decreases in intensity with increasing distance from the apex of the plant; whereas in woody plants, the growth of lateral shoots is more inhibited the further they are from the terminal or dominant shoot (Luckwill, 1968).

Many fruit trees exhibit strong apical dominance of individual branches growing from the main trunk. Apical dominance has a direct relationship with tree form and subsequent yield potential (Martin, 1987). In apples, the control of apical dominance is of importance for the production of side branches (feathers) on maiden trees (Luckwill, 1972).

It has been suggested that there are a lot of factors influencing apical dominance including effects of endogenous plant hormones. Martin (1987) suggested that the bud did not grow when the leaf was attached to the plant because the leaf prevented bud growth by extracting all available water and nutrients from the bud, which were available for translocation, to the shoot and root apex; the apex being a site of nutrient accumulation (Rubinstein and Nagao, 1976).

Phillips (1975) concluded that the interaction of a nutritional and hormonal condition must be appropriate to allow bud

outgrowth. In the hormonal system, auxins seem to be a primary component of the inhibitory correlative signal. It has been also been suggested that gibberellins also play a role in regulation of bud growth (Phillips, 1975). Luckwill (1968) suggested that in the growing apple shoot where both auxin and GA are synthesized. GA stimulated either production or downward movement of auxin. Auxin, in turn, promotes the transport of carbohydrates and organic nitrogenous nutrients to the apex to be used in the production of more leaves and internodes. (Luckwill, 1968).

Cytokinin synthesized in roots can also be influenced, either in synthesis or utilization, by auxin within lateral buds, or by the distribution between meristems in the shoot (Phillips, 1975). Martin (1987) suggested that auxin promotes cytokinin breakdown; cytokinin is known to initiate cell division activity. Sachs and Thimann (1964) showed that lateral buds of pea were released from apical dominance by direct application of kinetin. Woolley and Wareing (1972a. and 1972c.) indicated that lateral buds outgrowth required a supply of cytokinin from roots. This suggests that bud inhibition is a deficiency in endogenous cytokinins (Phillips, 1975).

The interaction of three plant hormones, auxin, GA, and cytokinin, seems obvious. Woolley and Wareing (1972c.) suggested that the lateral buds outgrowth is under cytokinin control, but the lateral shoot growth after cytokinin-induced bud outgrowth is promoted by GA. Phillips (1975) concluded that the role of cytokinin was to initiate cell division activity and that GA was required for the subsequent enlargement of newly formed cells in the bud.

Arney and Mitchell (1969) suggested that abscisic acid (ABA) synthesized within lateral buds also has an inhibitory effect on the

buds. Application of auxin can increase the ABA content and lateral bud inhibition (Knox and Wareing, 1984). Tucker and Mansfield (1973) found the cytokinin level in inhibited buds of *Xanthium strumarium* was much higher than in the released buds. They also suggested that ABA accumulation in the buds themselves was induced by auxin and prevented the outgrowth, even if there was cytokinin present in the buds. In apples, Theron et al. (1987) suggested that there are two different mechanisms of bud inhibition existing in apple nursery trees. The first mechanism is related to node position of the bud which inhibition increases with increasing age of the bud and is related to ABA. Another cause of axillary bud inhibition is that imposed by subtending leaf. This inhibition decreases with increasing leaf age and is possibly auxin related mechanism (Theron et al., 1987).

Thus, the requirement of full outgrowth of lateral shoots controlled by the complex hormone system is the capacity of the previously inhibited buds to synthesize the hormones required to overcome the inhibition and only gradually and sequentially to balance other factors e.g., nutrient and water supply (Phillips, 1975).

<u>Branch angle</u>

Branch angle is another component of apple tree morphogenesis. This angle is normally quoted as the angle between the axis of the main trunk and the apparent axis of the branch at the point of attachment. Main branches with narrow angles to the tree trunk are structurally weak and easy to break under heavy fruit load. They are also upright and have very strong vegetative growth which in turn delays flowering. The crotch angle plays a role in light interception within the canopy. This is particularly important for red skinned apple varieties, because anthocyanin development is influenced by light intensity and duration (Filipovich, 1976).

Verner (1955) showed that apple branch angle formation gradually increases over the first period of shoot growth, from 5° or less to as much as 80°. He also demonstrated that branch angle increases from the tip to the base of the tree. On newly planted trees, when 4 or more shoots were above a new branch, its angle was 50°-90°; but where there were no shoots above the branch, it was in the very narrow range of 0°-40°. Jankiewicz et al. (1973) concluded that there was an interaction of factors determining the formation of branch crotch angle such as negative geotropism, geoepinasty, mechanical pressure of tissues, and vascular connection. A shoot will grow straight upwards, as seen in the upmost branches of decapitated apple trees, caused by negative geotropism with elongation being faster on the lower side. Lower shoots grow out horizontally, which is explained by geoepinasty balanced by negative geotropism. The mechanical effect of tissue accumulating in the crotch may push the base of the young shoot to increase the angle from the main axis. The branches which have narrow angles may have a weak vascular

connection to the main axis at the time of formation (Jankiewicz et al., 1973).

Ferree (1981) concluded that branch angle is hormonally controlled, and plant hormones produced from the shoot tip, particular auxins, are very closed concerned. Verner (1938) showed that a continuous supply of IBA in lanolin paste over the cut end of and apple nursery tree without any branches, resulted in development of wide crotch branches throughout the entire tree. Jankiewicz (1970) suggested that in crotch angle formation, auxins act on geotropism and geoepinasty and interact with mechanical pressure exerted on a branch base by the tissues situated in the crotch. Crabbé (1984) suggested that not only the plant hormones from the shoot tip but also ones produced from the roots influence the crotch angle. Faust and Zagaja (1984) suggested that it is possible for a naturally wide crotch angle tree to have a high cytokinin content. Williams and Billingsley (1970) reported that wide crotch angle can be obtained in young apple trees by applying a mixture of gibberellin and cytokinin in a lanolin paste to the dormant buds.

2.2.3. Variety effects

Scion

Apple (*Malus domestica* Borkh.), has a chromosome number of (2n) = 34. It belongs to the family Rosaceae and has been classified into the sub family Pomoideae. This sub family is characterized by having fruit consisting of two to five carpels enclosed in a fleshy covering. Apple trees are deciduous, rarely evergreen or shrubs, and rarely with spiny branches. The genus *Malus* consists of about 25 to 30 species and several sub-species of so-called 'crab apple'. Most of the domestic cultivars have been selected and improved by man for thousands of years and it is difficult to know their origin. Most of the cultivated apples usually are considered to have *Malus pumila* Mill. as the common parent. But there are other species, such as *M. sylvestris*, also have been involve in its evolution (Brown, 1975; Westwood, 1978).

Since apple has been cultivated, selected and improved for a very long time, many plant characteristics, in particular fruit quality, are important for acceptability of a new variety. The fruit colour and appearance seem to be a prime factor for the market acceptance (Sistrunk and Moore, 1983). In many major cultivars, mutants occur naturally and artificially. These mutants, or so-called "sports", show some variation of characteristics such as colour of the fruit, growth habit, disease resistance and bearing habit. Some selections develop a high proportion of lateral spurs rather than long lateral branches; this is called spur type growth habit. Nearly all apple cultivars are of standard type, i.e., non-spur growth habit. The only known and recognized varieties that occur with only spur type form, are 'Lady', 'Grove', 'Ackmene', and 'Bernerrosen'. The first recorded spur type apple mutation of 'Delicious' was the 'Okanoma', a

31

spur sport found in the Knopp Orchard, Omak, USA, in 1921. Since 1955, spur sports for most major apple cultivars have been identified and introduced, the most widely cultivated being those of 'Delicious', 'Golden Delicious', and 'McIntosh' (Fisher and Ketchie, 1981).

The spur types display distinct differences, compared with standard parents, assuming similar cultural practices. The main difference is a genetically controlled compact growth habit, such as reduced internode length, limited side branching on shoots and prolific development of fruit spurs. Most of the spur types have a tendency to produce very upright-growing branches, especially in the 'Delicious' cultivars. There is some indication that 'Oregon Spur Delicious' tends to form wider crotch angles than other strains. The standard types tend to produce more vegetative growth and form an extensive branch framework in their first few years. The spur types produce trees which are precocious in bearing and crop more heavily and regularly in the early years (Brown, 1975; Fisher and Ketchie, 1981). In 'Delicious' spur types, internodes and shoots are only 80% as long as those of standard type. The fruit set per 100 blossoming clusters of 2-year-old 'Delicious' trees were 20% more on spur type than on standard type. (Westwood and Zielinski, 1966).

According to Lapins (1976), the compact growth habit in apple trees is determined by a single dominant gene designated Co. When the Co gene is present in apples almost all lateral buds develop into spurs. The Co gene may express itself in a various ways, such as reducing shoot growth and internode length, and promoting spur formation. According to Zagaja and Faust (1983), it appears that internode length control is not restricted to the Co gene but other mechanisms for internode reduction also exist. The genetic system responsible for the occurrence of short

internodes in genetic dwarfs appears as a product of a joint expression of both polygenic and single gene control systems. Some of the polygenically controlled characters are vigour, spurriness, wide crotch angle and precocity (Faust and Zagaja, 1984). Looney et al. (1988), worked on spur strains of McIntosh apple trees and suggested that the genetic control of spur type growth habit is through the endogenous plant hormone system. They found that a critical level of GA or GA synthesis pathway in actively growing shoots is probably quantitatively rather than qualitatively genetic controlled. Cytokinin, on the other hand, is also involved in the genetic control system because it can reduce the overall GA biosynthesis. Thus, both GA and cytokinin play a role in defining the spur type growing habit as found in the 'McIntosh Wijcik' clone, which is both dwarf and spurry, and has high cytokinin and low GA activities. Looney et al. (1988) also suggested that those of its progeny with the Co gene exhibit high cytokinin activity, but their tendency to lateral branch development depends on vigour which also ,in part, is controlled by the endogenous level and activity of GA.

Different cultivars vary in their overall system of growth and fruiting. Growth habit refers to the overall growth pattern of the tree including the degree of branching, branch orientation (upright or spreading), and branch crotch angle. Fruiting habit refers to the overall pattern of fruiting and including fruiting position on the ends of long or short shoots, age of spurs producing most of the crop; and location of the crop on the scaffold limbs. The French system has been used by Stebbins (1980) to classify apple cultivars into four groups according to growth and fruiting habit:

Type I consists of spur types characterized by 'Starkimson Delicious'. Spur types which tend to form few lateral on the main scaffold limbs. Fruiting occurs on numerous, long-lived, short spurs. So the zone

of fruiting tends to remain close to the trunk as long as this area is exposed to sufficient light for flower initiation.

Type II is characterized by the standard habit or non-spur strains of 'Delicious'. Because branching is more frequent than in Type I, there is a greater tendency for the fruiting zone to move away from the trunk. The tree may develop too many medium-size branches which create a very dense canopy, unless excess branches are wisely removed.

Type III cultivars are characterized by standard habit 'Golden Delicious'. They tend to be spreading with wide crotch angles and frequent branching. They also tend to bear early with most of the fruit on spurs and shoots which are generally 1 to 3 years of age. The fruiting zone on these cultivars tends to move rapidly away from the trunk to the outside of the tree.

Type IV, the tip bearers, are characterized by 'Rome Beauty' and 'Tydemans Red'. They tend to have upright main scaffold limbs with narrow angles and frequent branching. Since most of the crop is produced on the ends of previous years' shoots, a weeping terminal habit develops. The lower half of many shoots will be leafless and less fruit. There is a strong tendency for the fruiting wood to move toward the ends of the branches. (Ferree, 1981).

Rootstock

An apple tree generally consists of two distinct parts or varieties growing together as a unit. The scion, or fruiting portion, is selected for its fruit quality and its tree growth habit. The other portion is the rootstock, or root portion, which is selected for the effects on tree-size control, resistance to pests and diseases, and the tree support (Tukey, 1981). There are two groups of rootstocks, seedling and clonal. Seedling rootstocks are those developed from germinated seeds. They have certain advantages; the production of seedlings is relatively simple and economical, it has a good anchorage, and most seedlings do not retain the viruses occurring in the parent plant. However, they have the disadvantage of genetic variation which may lead to variability in growth and performance of the scion of the grafted trees. Clonal rootstocks are propagated vegetatively from a selected and improved parent plant. They have specific influences on the scion such as disease resistance, growth or flowering characteristics. Each individual clonal rootstock plant has the same genetic components and can be expected to have identical growth characteristics in a given environment (Hartmann and Kester, 1983).

Vyvyan (1955) showed that an apple scion could grow more vigorously on vigorous rootstocks than it would on its own roots. Most apple scion varieties are inherently quite vigorous and selection has been made for other characteristics than vigour. This contrasts with apple rootstocks, where the wide range of rootstock vigour has been the dominant aspect of selection over a long period (Rogers and Beakbane, 1957).

The most significant rootstock effect on a given scion cultivar is control of tree size and shape. In apples, the correct rootstock

selection can be obtained for the complete range of tree size from very dwarfed to very vigorous. Most notable is the series of clonal, apple rootstocks collected and developed at the East Malling Reseach Station in England, beginning in 1912, and designated the East Malling-Long Ashton (EMLA) or M series. They were classified into four groups according to the degree of vigour imparted to the scion cultivars: dwarf, semidwarf, vigorous and very vigorous (Hartmann and Kester, 1983).

Apart from growth control, resistance to insect pests and diseases, precocity and yield efficiency have also been considered. For example, the Malling Merton (MM) series were specially selected, for resistance to woolly aphids (Tukey, 1964).

Prediction of rootstock effects cannot be made without considering the entire tree. The particular cultivar used as the scion can also modify the rootstock influence (Hartmann and Kester, 1983). For example, some vigorous cultivars such as 'Gravenstein' and 'Mutsu' would be perhaps twice as large on M9 dwarf rootstock than 'Jonathan' or 'Golden Delicious'. Spur types are much smaller on dwarf rootstocks than are the parent cultivars (Westwood, 1978).

It has been found that the rootstock modifies the scion more than the scion modifies the rootstock (Rogers and Beakbane, 1957). In some cases, the rootstocks show some effects on the branching habit e.g., MM111 produces a tree somewhat similar in overall size to MM106, but is much more upright, less branching, and not as early to come into heavy cropping. M7 has a very fibrous root system and the growth of the scion on it tends to exhibit the same tendency to be fine, spreading, and more limiting in growth. MM106 produces branches with wide crotch angles, vigorous trees, early fruit and large fruit size. But trees on MM106 are slow to mature, and are susceptible to early autumn freezes and

Phytophtora crown rot (Tukey, 1981).

The most dwarfing rootstocks e.g., M27, M9, M26, M7, usually require staking or trellising supports, particularly in the early years and when heavy annual cropping is desired. Their poor anchorage is due to the brittle nature of the roots. However, the dwarfing effect is not because of a small or a shallow root system. M9 has been found to root as deeply as do vigorous rootstocks in the same soil. In addition, some of the more vigorous rootstocks, which may be as vigorous as seedlings, such as M2, MM104 and MM109 are not as well anchored as seedlings (Westwood, 1978).

Some rootstocks affect not only the tree growth but also fruit yield. On a physiological basis, the balance between root and top affects yield. This in turn has effects on flower initiation, fruit set, and fruit growth. The rootstock upon which a scion is budded or grafted has a significant effect on the precocity of the scion. It has been observed that the rootstocks which have a dwarfing effect on the scion are associated with early cropping. In M1 rootstock, early flowering is achieved to a greater extent than expected from its size-controlling characteristics. Thus, in general, first flowering and fruiting of a young apple tree can be modified by the rootstock, and those rootstocks that restrict vegetative growth enhance precocity (Bukovac, 1981; Westwood, 1978).

There are three considered approaches to explain the mechanism of the scion and rootstock interrelationship which influence the growth, flowering, and fruiting response:

1. nutrient uptake and utilization,

2. translocation of nutrients and water, and

3. alterations in endogenous growth factors.

It has been found that dwarf apple trees often contain higher concentration of nutrients than the vigorous ones. Young apple

trees on M9 rootstocks, were fruitful and this was found to be associated with the accumulation of starch in the shoots early in the season. Early storage of starch would be considered to be favourable for the initiation of flower bud primodia. The apple trees on vigorous rootstocks failed to show such starch storage. New growth would be stimulated by the increased supply of water and nutrients from the vigorous rootstock. This would not allow for storage of carbohydrates, as is the case with dwarfing rootstocks (Hartmann and Kester, 1983).

The dwarfing effect could indicate that translocation is involved, due either to a partial blockage at the graft unions or to a reduction in movement of water and nutrient material (Hartmann and Kester, 1983). Simons (1986) found that the development of the graft union showed some abnormal morphological characteristics associated with the degrees of dwarfing. Excessive non-functioning phloem was found in the extreme dwarfing rootstocks, e.g. M27, M9, M26 (Simons and Chu, 1984). Jones (1986) showed that dwarfing rootstocks lead to a marked depletion in the constituents of the xylem sap stream; and this depletion appeared to include the cytokinin content. He suggested that a possible mechanism which related the depletion of nutrients and growth regulators moving into the scions via the xylem sap to dwarfing. This may operate in intact trees and could control scion vigour.

Endogenous growth regulators have been shown to have a very important role in scion and rootstock relationships. Dwarfing characteristics of some rootstocks can be attributed to their own low production of endogenous growth promoters or their inability to utilize or conduct these substances produced by the scion (Hartmann and Kester, 1983). Lockard and Schneider (1981) showed that the grafted bark ring of dwarfing M26 apple caused reduction in downward movement of auxins,

subsequently reducing cytokinin production in the roots. They also quoted Gur and Samish (1968) that the bark of the more dwarf apple rootstock caused a higher rate of auxin destruction than the bark of the less dwarf clones. Dwarfing M9 rootstocks were found to contain lower GA-like substances than the more vigorous M1 and M25 rootstocks. Either lower production or the more rapid destruction could be the case for the low GA levels in the more dwarfing rootstocks (Hartmann and Kester, 1983).

2.2.4. Cultural Techniques

The external factors which influence apple tree form are environmental factors including cultural techniques. Those, which include training, limb spreading, pruning, etc., are used extensively to create and maintain a desired tree shape.

"Training" is defined as an integrated technique accomplished by pruning to obtain a desired tree shape and framework; and is mainly achieved during the first years of a tree's life. The main objective of tree training practices on young apple trees is to develop a branch framework that results in optimum light penetration to improve color, size, and quality of fruit. Branch angle, or the crotch angle of young apple trees is very important (Ferree, 1981; Tukey, 1981; Westwood, 1978).

In some apple cultivars, particularly spur types, where the natural growth habit favours undesirable upright growth, limb spreading is essential in training the trees. Spreading of limbs should generally not exceed angles of 60°, and less is often suggested. Limb spreading can retard shoot growth on limbs because branch orientation is changed to a more horizontal position which alters plant hormone content, redistribution and/or ratios of plant hormones. Limb spreading helps accomplish several very important targets on a developing tree:

1. Assists in shaping a tree.

2. Assures strong scaffold branches.

3. Helps control growth and minimizes pruning.

4. Encourages strong axillary bud formation that may develop into strong fruiting spurs.

5. Encourages and increases flower bud formation.

6. Allows light penetration onto all portions of a limb.

7. Increases fruit-set.

8. Reduces limb rub of apples because the fruit can hang without touching the limb. (Greene, 1981).

Since the purpose of training is to develop a tree form and orientation that facilitates management techniques and optimizes the light available to the tree and orchard, the pyramidal tree shape maximizes the amount of foliage in the well-exposed shell (Ferree, 1981). In some other systems of training such as four leaders, at the planting time, a branched tree is cut back and reduced to four wide-angled branches. If a central leader tree is desired, all side branches are cut off and the leader is headed back to the desired height. In a hedgerow system, the trees particularly on dwarf rootstocks, should be trained to a central-leader system to encourage upright growth to a height of 3 to 4 meters. It is important that the newly planted trees be pruned back enough to ensure that the top is in good balance with the root system. (Westwood, 1978).

Pruning is a dwarfing process and can be used to maintain any desired tree size. Removal of a branch not only removes stored carbohydrates, but also reduces the potential leaf surface, number of growing points or tree height and spread. Root growth is also correspondingly reduced by pruning and will be delayed until resultant vigorous shoot growth has responded to pruning. Although the whole plant or limb is dwarfed by pruning, this invigorating growth response occurs in the area of the cut. This invigorating effect decreases as the distance from the cut increases. Lateral buds that would normally remain dormant are released to grow; and the larger the cut the more vigorous will be induced growth. Another general principle is that pruning delays flower and fruit bearing of young trees. Pruning limits the number of

41

growing points of young trees and stimulates growth of the remaining buds and carbohydrates do not accumulate for flower bud initiation but are used by the vigorous vegetative growth. It is a general practice to prune young trees as little as possible in the early years but in some of the very intensive plantings, pruning is particularly important and may be necessary. Although pruning is done in winter, summer pruning can also restrict vegetative growth and induce the formation of flowering spurs. Responses vary widely depending on time and type of pruning, environmental conditions, tree vigor and cultivar. Summer pruning generally restricts tree growth more than an equivalent amount of dormant season pruning. It has been suggested that in vigorous young trees, summer pruning may be to help devitalized and encourage them to form flower buds. In intensive plantings, summer pruning by heading back of a leader controls tree size and form and also encourages fruiting. Another concern associated with summer pruning is winter injury because these trees do not harden off as early as unpruned trees. (Ferree, 1981; Greene, 1981; Tukey, 1981).

Branch thinning and heading back produce different physiological responses and each also has a role in developing an efficient tree with a good balance between vegetative and reproductive vigour. Thinning-out removes an entire shoot, spur, branch, or limb while heading-back removes a portion leaving another portion from which new growth can develop. Generally, thinning-out improves light conditions in the tree and increases carbohydrate reservation which in turn encourages flower bud initiation. Heading-back encourages more vegetative growth and the result tends to be fewer spurs and less flower bud initiation. But these cuts are particularly useful with young trees to thicken limbs, to develop lateral shoots, and to balance the scaffold branches. It is beneficial to use these cuts on spur-type apple trees since these cultivars often do not

form sufficient lateral shoots. When the tree ages, thinning-out becomes more important to improve light penetration and spray distribution throughout the tree. The principle fruiting unit for most apple cultivars are spurs, pruning is to maintain balanced spur vigour. To do this, older pendant spurs are removed and new spur growth from shoots is encouraged. (Ferree,1981; Greene, 1981).

According to the cultural classification by Stebbins (1980) as described above, in Type I cultivars (spur type), heading-back cuts are needed in the training years to develop lateral shoots on the primary scaffold by forcing potential spur buds into vegetative extension shoots. It is not necessary to prune this type to renew fruiting wood as it is with other growth types. Type II cultivars need more thinning-out of young wood to induce spurs and retain the fruiting zone in the tree interior. Type III cultivars tend to have brittle wood, consequently heading-back cuts are required to thicken the branches in order to support the early crops. In Type IV (tip bearing) cultivars, delayed spring pruning can often induce lateral shoots on the lower half of the shoot that normally would be bare. It is also important to use many small thinning-out cuts at the branch extremities to ensure a high percentage of fruit spurs in the 1- to 3-year-old wood. But it is a mistake to begin pruning branches of these cultivars from the trunk outward, as this practice will result in large amounts of blind wood (previous season's wood with no lateral growth) (Ferree, 1981).

Pruning also creates hormonal changes within the tree. Severe winter pruning doubled the contents of auxin and gibberellins and increased the cytokinin contents in the conductive tissues of the tree during the beginning of growth in the spring. Excessive growth of the pruned tree followed this high level of plant hormones, although the

43

hormone levels dropped later and continued at relatively low levels for the remainder of the growing season. (Ferree, 1981).

Since some roles of morphogens which affect apple tree form are understood, growth regulator application can be used to obtain the desired tree form. In pruning and training young apple trees, the common problem is reluctance to develop lateral branching. Heading back the shoots can induce more lateral shoots and spurs but this often produces an undesirable cluster of vigorous upright shoots with narrow crotch angles and not enough suitable branches to form the first set of scaffold limbs. Naphthaleneacetic acid (NAA) has been applied to the second, third and forth buds below the heading cut (tip treatment), by Forshey (1977). The result was less of a cluster of shoots at the top associated with an increase in the number of side branches arising form the middle section. In addition, these side branches tended to develop wider and more desirable crotch angles than untreated trees (Raese and Looney, 1981). Filipovich (1976) reported an increase in crotch angle on young apple trees by using 200 ppm of indole butyric acid (IBA) or 25 ppm of 2,3,5 triiodobenzoic acid (TIBA) prepared in a lanolin paste, treated after bud burst.

It is obvious that all cultural techniques alter many physiological processes of apple trees. The success of a cultural practice programme for a particular approach depends on the ability of the manager to choose the right integrated techniques for his situation. Regardless of the chosen approach, better results can be obtained if the techniques are applied with a knowledge of the physiological responses of the tree (Ferree, 1981).

2.3. Apple tree morphogenesis and nursery tree management

In the past, orchardists aimed to develop large vigorous trees and pruned hard to produce strong limbs carrying a limited number of fruit. Nowadays, the aim is to develop a compact tree producing fruit as early as possible. In Australia, most newly planted apple orchards use the central leader type of trees. The central leader, a pyramid-shaped tree with a central stem, or leader, makes better use of the available space and also increases the penetration of light into the canopy to produce more fruitful trees (Baxter, 1981).

In this system a common problem is the lack of development of lateral branches because many important apple cultivars produce few branches in the nursery. The normal practice is to head back the shoots to force more lateral shoots at planting time. However, heading often results in an undesirable cluster of vigorous upright branches with narrow crotch angles and not enough branches to form the first set of scaffold limbs (Raese and Looney, 1981).

In Europe, orchardists generally plant trees that have 5 to 10 side branches or feathers when they come from the nursery (Nickell, 1983). Once the tendency to branch is developed in a tree, little pruning or heading back is required to continue the tendency to branch. Branched nursery trees develop a greater fruiting volume early in the life of the orchard and are therefore more productive (Raese and Looney, 1981; Nickell, 1983). The use of these trees in high density planting systems is particularly important because the economic viability of these systems is dependent upon high levels of cropping from an early stages in the life of the orchard (Quinlan, 1978).

45

2.3.1. Chemical application and other practices to induce branching

Some growth regulators have been used as branching agents commercially. M&B 25,105 (n-propyl 3-*tert* butylphenoxy acetate), for instance, has been successful in inducing branching of nursery trees. This chemical temporarily checks apical dominance by inhibiting the basipetal movement of auxin in treated shoots (Duckworth et al., 1979). The result is production of lateral shoots from axillary buds at internodes below the shoot apex (Quinlan, 1980). M&B 25,105 applied to cv. 'Gloster' (Wertheim, 1987), 'Schone van Boskoop' (Wertheim, 1978a), 'Spatan' (Quinlan, 1978), and many other cultivars (Anon., 1976) as nursery or young apple trees increased branching and produced wide angled branches. For some cultivars such as 'Topred Delicious', the chemical applied up to 2000 ppm was unsuccessful and stunted the trees (Strydom and Honeyborne, 1980).

Cytolin (Promalin) the mixture of BA (6-benzylamino purine) and GA_{4+7} (Gibberellin $_{4+7}$), in 1 BA : 1 GA_{4+7} ratio, has been used as branching agent. Johann (1983) found that in 'Boskoop' and 'Gloster' nursery apple trees, the application of the combination of Promalin and M&B 25,105 produced more branches and wider branch angles compared to the chemicals applied alone. In many trials, it has been found that BA applied alone can produce branches in nursery apple trees as effectively as or more effectively than applied in the form of mixture with GA_{4+7} (Edgerton, 1983; Popenoe and Barritt, 1988; Elfving, 1984, 1985). Elfving (1984) suggested that GA_{4+7} had less physiological effect on branch induction. In spur type 'Delicious' ('Redchief' and 'Campbell'), the application of BA followed by GA_{4+7} two weeks later

produced more branches than BA applied alone or BA followed by GA$_3$ (Popenoe and Barritt, 1988). Cytolin has also been used in young apple trees in the orchard to induce branching. In Tasmania, Cytolin was applied to one year old spur-bearing and non-spur bearing types of 'Red Delicious' trees and it was found that although there was no effect on non-spur bearing trees, the spur-bearing trees were induced to branch (Koen et al., in press).

Some other chemicals have also been used to induce branching but most of them have some undesirable side effects, for example "Off-Shoot-O" (fatty acid methylester) selectively kills or checks growth of shoot tips (Quinlan,1978). "Dikegulac", used by Ramirez et al. (1983), has been found to give an effect on branching but also greatly reduced branch angle and the main stem growth.

Apart from chemical application, some other mechanical treatments have been applied to induce branching such as removing young leaves and the the tips of the shoots. It has been found that shoot tipping produced a high percentage of branched trees but branch formation was just below the excised tip with narrow branch angles (Ramirez et al., 1983; Wertheim, 1978a). The removal of young leaves has been thought to remove the site of auxin production and has been found to induce branches in apple nursery trees (Wertheim, 1978a,b; Popenoe and Barritt, 1988).

2.3.2. Nursery practices and branching

It has been shown that chip-budding gave a higher percentage of success and greater labour productivity than T-budding (Howard et al.,1974; Kviklis, 1986). Howard et.al. (1974) showed that the use of chip-budding produced larger and more uniform one year old trees with more and longer lateral branches compared with T-budding. They also suggested that the superior growth of trees budded by chip-budding was associated with the formation of a better union between scion and rootstock.

The height of budding is also important in producing good quality nursery trees. Jotic (1985) suggested the ideal one-year-old nursery tree as," 15-20 mm. in diameter above the graft union, 1.5 metre high with well developed root systems and preferably well branched between 40 and 70 cm. above the ground level". High budding has the advantage of raising the branches to a height where they can be used to obtain early cropping (Parry, 1986).

In addition, the early establishment and anchorage of young trees may be related to the root development from the buried rootstock shank. That is the portion of the rootstock that was above the soil level in the nursery and was buried at the time of planting trees in the orchard (Jackson et al., 1984). Rom and Motichek (1987) suggested that the growth habit of the scion cultivar can influence the development of adventitious root on the buried rootstock shank. Barritt (1988) also found that spur type cultivars had less rooting on the rootstock shank than the more vigorous non spur type ones. He also suggested that the failure of some apple cultivars to anchor firmly when planted deep might be associated with scion tree type.

3. General Materials and Methods

3.1. Varieties

The scion varieties used in the experiments were mainly spur type 'Red Delicious' selections except where otherwise noted in the methods for individual trials. 'Red Delicious' is the most important variety for the apple growing industry in Tasmania. Strains of 'Red Delicious' have been selected in Tasmania on the basis of their skin colour. Among the selected strains spur and semi-spur types show distinct vegetative growth characteristics with typically few lateral shoots produced in the early stages of growth. The spur type 'Red Delicious' strains being used in the experiments have been allocated the code names Tas. Ag. no.2, Tas. Ag. no.5, and Tas. Ag. no.8. In addition, a semi-spur type (Tas. Ag. no.1) and a standard type (Tas. Ag. no.20) were also used.

'Golden Delicious', another important variety for the apple industry in Tasmania, was also used in the scion variety trial.

A Japanese apple variety, 'Red Fuji', which has been introduced into Tasmania recently was also used in some experiments. Two strains of 'Red Fuji being' used, Naga Fu no.2 in the preliminary observations and Naga Fu no.1 in the scion variety trial.

The rootstocks used in the trials were mainly either MM106 or seedling, except as noted in methods for individual trials. These rootstocks are widely used in Tasmania because they produce a good anchorage root system to support the free standing trees. Virus-free MM106 and other clonal rootstocks, used in the rootstock trial, were all the East Malling-Long Ashton (EMLA) series except 'Northern Spy'. Seedling rootstocks used in the trial at Grove Research Station were

grown from 'Sturmer' seeds. Those used in the trials at Forest Home Nursery were grown from 'Granny Smith' seeds.

3.2. General cultural practices

The trials on nursery trees were conducted in two different locations. The first location, at the Grove Research Station, is in the southern part of Tasmania (Australia), on a latitude approximately 43° south. The trial site was in an established nursery area with a flat, deep, well drained alluvial soil. The second trial location was a commercial nursery (Forest Home Nursery) about 13 km. west of Grove Research Station where the soil was also alluvium. The trial on one-year-old trees was conducted at Rookwood, a commercial orchard which is about 10 km. west of the research station. This soil was also alluvium but with a hard pan at a depth of about 1.5 m.

3.2.1. Grove Research Station
Plant materials and propagation:

All plant material used in the trials was supplied from the research station. The roots and tops of the rootstocks were trimmed before planting. The rootstocks were lined out in September 1986, 25 cm. apart in rows (except in the plant spacing trial) with 1 m. spacing between rows. In February 1987, the rootstocks were chip budded (Hartmann and Kester, 1983), after having grown in the nursery for one season. The height of budding was 25 cm. above ground level, except in the budding height trial. Buds were completely sealed with plastic budding tape, which was removed at the same time as the rootstock was cut back to the bud during June 1987.

Weed control:

A pre-emergence surface applied herbicide (Surflan®[1]), used to control grasses and broad leaved weeds, was applied immediately after lining out. Periodic rotovating and hand hoeing was done as required. As the trees established, Surflan was also applied after hilling-up and rotovating. Another systemic post-emergent herbicide, Fusilade® was applied as necessary for supporting control of specific weeds.

Pest and disease control:

1. Insecticides:	Superior Oil®	Lannate®	
	Cothion®	Kilval®	
	Thiodan®		
2. Fungicides:	Cuprox®	Delan®	
	Bayleton®	Baycor®	
	Agridex®		

All spray materials were carefully selected, from the many alternatives available on the market, for compatibility with an integrated pest control programme. This ensured the survival of predatory mites (*Typhlodromus pyri*), which since 1983, have kept European Red Mite populations under control, without the need for any miticide sprays. Insecticides were sprayed as pests became apparent, depending on pest severity. Some insecticides were applied as a preventive spray, for example Kilval was used to prevent Wooly Aphid build up in November 1987. Fungicides were applied every 10-14 days as preventive measures for Black Spot and Powdery Mildew.

---

[1]® Registered trade mark

Fertilizer programme:

In the 1986-1987 growing season, a 6-5-5 (N-P-K) fertilizer was applied to the soil at 150 kg/ha. in September, and at 200 kg/ha. in December. Zinc superphosphate was also applied at 250 kg/ha. There were two foliar sprays of fertilizer; zinc sulphate at 1 kg. per 100 litre (1000 l/ha.) and Solubor® (Boron) at 125 g. per 100 litre (2000 l/ha.).

The surface soil analysis (0-150 mm. profile) of the trial site in January 1988 found that the pH was 5.8. The levels of phosphorus (38 ppm) and potassium (200 ppm), and the conductivity (0.11) were all in the accepted optimum ranges for apple orchards (Temple-Smith, 1984). In the 1987-1988 growing season, Zinc superphosphate was applied at 125 kg/ha. As the leaf iron levels were found to be deficient, foliar applications of Iron pholate were applied at 65 g/100 litre (700 l/ha.) on 9 November 1987, and at 20 g/100 litre (2000 l/ha.) on 4 and 21 December 1987. Solubor was also applied at 125 g/100 litre (2000 l/ha.) in November 1987.

Irrigation:

During the growing seasons, the trial site was irrigated by fixed standing sprinklers, applying up to 25 mm/week depending on weather conditions. Grove Research Station is part of the Australia Bureau of Meteorology network of weather stations and a detailed record of the weather for the period of the experiments is available from the Bureau's archives.

3.2.2. Forest Home Nursery

Plant materials and propagation:

The plant material used in these trials was supplied from the Grove Research Station, except the seedling rootstocks, which were grown from 'Granny Smith' apple seeds. The rootstocks were lined 15-20 cm. apart in rows and 90 cm. spacing between rows, and were grown on the trial site for one season before chip budding was undertaken in February. The M2 rootstocks were budded 20-25 cm. above ground level, but the seedlings were budded 40-50 cm. above ground level due to their stem size. The buds were completely sealed with budding tape, which was removed at the time the rootstocks were cut back to the bud during June.

Weed control:

A pre-emergence herbicide, Simazine, was applied post planting at 4 l/ha. by hand lance to a 30 cm. wide strip of tree line between rows. Cultivation was initially by rotovator to control weeds with later spot sprays of Tryquat® and hand hoeing as supplementary control.

Pest and disease control:

1. Insecticides:	Methedathion	Chlorpyrifos
	Methomyl	Endosulfan
	Bromopropylate	
2. Fungicides:	Biteranol	Penconazole
	Mancozeb	Bupirimate
	Fenarimol	Copper Hydroxide

54

Insecticides were sprayed as pests became apparent, depending on pest severity and spray compatibility. Fungicides were applied every 10-14 days, depending on disease pressure.

Fertilizer programme:

After soil analysis, the pH was adjusted to 6.5-6.8 by incorporating lime during ground preparation; P was applied at the rate of 1 tonne/ha. K_2SO_4 and $MgSO_4$ were applied prior to planting in approximately equal proportions at 250 kg/ha.

Nitram® (34% N) was applied sequentially, only along the row line to the budded trees, at 10 g/tree in October, 15 g/tree in mid December, and 20 g/tree in early February.

Irrigation:

The trial site was irrigated by a travelling irrigator, aimed to supply on average 25 mm/week depending on weather conditions. In extremely hot conditions two irrigations were applied per week.

3.2.3. Rookwood

Plant materials and management:

The one-year-old trees of 'Red Delicious' (Tas. Ag. no.2) on seedling rootstocks were planted in the orchard in August 1987 at the spacing of 5 x 2.5 m. The trees were supplied from the Grove Research Station. A 6-5-5 (N-P-K) + Mg fertilizer was applied at 0.5 kg/tree a month after planting. Nitrophoska Blue TE® (12-5-14) was also applied at the rate of 250 g/tree. Both fertilizers were sprinkled around the base of the trees. A spray of Hydromag® (Magnesium) in 1% solution was also applied at 15 kg/ha. The trees were irrigated by fixed standing sprinklers, aimed to supply up to 20 mm/week every week from December 1987 to March 1988 depending on the weather. Two sprays of Lorsban® at 1.5 kg/1500 litre (1000 l/ha.) were applied to control insect pests. Delan®, Dithane-M45®, and Copper oxychloride were used as fungicides.

Weed control:

Surflan was applied as a pre-emergence application at the rate of 6 l/ha. once after planting. Hand hoeing was also applied as required. Roundup®, another systemic herbicide was applied, as spot application, as required at 2.5 l/ha.

3.3. General experimental design, data collection, and statistical analysis

In most of the experiments, the randomized complete block design was used except where noted in methods for some individual experiments. With seedling rootstocks the blocking took account of natural variation in rootstock size. Clonal rootstocks did not require blocking in this manner but were generally blocked according to field position. In all experiments at Forest Home Nursery where the budded trees were already in place, the trees were selected as uniform as possible in terms of both scion and rootstock size. All plots in the commercial nursery were buffered at least by single trees. In other experiments plots included treated buffer trees if total tree numbers permitted.

At the time the rootstocks were cut back to the bud, the diameters at the bud and ground levels, and the height of budding were measured. For the experiments with treatments applied during the growing period, trunk diameter above the graft union, length of the leading shoot, and length and number of the lateral shoots were measured prior to treatment. At the end of the growing season, the final growth of the trees for all the experiments was measured as trunk diameter above graft union, length of the leading shoot, number of lateral shoots, and length and angle of the lateral shoot to the vertical. The trunk diameter was measured by using a vernier caliper. The angle to the vertical of the lateral was measured by using a simple protractor.

In line with the experimental design preferred in these experiments, the continuous variables for the growth parameters were assumed to possess a normal error distribution and were analysed using

analysis of variance procedures. However, the discrete variable, number of lateral shoots, was assumed to follow a Poisson distribution and therefore a log-linear analysis of deviance model was fitted (McCullagh and Nelder, 1983). Most of the analyses were performed by using Genstat, a statistical program package. Results are expressed at a level of significance determined from published tables (Steel and Torrie, 1981), with a least significant difference calculated from the error mean square term in the analysis of variance. The graphical results are presented with a standard error of the difference between means shown as a bar at 5% level. Other analysis techniques were also used, regression analysis used in the preliminary observations and experiment 4.4.2, and chi-square test used in experiments 4.3.3 and 4.4.1.

3.4. Mechanical treatments and growth regulator applications

All the mechanical treatments, removal of leading shoot tip, young and mature leaves, and first-formed lateral shoots and buds, were applied by hand. The leading shoot tips were removed by pinching off the tips. The young and mature leaves were removed by pulling the leaves down gently, by one hand while holding the stem by the other hand, until the leaves separated from the stem without any damage to the axillary buds. The first-formed lateral shoots and buds were removed by grasping the shoots by fingers or buds by finger nails, and pushing to the side plane of the stem and leaf until it separated from the stem; while the other hand was supporting at the subtending leaf and the stem to prevent the breakage of the petiole.

The growth regulators which were used in various trials were:

1. BA (6-Benzyladenine) which was used in two different forms in separate trials. BA in the growth regulator screening trial at Forest Home nursery, was an anhydrous solid 97% a.i., supplied by Sigma Chemical Company, St. Louis, USA. A stock solution of BA was prepared by dissolving the compound in a small amount of water and stirring while adding a few drops of 1N NaOH until the BA completely dissolved. More water was then added to dilute to the required concentration. In another trial the BA and Gibberellin$_{4+7}$ were used at the Grove Research Station, BA was supplied as 2% a.i. liquid concentrate by Abbott Laboratory, North Chicago, USA.

2. Gibberellin$_{4+7}$ (GA$_{4+7}$) was supplied as 2% a.i. liquid concentrate by Abbott Laboratory, North Chicago, USA.

3. Cytolin®(BA+GA$_{4+7}$) was supplied as liquid mixture of

2% a.i. BA and 2% a.i. GA$_{4+7}$ by Schering Pty. Ltd. Australia.

4. Cultar® (PP333, paclobutrazol), with the chemical composition of (2RS,3RS)-1-(4-chlorophenyl)-4,4-dimethyl-2-(1H-1,2,4-triazol-1yl) pentan-3-ol, was supplied by ICI Australia Pty. Ltd. as suspension concentrate at 25% a.i.

5. M&B25,105® (N-propyl-3-t-butylphenoxyacetate) was supplied as 75% a.i. liquid concentrate by May and Baker Australia Pty. Ltd.

6. Thidiazuron® (N-phenyl-N'-(1,2,3,-thiadiazol-5-yl) urea) was supplied as 50% a.i. wettable powder by Cotton Grower Services Pty. Ltd. Australia.

7. NAA (1-naphthaleneacetic acid) was supplied as 2% a.i. liquid concentrate by Kendon Chemical & Manufacturing Co. Pty. Ltd. Australia.

In all the growth regulator applications a wetting agent, Tween 20® (Polyoxyethylene sorbitan monolaurate), at 1000 ppm was added to all the solutions except the M&B25,105 (Anon, 1976).

Thidiazuron, M&B25,105, BA, and NAA (in experiments 4.4 and 4.6) were prepared as stock solutions at suitable concentrations being enough for each application when it was diluted to the required spray concentrations. The stock solutions were freshly prepared one day before the application took place.

A domestic, hand sprayer with a one-litre container was used to apply the chemicals. The sprays were applied to the leading shoot tip as the length reached 50 cm. in the nursery trees and 5 cm. in the one-year-old trees. The sprays were applied directly to the 5 cm. of leading shoot growth until run off just commenced. Screens were used to prevent sprays drift to other trees but some vertical drip loss onto lower foliage on

60

the treated trees did occur.

4. Experimental

4.1. Preliminary observations

In order to provide some guide to nursery practices, which may be of value in determining tree form and to establish interrelationships between the various aspects of tree growth, preliminary observations were carried out on young orchard trees. The need to obtain preliminary data on how these interrelationships changed with stock/scion selection combinations was regarded as crucial in both the planning and interpretation of later experiments.

As the trees for the two observations were already established in the orchard not all nursery factors could be considered and observations were restricted to budding height and diameter of rootstocks. The random variation in these two parameters, which occurs in commercial nursery management, was used to analyse correlations between different aspects of growth, particularly branch induction, growth and angle.

4.1.1. Nursery trees

The aim of these observations was to examine the field relationship between rootstock size and the growth of the scion buds.

Methods:

Four groups of nursery trees i.e., two strains of spur type 'Red Delicious' (Tas. Ag. no. 2 and no.5) on seedling rootstocks, semi spur type 'Red Delicious' (Tas. Ag. no.1) and 'Red Fuji' (Naga Fu no. 2) both on MM106 rootstocks, were available in a trial planting at Grove Research Station. All trees were prepared according to normal nursery practice and had been growing in the orchard for one season. Height of budding, and diameter of the rootstock at both the budding and soil levels were recorded before the bud burst in August 1986. The volume of the rootstock portion was calculated according to the formula below:

$$\text{volume} = \pi h [r_2^2 + r_2(r_1-r_2) + (r_1-r_2)^2/3]$$

when $\pi = 3.1416$

$h =$ the height of budding

$r_1 =$ the radius of the rootstock portion at soil level

$r_2 =$ the radius of the rootstock portion at the bud level.

The growth of the scion was measured, when the growth ceased at the end of the trees' second growing season in May 1987, as the length of the main shoot and the number and length of the branches. The branching height from the soil level and the angles of the branches to the vertical were also measured.

The parameters of the rootstock size including volume,

63

height of budding, diameters at both soil and the bud level, and of the growth of the scion were analysed for significant correlations.

Results:

Table 1. shows means and standard errors for all parameters measured on each rootstock scion combination. Details of correlations are given in Tables 2 to 5.

The length of the main shoots and the diameter of the rootstocks at both levels were significantly correlated ($p \leq 0.01$); but the length of the main shoots and the height of budding had no significant correlation except for Tas. Ag. no.1 on MM106 rootstocks which gave a significant ($p \leq 0.01$) negative correlation. The volume of the rootstock and the length of the main shoots, all showed significant correlations ($p \leq 0.05$) except for Tas. Ag. no.1 on MM106 rootstocks.

The number of branches with the volume or the diameter at both levels of the rootstocks each gave significant ($p \leq 0.01$) correlations except for Tas. Ag. no. 2 on seedling rootstocks. The height of budding and the number of branches, however, gave no significant correlation except Naga Fu no. 2 on MM106 rootstocks which gave a weak but significant negative correlation ($r = -0.174$) ($p \leq 0.05$).

The total and mean length of branches was significantly correlated with the volume and the diameter at both levels of the rootstocks ($p \leq 0.01$) except Tas. Ag. no.1 on MM106 rootstocks. Similarly, the mean length of branches was not correlated with the volume or the diameter of the budding level of the rootstocks for Tas. Ag. no.1 on MM106 rootstocks. The height of budding and the length of branches had no significant correlation except for Naga Fu no. 2 on MM106 rootstocks

64

which gave a negative correlation between the height of budding and total branch length (p≤0.01). There was a weak negative correlation between the height of budding and mean branch length (p≤0.05).

All the parameters of rootstock size and the angle of the branches to the vertical gave no significant correlations except for Tas. Ag. no. 5 on seedling rootstocks (p≤0.01) and for Naga Fu no.2 on MM106 rootstocks, where the height of budding and the branch angle were negatively correlated (p≤0.01).

The branching height had a significant correlation with both volume of the rootstocks and the height of budding (p≤0.01). The diameter of the rootstocks at both levels and the branching height had no significant correlation except for Naga Fu no. 2 on MM106 rootstocks for which the diameter at the bud level and the height of branching had a negative correlation (p≤0.01).

The length of scion before the first lateral shoot for Tas. Ag. no.1 on MM106 rootstocks and Tas. Ag. no.2 on seedling rootstocks gave no significant correlations with any of the parameters of rootstock size. For Naga Fu no.2 on MM106 rootstocks, the length of scion before the first lateral shoot gave no significant correlations with the parameters of rootstock size except the height of budding (p≤0.01). In comparison, Tas. Ag. no.5 on seedling rootstocks gave negative significant correlations between the length of scion before the first lateral shoot and the parameters of rootstock size (p≤0.01), except diameter of the rootstock at the bud level.

The diameter of the main shoots just above the graft union, had no significant correlation with either volume of the rootstocks or height of budding. The diameter of the rootstock at both levels each gave significant correlations with the diameter of the main shoots (p≤0.01) except for Tas. Ag. no. 2 on seedling rootstocks.

Table 1. Means and standard errors of scion growth and rootstock parameters in four different scion/rootstock combinations.

Means	Naga Fu no.2 on MM106	Tas. Ag. no.1 on MM106	Tas. Ag. no.5 on seedling	Tas. Ag. no.2 on seedling
Tree trunk diameter (cm.)	1.51 ± 0.02	1.58 ± 0.01	1.57 ± 0.02	1.62 ± 0.01
Length of leading shoot (cm.)	121.9 ± 1.41	122.2 ±1.14	121.4 ± 1.51	130.4 ± 1.12
Number of lateral shoots per tree	4.48 ± 0.29	2.80 ± 0.24	6.76 ± 0.35	5.89 ± 0.26
Average length of lateral shoots (cm.)	20.51 ± 1.21	13.92 ± 1.23	23.30 ±1.35	19.21 ±1.16
Angle of lateral shoot to the vertical (°)	79.36 ± 0.67	71.40 ± 0.69	61.23 ± 0.69	63.34 ± 0.49
Branching height (cm.)	50.78 ± 0.99	45.80 ± 0.78	59.78 ± 0.78	56.44 ± 0.73
Length of scion before the first lateral shoot (cm.)	5.78 ± 0.16	8.28 ± 0.27	7.65 ± 0.26	6.74 ± 0.20

Table 1. (Cont.) Means and standard errors of scion growth and rootstock parameters in four different scion/rootstock combinations.

Means	Naga Fu no.2 on MM106	Tas. Ag. no.1 on MM106	Tas. Ag. no.5 on seedling	Tas. Ag. no.2 on seedling
Rootstock volume (cm^3)	49.92 ± 1.18	53.80 ± 1.39	69.69 ± 2.04	72.13 ± 1.66
Budding height (cm.)	33.99 ± 0.67	30.35 ± 0.68	40.09 ± 0.72	39.37 ± 0.50
Rootstock diameter at ground level (cm.)	1.52 ± 0.02	1.65 ± 0.02	1.67 ± 0.02	1.75 ± 0.02
Rootstock diameter at bud level (cm.)	1.22 ± 0.02	1.35 ± 0.02	1.27 ± 0.02	1.27 ± 0.02
Number of observed trees	151	89	87	132

Table 2. Correlation coefficients (r) of scion and rootstock measurements of Tas. Ag. no.5 on seedling rootstocks.

Scion measurements	Volume	Budding height	Rootstock measurements Diameter at bud level	Diameter at ground level
Leading shoot length	0.313	0.028	0.417	0.347
Number of lateral shoots	0.328	0.204	0.327	0.313
Total length of lateral shoots	0.379	0.118	0.460	0.436
Mean length of lateral shoots	0.309	0.041	0.429	0.390
Angle of lateral shoots to the vertical	0.392	0.305	0.229	0.301
Branching height	0.484	0.768	-0.162	0.134
Tree trunk diameter	0.189	-0.009	0.284	0.245
Length of the leading shoot before the first lateral shoot	-0.292	-0.201	-0.351	-0.404

n=87, $\approx r_{df=85}$ (at p=0.05) = 0.211

$\approx r_{df=85}$ (at p=0.01) = 0.275

68

Table 3. Correlation coefficients (r) of scion and rootstock measurements of Tas. Ag. no.2 on seedling rootstocks.

Scion measurements	Volume	Budding height	Rootstock measurements Diameter at bud level	Diameter at ground level
Leading shoot length	0.250	-0.095	0.424	0.340
Number of lateral shoots	0.092	-0.014	0.162	0.097
Total length of lateral shoots	0.349	0.137	0.303	0.322
Mean length of lateral shoots	0.288	0.126	0.250	0.237
Angle of lateral shoots to the vertical	0.086	-0.048	0.154	0.144
Branching height	0.375	0.604	-0.117	0.164
Tree trunk diameter	0.130	0.016	0.093	0.132
Length of the leading shoot before the first lateral shoot	-0.031	-0.102	-0.054	-0.100

$n=132$, $\approx r_{df=130}$ (at $p=0.05$) = 0.171

$\approx r_{df=130}$ (at $p=0.01$) = 0.235

69

Table 4. Correlation coefficients (r) of scion and rootstock measurements of Tas. Ag. no.1 on MM106 rootstocks.

Scion measurements	Volume	Budding height	Rootstock measurements Diameter at bud level	Diameter at ground level
Leading shoot length	0.056	-0.359	0.477	0.369
Number of lateral shoots	0.258	-0.062	0.281	0.407
Total length of lateral shoots	0.284	-0.050	0.295	0.417
Mean length of lateral shoots	0.133	-0.096	0.206	0.288
Angle of lateral shoots to the vertical	-0.178	-0.134	-0.094	-0.018
Branching height	0.679	0.780	-0.168	0.199
Tree trunk diameter	0.067	0.056	0.255	0.299
Length of the leading shoot before the first lateral shoot	-0.022	0.103	0.024	0.040

n=89, $\approx r_{df=87}$ (at p=0.05) = 0.209

$\approx r_{df=87}$ (at p=0.01) = 0.275

Table 5. Correlation coefficients (r) of scion and rootstock measurements of Naga Fu no.2 on MM106 rootstocks.

Scion measurements	Volume	Budding height	Rootstock measurements Diameter at bud level	Diameter at ground level
Leading shoot length	0.373	-0.058	0.462	0.482
Number of lateral shoots	0.320	-0.174	0.498	0.577
Total length of lateral shoots	0.268	-0.244	0.497	0.586
Mean length of lateral shoots	0.238	-0.182	0.436	0.493
Angle of lateral shoots to the vertical	-0.129	-0.220	0.129	0.045
Branching height	0.627	0.731	-0.233	0.076
Tree trunk diameter	0.097	0.104	0.496	0.484
Length of the leading shoot before the first lateral shoot	-0.063	-0.143	0.241	0.143

$n=151$, $\approx r_{df=149}$ (at $p=0.05$) = 0.160

$\approx r_{df=149}$ (at $p=0.01$) = 0.209

71

4.1.2. One-year-old orchard trees

The aim of this observation was to examine field relationships between the growth of the leading shoot and branch production after transplanting into the orchard.

Methods:

Sixty, one-year-old 'Red Fuji' (Naga Fu no. 1) apple trees on seedling rootstocks were available in a trial planting at Grove Research Station. All trees were transplanted from the nursery area and had been growing in the orchard for one season. At the end of the 1985-1986 growing season (July), the trunk diameter and the length of the main shoot above the grafted union, and also the length of last season growth of the main shoot were measured. Branch production was also recorded as number and length of branches categorized into current and last season growth. Angle of the branches to the vertical was also measured. All the parameters were compared and analysed using regression analysis.

Results:

Table 6. shows means and standard errors for all growth parameters. The tree trunk diameter was significantly correlated ($p \leq 0.01$) with length of the leading shoot (Figure 3) and branches (Figure 4), and the number of branches (Figure 5). The total length of branches and leading shoot, in both the last and the current growth season (Figures 6 and 7), also significantly correlated with the tree trunk diameter ($p \leq 0.01$).

Table 6. Means and standard errors of tree growth of one-year-old 'Red Fuji' apple trees on seedling rootstocks.

Tree growth parameters	Means and standard errors
Tree trunk diameter (cm.)	1.81±0.03
Length of leading shoot (m.)	1.58±0.02
Length of the current leading shoot growth (cm.)	34.73±1.20
Length of the current branch growth (cm.)	8.05±1.71
Length of the last season branch growth (cm.)	229.45±15.16
Angle of the branches to the vertical (°)	55±1.18
Number of branches per tree	7.3±0.20

Figure 3. Regression analysis of tree trunk diameter and leading shoot length of one-year-old 'Red Fuji' apple trees on seedling rootstocks.

$y = 0.6999 + 0.4871x \quad R = 0.61$

Leading shoot length (m.)

Tree trunk diameter (cm.)
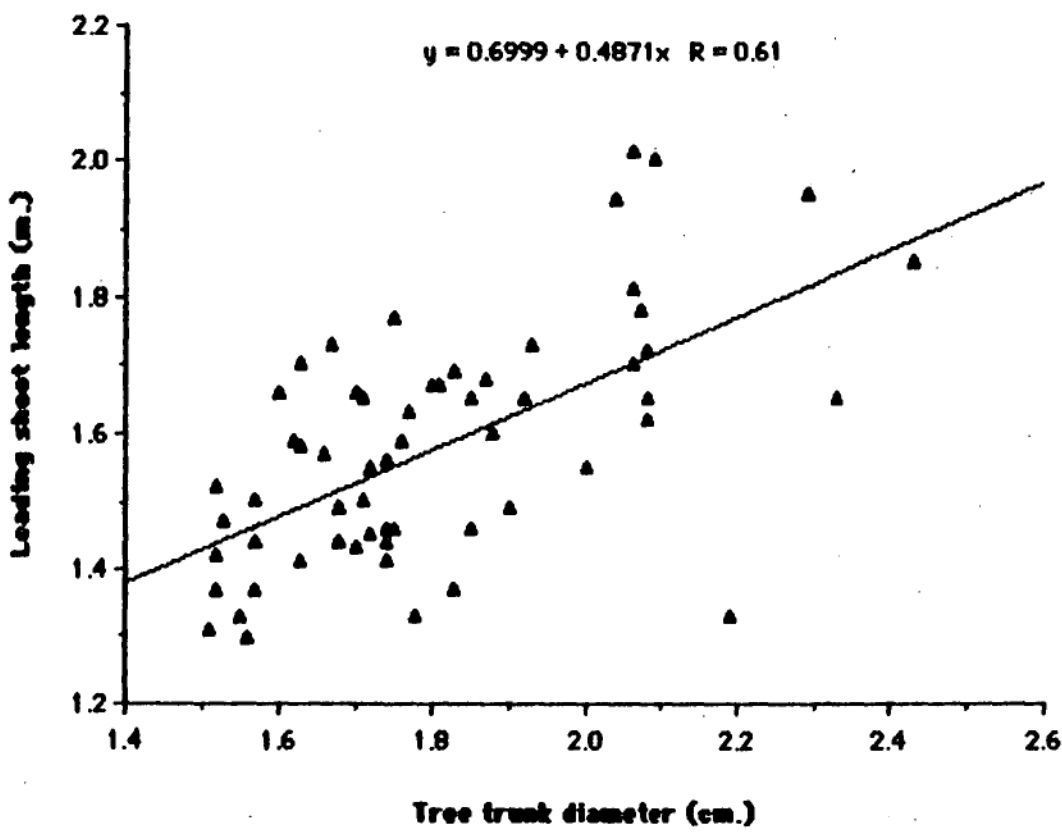
Figure 4. Regression analysis of tree trunk diameter and branch length of one-year-old 'Red Fuji' apple trees on seedling rootstocks.

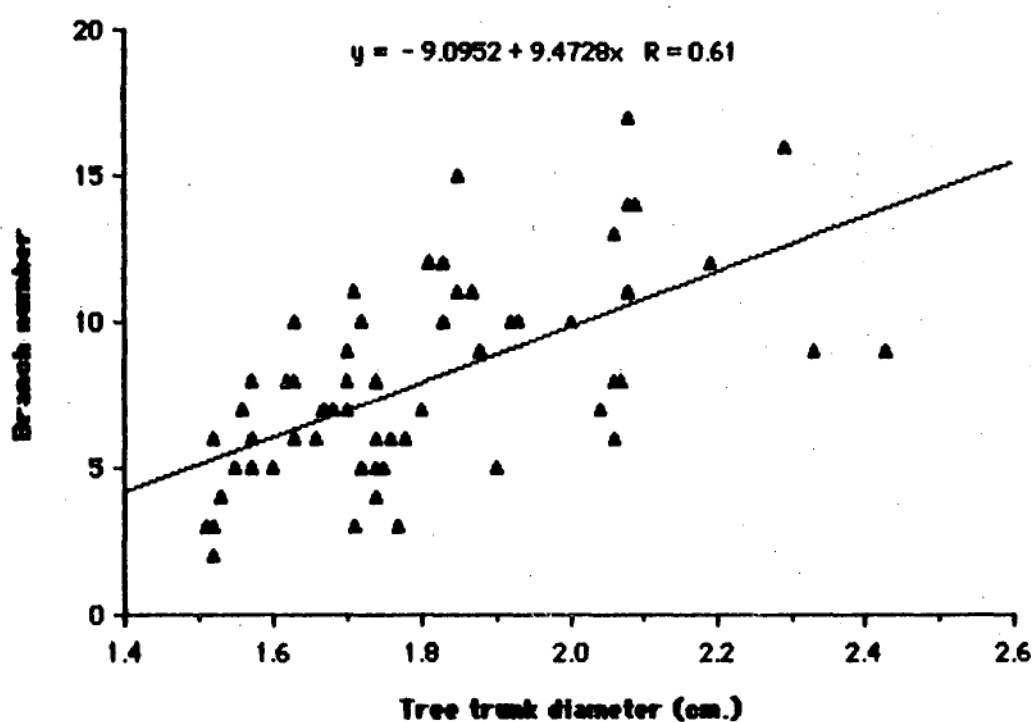$y = -392.6966 + 349.1947x$ $R = 0.62$
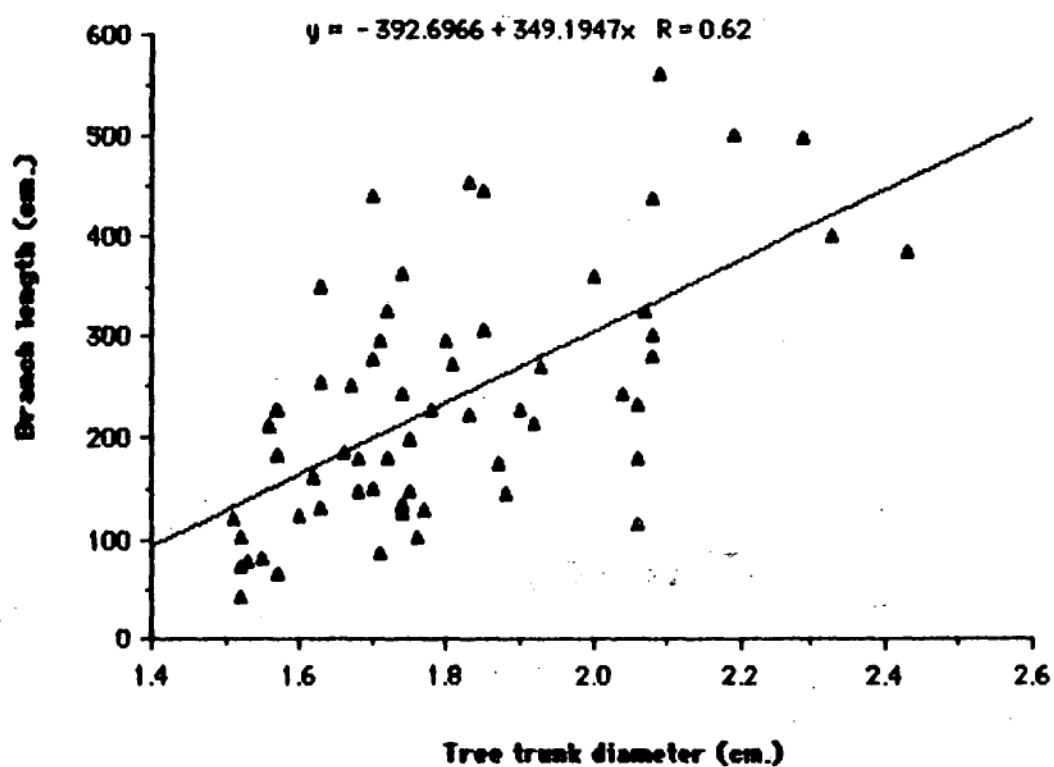
Figure 5. Regression analysis of tree trunk diameter and branch number of one-year-old 'Red Fuji' apple trees on seedling rootstocks.
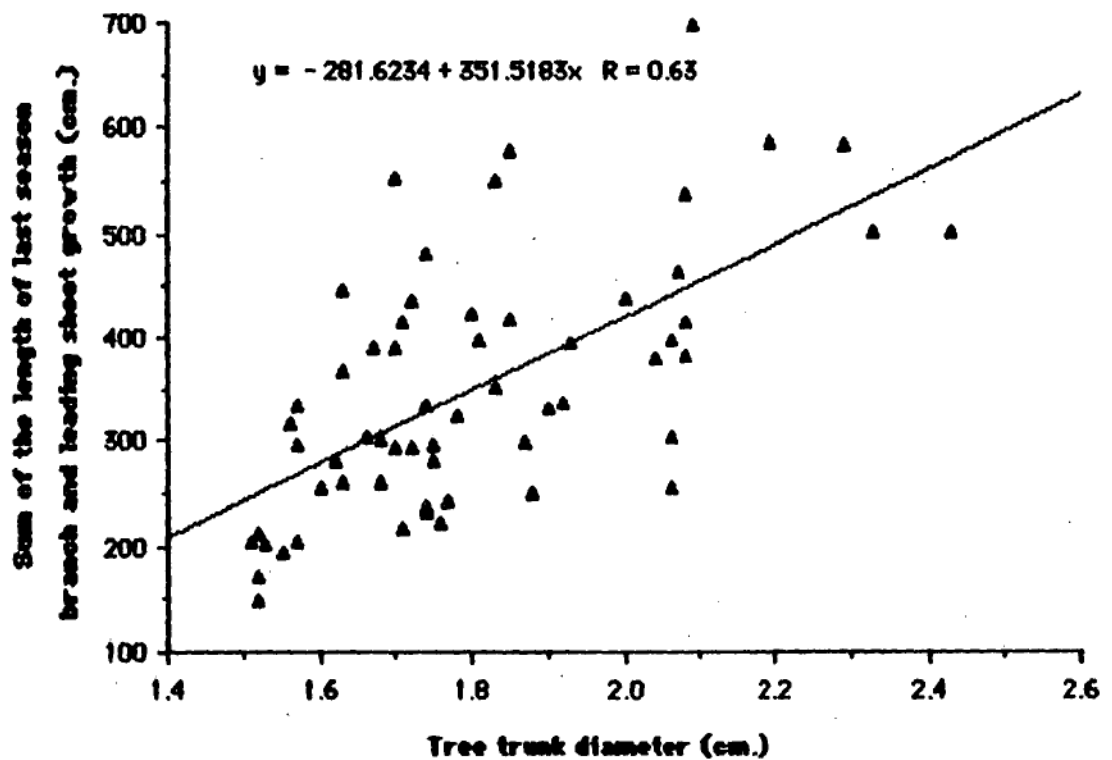
Figure 6. Regression analysis of tree trunk diameter and sum of the length of the last season branch and leading shoot growth of one-year-old 'Red Fuji' apple trees on seedling rootstocks.

Figure 7. Regression analysis of tree trunk diameter and sum of the length of the current season branch and leading shoot growth of one-year-old 'Red Fuji' apple trees on seedling rootstocks
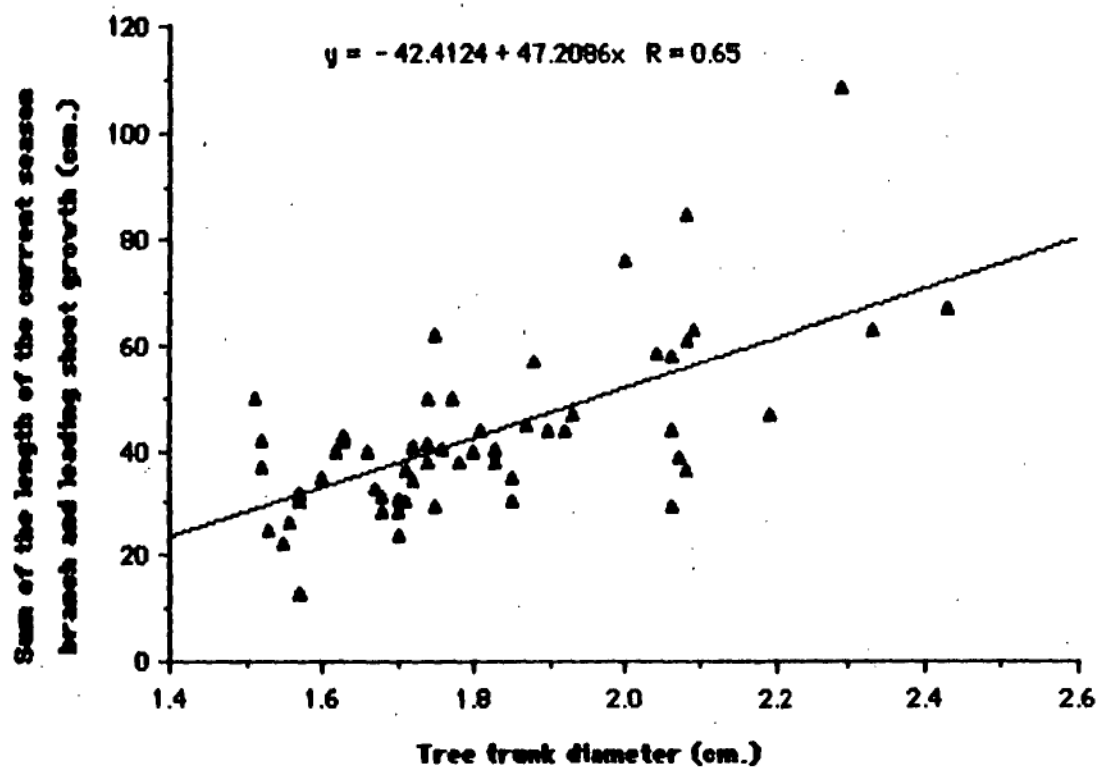
Discussion:

As expected the general growth habit of the nursery trees in these observations reflected the different rootstock and scion characteristics. Although the material contained different combinations of both scion and rootstock, it is possible to describe the growth of the trees almost entirely in terms of the rootstock influence or the scion's own growth habit. The two rootstocks (MM106 and seedlings) can be compared in terms of the scion growth. MM106 rootstocks which normally produce semi-dwarf trees, produced trees with less and shorter lateral shoots than the seedling rootstocks. However, MM106 produced trees with wider crotch angles than seedling rootstocks which agrees with the finding of Tukey (1981). The vigour and branching habit of the scion also varied between scion varieties. It is therefore necessary to separate the influence of different rootstocks on scion growth as well as to identify the scion's own growth characteristics on a given rootstock variety.

The measurements of the rootstock, height of budding, and the diameter of the rootstock at both ground and bud levels, were used to calculate volume of the rootstocks. The volume was considered to represent the true size of the rootstock better than the diameter at either level or the bud level alone. The regression analyses indicate there was a correlation between the rootstock size and the growth of the scion; the bigger rootstock produced the larger trees. The results also indicated the volume of the seedling rootstocks was larger than MM106 rootstocks. This is in accordance with the predictable observation that trees on seedling rootstocks grew more vigorously (taller and more branches) than the trees on MM106 rootstocks with each of the scion varieties.

Although the differences in the height of budding affected

the rootstock volume alone, it gave fewer correlations to the scion growth parameters than either the diameter at both levels or the volume of the rootstocks. It suggested that the diameter of the rootstock has a stronger direct relationship to the growth of the scion portion than the volume.

The height of branching is important. Lateral shoots produced at the optimum height in the early stages of growth in the nursery, should be retained as the primary branches as the trees mature. The results showing that height of branching gave the strongest correlations to the height of budding simply indicate a taller tree when the bud starts to grow.

The results from the observation on one-year-old 'Red Fuji' trees (4.1.2) suggest that tree growth measured as length of the leading shoot, the length and number of lateral shoots in the current growth season had been reduced compared to the last season's growth. It is possible that the damage to the root system at the transplanting period could be the cause of the reduction of growth in the first year in the orchard.

The results also suggest that the trunk diameter relates to the growth of the whole tree because it gave significant correlations to other growth parameters, i.e. number of lateral shoots and shoot growth. Van Oosten (1978), suggested that the thickness of the stem and the number of lateral shoots on one-year-old apple trees were important factors for early production in the orchard. Preston (1967) recognised the stem thickness/tree size relationship when he initiated the use of crop per unit trunk cross-sectional area as an indication of the fruitfulness of apple trees. Orchardists should plant trees with bigger tree trunk diameter to assure better vegetative growth during the early years of growth.

4.2. Variety trials

Preliminary observations indicated some effects of a limited range of nursery practices and rootstock/scion relationships on growth and branching habit. The following section contains two experiments which further explore the relationships between the scion and rootstock varieties. The first experiment evaluates the natural growth habits of different apple scion varieties, on the same rootstock variety. The second is an observation of the effect of a range the rootstock varieties on the growth of one strain of spur type 'Red Delicious' which is typically difficult to manage for branch development in commercial orchard practice.

<u>4.2.1. Scion variety trial</u>

<u>Methods:</u>

Five scion strains i.e., 'Red Fuji' (Naga Fu no.1), 'Golden Delicious' (FVF no.1), spur type 'Red Delicious' (Tas. Ag. no.5), semi-spur type 'Red Delicious' (Tas. Ag. no.1), and standard type 'Red Delicious' (Tas. Ag. no.20), were chip budded on to MM106 rootstocks in the nursery area at Grove Research Station in February 1987, as described in the General Materials and Methods section. Experimental design consisted of 4 replicates of the 5 treatments (cultivars) in a randomized complete block design, with ten tree plots.

<u>Results:</u>

Results are shown in Table 7. The 'Red Fuji' trees were significantly taller than spur and semi-spur type of 'Red Delicious' on MM106 rootstocks than the other varieties (p≤0.05). There were no significant differences in tree height or mean length of lateral shoots among the three strains of 'Red Delicious' or 'Golden Delicious'.

'Red Fuji' and 'Golden Delicious' produced more lateral shoots per tree compared with the three strains of 'Red Delicious'. There were no significant differences in the number of lateral shoots between the spur and semi-spur types of 'Red Delicious', while the standard type produced significantly (p≤0.05) more lateral shoots than both.

With regard to trunk diameter, there were no significant differences between any of the cultivars.

'Red Fuji' produced significantly wider branch angles than

the other cultivars (p<0.05). There were no significant differences in branch angles between the three strains of 'Red Delicious' or 'Golden Delicious'.

Table 7. Means of the growth parameters of five scion cultivars on MM106 rootstocks.

Means	Red Fuji	Spur type 'Red Delicious'	Semi-spur type 'Red Delicious'	Standard type 'Red Delicious'	Golden Delicious	LSD[1] (p=0.05)
Tree height (cm.)	154	123.6	125.2	133.5	134.6	21.6
Number of lateral shoots per tree	7.15	2.05	1.59	3.56	7.24	1.38
Tree trunk diameter (cm.)	1.51	1.24	1.29	1.37	1.34	ns[2]
Average length of lateral shoots (cm.)	19.1	11.3	8.2	13.3	13	ns
Angle of lateral shoots to the vertical (°)	75.6	59.3	63.7	63.1	63.3	5.7

[1]Least significant difference at 5% level.
[2]Non-significant difference.

Discussion:

The results suggest that the scion varieties performed differently on a given rootstock. 'Red Fuji' grew the most vigorously. 'Golden Delicious' grew less vigorously than 'Red Fuji', but both produced more lateral shoots per tree than the 'Red Delicious' cultivars. The three strains of 'Red Delicious' on the same variety of rootstock were similar in growth. Thus, there is apparent variation in growth and branching habit of scions on the same rootstock, as early as the nursery stage of growth. The most obvious difference is that both 'Golden Delicious' and 'Red Fuji' have a high potential to produce lateral shoots in the early stage of growth while 'Red Delicious' has not.

This trial has shown clearly that 'Red Delicious' types ranging from spur to standard, have a limited potential to produce lateral shoots at a very early stage of growth in the nursery. It has been reported that the spur type strains of apples have a potential to flower very early, but have weak potential to branch early (Fisher and Ketchie, 1981). Thus, the potential for early production would be reduced by the small fruiting area as the tree matures.

4.2.2. Rootstock variety observation

Methods:

This observation was to study the influence of the different rootstocks on spur type 'Red Delicious' (Tas. Ag. no.5). Twelve clonal rootstocks were compared at Grove Research Station. Those used were the EMLA series M1, M2, M9, M25, M26, M27, MM106, Merton 778, Merton 779, Merton 789, Merton 793, and Northern Spy (N Spy). Each group consisted of 20 rootstocks, except the N Spy plot, which had only 17. They were planted as a single plot in random order one season before budding.

Rootstock volume was measured prior to the start of growth. Leading shoot length, trunk diameter above the graft union, average branch number and average branch length were measured at the end of the growing season. Nursery management was described in the General Materials and Methods section. The height of budding for M27 rootstocks was 15 cm. as they were too short to be budded at 25 cm.

As the design was not a replicated trial, only means and standard errors for each rootstock plot were calculated and are presented below.

<u>Results and discussion:</u>

Details of the scion growth on the various rootstocks are given in Figures 8 to 12. Only 9 of the 20 buds of Tas. Ag. no.5 were successfully accepted by M9 rootstocks. Budding was fully successful for the other rootstocks.

The compatibility of the scion and the rootstock was the first influence to be noted. The M9 rootstock had less than 50% successful buds, suggesting that this rootstock scion combination should be avoided. The reasons for the incompatibility are unknown.

Of the various rootstocks in this observation trial, M1 rootstocks produced the tallest trees with the most lateral shoots. This may have been due to the vigour of the rootstocks. The rootstocks M1, M2, M25, and the Merton series were the most vigorous. Most of them produced long leading shoots in comparison to the dwarf and semi dwarf rootstocks (M9 , M26, M27, and Northern Spy).

In terms of number of the lateral shoots per tree, the vigour effect was less pronounced as only M1, M2 and Merton 793 produced trees with a substantial number of lateral shoots. Other rootstocks which produced trees with a substantial number of lateral shoots per tree (but less than M1) were M9 and MM106 which are considered as dwarf and semi dwarf rootstocks respectively. Of the rootstocks which produced a substantial number of lateral shoots, the more vigorous ones produced the longer lateral shoots.

The volume of the rootstocks also showed some influence on the growth of the scion which is still closely related to the vigour of each rootstock. The more vigorous rootstocks and those with larger rootstock volume seemed to produce trees with larger trunk diameter.

The rootstock size is influenced directly by the inherent vigour of the rootstocks and their seasonal growing conditions. In this observation the size of the rootstocks was very variable. The vigour of each rootstock could therefore have been affected by the initial size of the rootstocks.

Usually, the study of rootstock effects on a given scion variety would be a long term study with the effects described as growth habit and productivity. The most obvious results at this stage are that M9 rootstock took very few successful buds of the spur type 'Red Delicious' (Tas. Ag. no.5), and that M1 rootstock produced trees with more and longer lateral shoots than other rootstocks. Observations also suggest that at the nursery stage, the spur type 'Red Delicious' (Tas. Ag. no.5) trees produce very few lateral shoots on some rootstock selections but produce more on others.

Figure 8. Means and standard errors of rootstock volume in the rootstock variety observation trial. The initial size of the rootstocks are designated as follows: vs=very small, s=small, M=medium, L=large
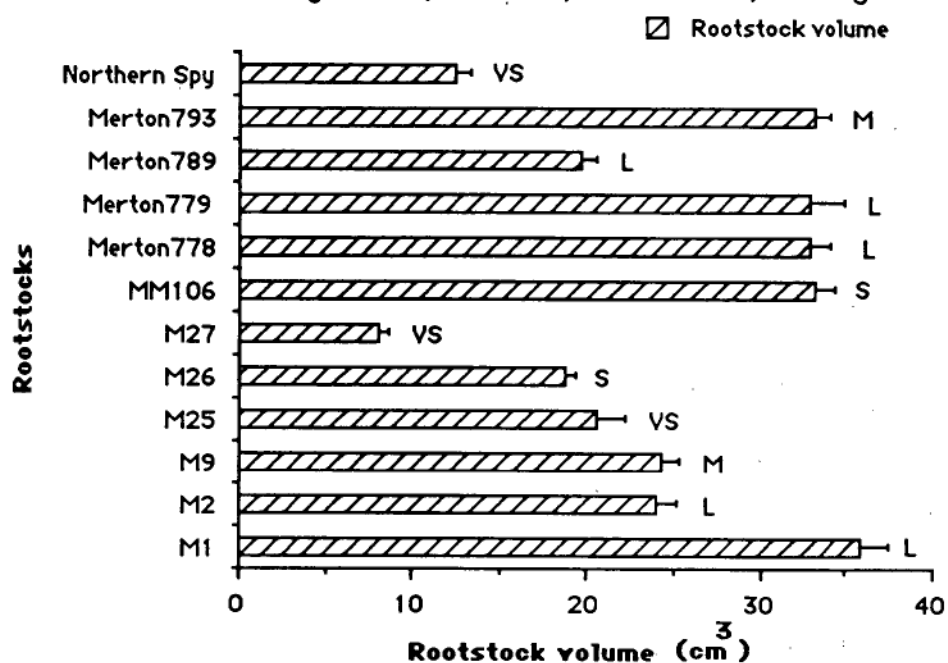
89

Figure 9. Means and standard errors of spur type 'Red Delicious' (Tas. Ag. no. 5) tree trunk diameters above graft union on various rootstocks
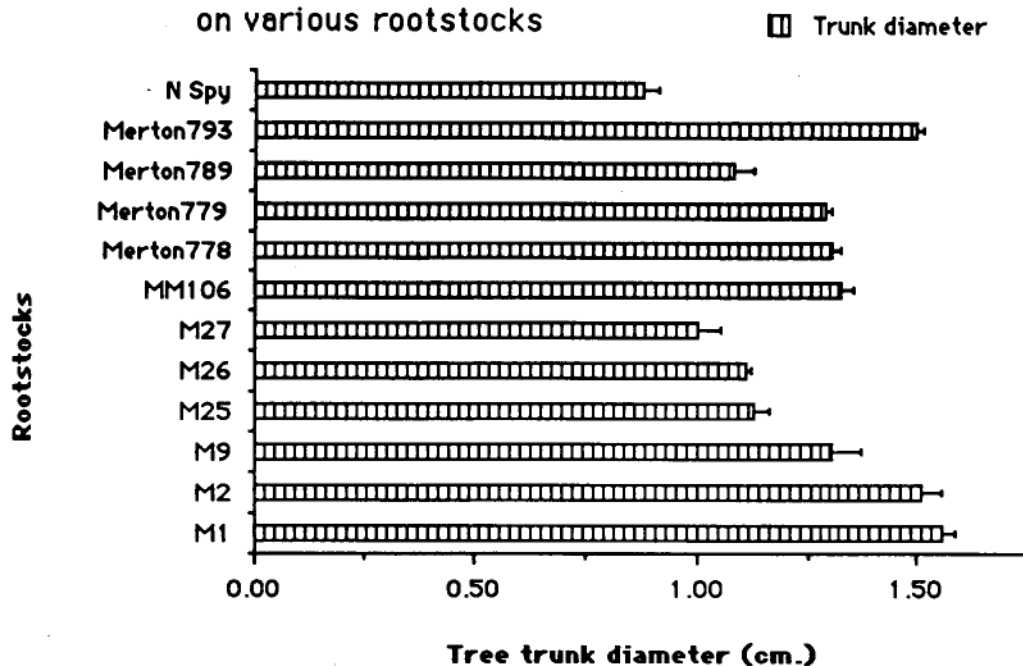
□ Trunk diameter

Tree trunk diameter (cm.)

Figure 10. Means and standard errors of spur type 'Red Delicious' (Tas. Ag. no.5) leading shoot length on various rootstocks

▨ Leading shoot length
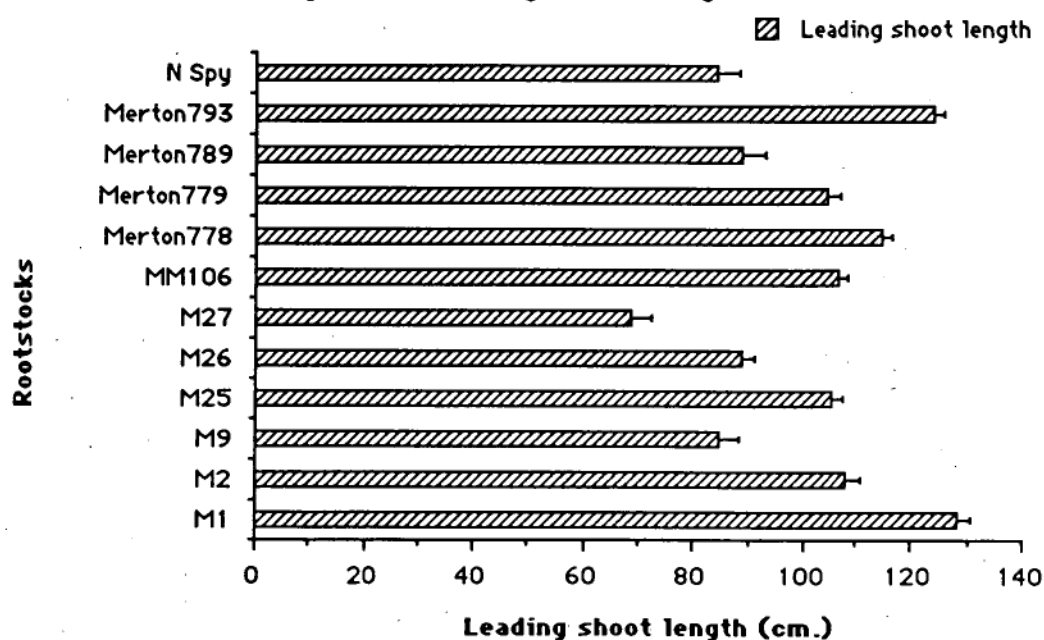

Leading shoot length (cm.)

Figure 11. Means and standard errors of average lateral shoot length of spur type 'Red Delicious' (Tas. Ag. no.5) on various rootstocks
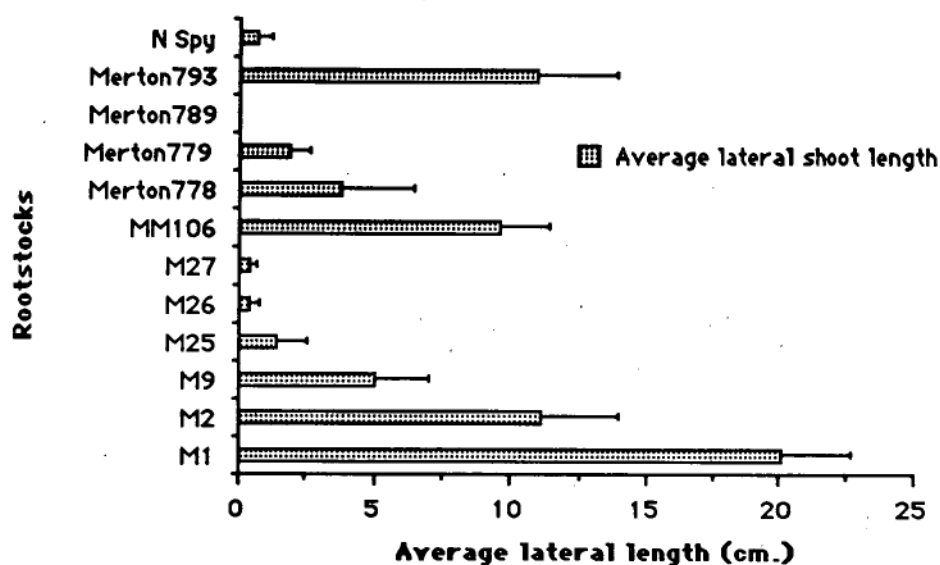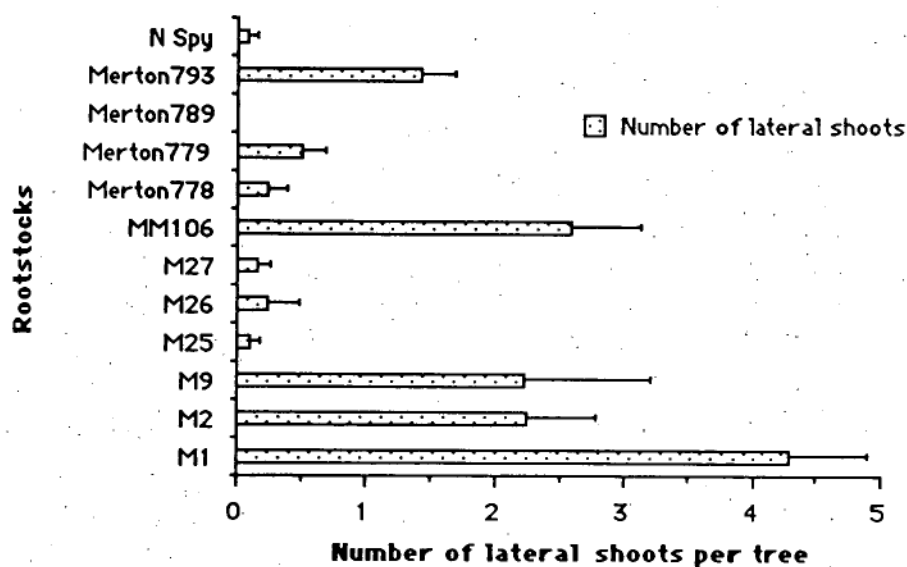

Figure 12. Means and standard errors of number of lateral shoots per tree of 'Red Delicious' (Tas. Ag. no.5) on various rootstocks

91

4.3. Nursery management trials

The four trials in this section examine some of the nursery management practices which could be used in a commercial nursery to influence the growth and lateral shoot formation of young spur type 'Red Delicious' apple trees. Each trial studies a single factor which has been reported in the literature as influencing lateral shoot formation.

4.3.1. Budding height

Methods:

Spur type 'Red Delicious' (Tas. Ag. no.5) scions were chip budded on to MM106 rootstocks at heights of 15, 25, 35 and 45 cm. above the ground. Each level was considered as a treatment with 10 trees per plot, with four replicates in a randomized complete block design.

Results:

There were no significant differences in any of the growth parameters (i.e., trunk diameter, length of the leading shoot, number of branches, and average length of branches) as shown in Table 8. The higher the rootstocks were budded, the higher the branches were produced. There were no significant differences in the average branching height as measured from the bud union. The rootstock volumes naturally increased as the rootstocks were budded higher.

Table 8. Means of rootstock volume and the growth parameters of the scion (Tas. Ag. no.5) on MM106 rootstocks at various heights of budding.

Means	Height of budding (cm.)				LSD (p=0.05)[1]
	15	25	35	45	
Rootstock volume (cm^3)	22.49	35.75	49.09	55.93	9.61
Tree trunk diameter (cm.)	1.34	1.29	1.31	1.27	ns[2]
Length of leading shoot (cm.)	108.6	105.9	110.7	107.8	ns
Number of lateral shoots per tree	1.43	1.68	1.76	1.33	ns
Average length of lateral shoots (cm.)	12	11.7	14.3	11	ns
Average branching height from graft union (cm.)	16.31	14.66	15.69	14.69	ns

[1]Least significant difference at 5% level.
[2]Non-significant difference.

4.3.2. Plant spacing

The plant spacing of the young apple trees in the nursery has been considered an important factor influencing growth of the trees. This trial was conducted to examine relationships between tree form and spacing in the nursery for a spur type 'Red Delicious' on MM106 rootstocks. The trial was also designed to detail the development of the trees during the growing period by measuring the growth sequentially during the season.

Methods:

MM106 rootstocks had been planted at a standard spacing of 1 meter between rows and at 15, 25, 35, and 45 cm. spacing within rows, as treatments at the Grove Research Station. The rootstocks had been growing for one season before budding with spur type 'Red Delicious' (Tas. Ag. no.5). The growth of the scion was measured sequentially, during the growing season, as length of the main shoot. Measurements were taken at 3 week intervals from 11 November 1987 to the end of the growing season in April 1988.

The apparent leaf area of the trees was also measured sequentially as the horizontally projected leaf area. Overhead photographs of a 0.5 m.^{2} fixed quadrat in each plot were taken at two week intervals from December 22 to March 23. The film used was Kodak high speed infra-red no. 2481, exposed according to the manufacturer's recommendation. Prints were prepared, photocopied on to 3M transparency films, cut to the quadrat size and passed through an electronic planimeter to determine ground cover as a proportion of the

quadrat area.

At the end of the growing season after budding, the various measurements of tree growth were also taken (described in General Materials and Methods section).

Results:

From the beginning of the growing season, the length of the leading shoot increased sharply until January 25, 1988, as shown in Figures 13 and 14. After January 25, the projected leaf area, as well as the leading shoot length increment, started flattening.

The trees planted at 15 cm. spacing produced significantly fewer lateral shoots per tree and less rootstock volume than those planted at the widest spacing (p≤0.05) (see Table 9). There were no significant differences in number of lateral shoots and rootstock volume between trees planted at 25, 35 or 45 cm. spacing within rows.

The other scion growth parameters, tree trunk diameter and length of leading shoot, measured after the growth had ceased (Table 9.), showed no significant differences among the trees growing at different within row spacings. The length of the lateral shoots increased as a significant linear regression (p≤0.01) when the tree were planted wider apart as shown in Figure 15.

Figure 13. Sequential measurements of leading shoot length of spur type 'Red Delicious' (Tas. Ag. no.5) on MM106.
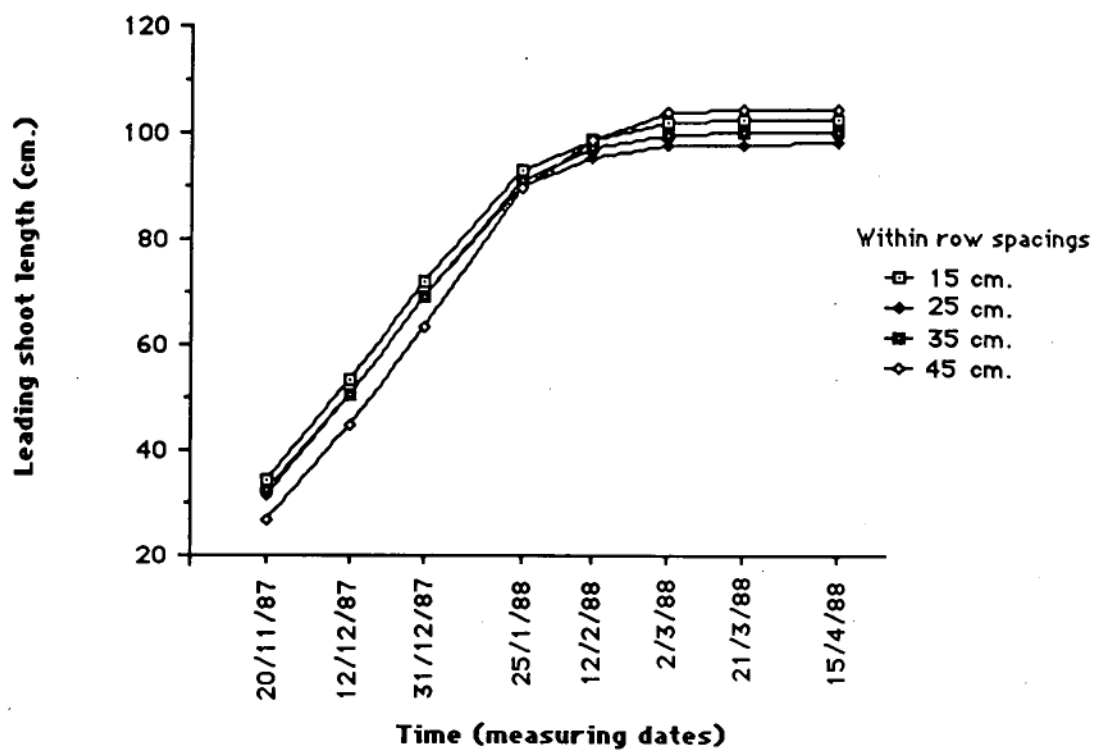
Figure 14. Sequential measurements of projected leaf area of spur type 'Red Delicious' (Tas. Ag. no.5) on MM106
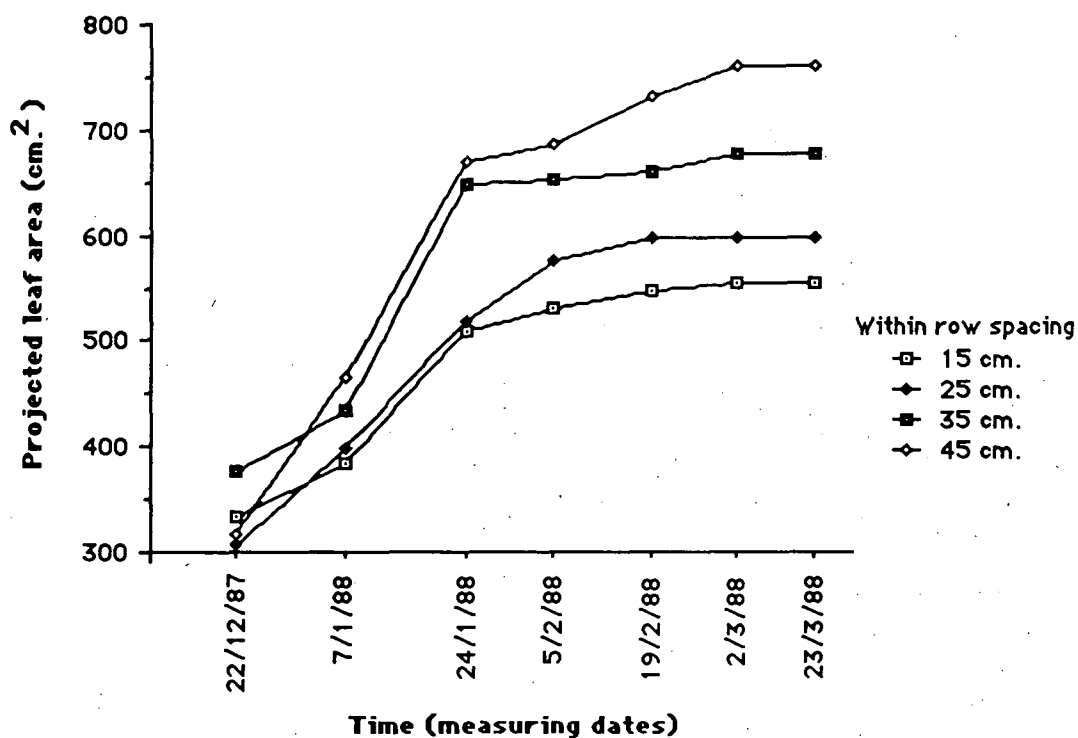
Table 9. Mean of rootstock volume and the growth parameters of the scion (Tas. Ag. no.5) on MM106 rootstocks at various plant spacings within the row.

Means	Spacing within row (cm.)				LSD (p=0.05)[1]
	15	25	35	45	
Rootstock volume (cm^3)	26.80	33.43	31.50	37.11	7.45
Tree trunk diameter (cm.)	1.21	1.26	1.26	1.40	ns[2]
Length of leading shoot (cm.)	127.3	122.7	124.7	129.6	ns
Number of laterals per tree	0.62	1.79	1.51	2.02	1.14

[1]Least significant difference at 5% level.
[2]Non-significant difference.

Figure 15. Mean of lateral shoot length of spur type 'Red Delicious' (Tas. Ag. no.5) on MM106 at various within row spacings.

$$y = -0.1 + 0.38x \quad R = 0.96 \; (p \leq 0.01)$$
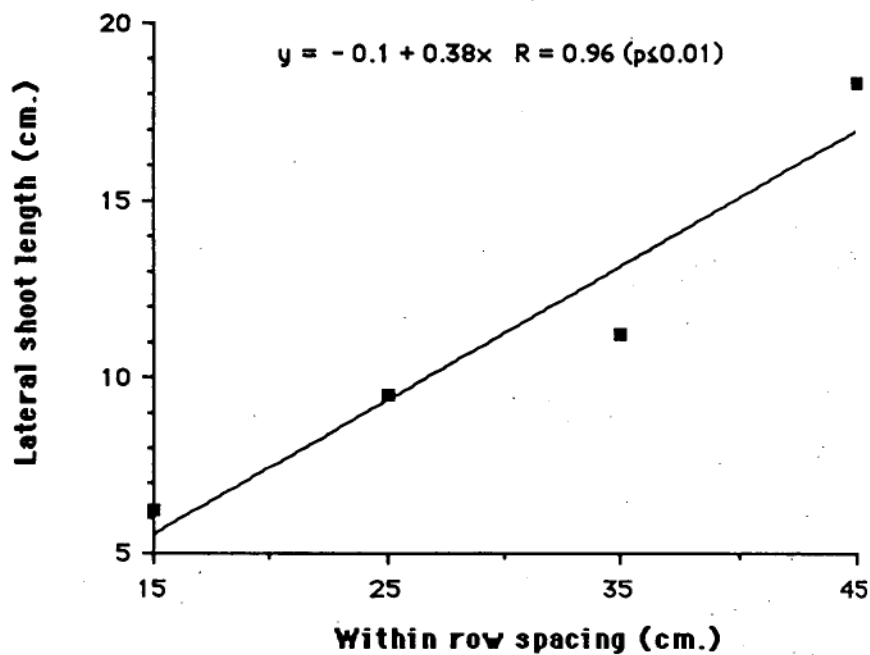
Discussion:

The results of the plant spacing trial (4.3.2), suggest that wider spacings within a row in the nursery, increase both radial and lateral growth. Only at 15 cm. was there an effect on number of lateral shoots and rootstock volume, but widening the plant spacing, generally resulted in the production of longer lateral shoots and greater projected leaf area. As the rootstocks were planted and had been growing for one season before budding, the growth of the rootstocks would have been affected by the plant spacing, so that the smaller rootstock volume at 15 cm. represents the sum of spacing influences in two season of growth (i.e. prior to and following budding).

The growth pattern of the leading shoot length showed no differences, but the growth of the leaf area showed that wider spacing produced more projected leaf area in the early stages of the growing season. It is possible that the lateral shoots of the trees on the wider spacings had more space to grow without shading from nearby trees; they produced more leaves and grew faster and longer than the lateral shoots of the trees on the close spacing. This could be applicable to both the first season of rootstock growth and the season after budding.

The productivity of a nursery is mainly judged on the number of satisfactory trees grown per unit area. The quality of the trees grown in this trial was generally good but those grown at wider spacings were the closest to ideal for orchard establishment.

The budding height results (4.3.1) confirmed the preliminary observation that the height of budding had no effect on the lateral shoot production. According to the preliminary observations, the volume of the rootstocks influenced the lateral shoot production and growth. Although the differences of budding height did directly affect the volume of the rootstocks; the results from both the preliminary observations and this trial, suggest that the size of the rootstocks, measured as a diameter, has a greater influence on volume than budding height. This could also of course be deduced mathematically as the volume is linearly related to length, but quadratically related to diameter. The effect of the budding height on the height at which the lateral shoots are produced is an obvious physical effect of no apparent physiological significance.

4.3.3. Young leaves and shoot tip removal

Wertheim (1978a. and 1978b.), found that young leaf removal induced lateral shoots with very wide crotch angles in nursery trees but that complete removal of the growing tip (tipping) produced a number of lateral shoots with very narrow angles. This trial examines the lateral shoot induction effects of both practices.

Methods:

Nursery trees of spur type 'Red Delicious' (Tas. Ag. no.5), on M2 rootstocks were used in this trial at Forest Home Nursery. There were four treatments: 1) control, 2) removal of the leading shoot tip by hand (pinching) on 19 December 1986, 3) removal of young unexpanded leaves by hand (4-5 leaves from the tip) on 19 December 1986. 4) removal of young leaves three times at 14 day intervals (starting on 19 December 1986).

Each treatment contained 5 trees with 2 buffer trees in each plot. All treatments were replicated twice in a randomized complete block design. The growth of the scion was measured before and after the treatment, and analysed as described in the General Materials and Methods section.

Results:

The leading shoot length of the trees in treatments **2** and **4** was significantly shorter ($p \leq 0.05$) than the control and treatment **3**, as shown in Figure 16. Pinching (treatment **2**) induced 4.2 branches per tree with significantly narrower angles to the vertical ($p \leq 0.05$), as shown in Figure 17, while the other treatments did not induce any branches.

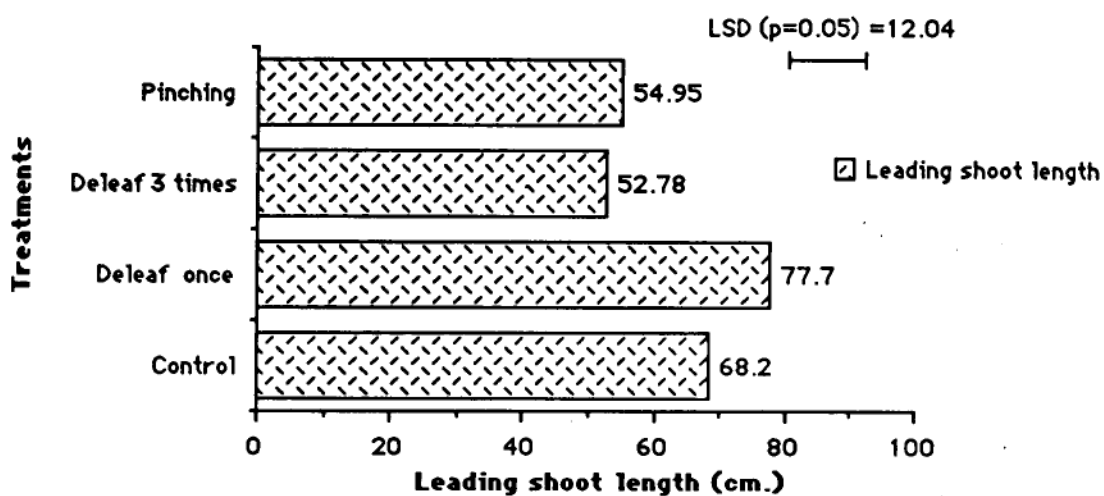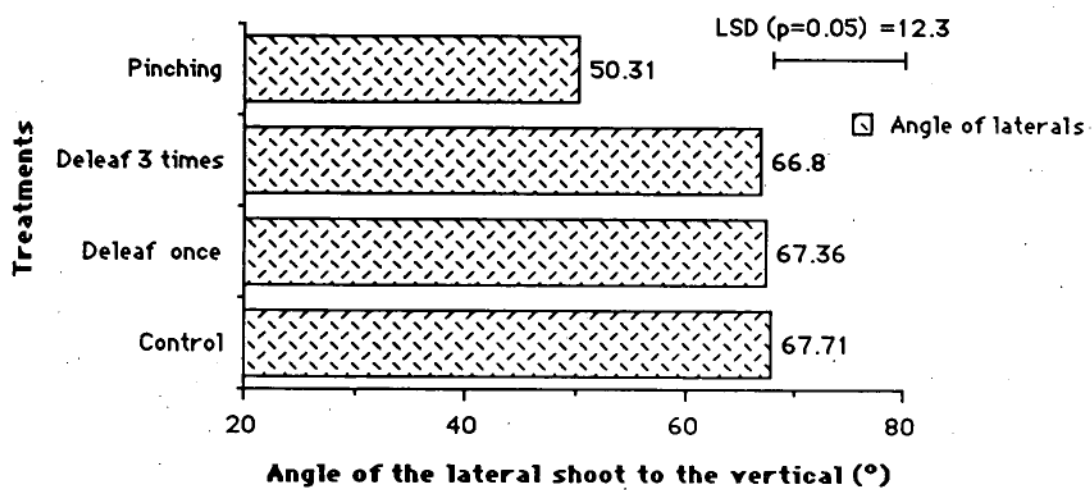**Figure 16.** Mean of the length of the leading shoots of spur type 'Red Delicious' (Tas. Ag. no.5) on M2.

LSD (p=0.05) =12.04

☑ Leading shoot length

- Pinching — 54.95
- Deleaf 3 times — 52.78
- Deleaf once — 77.7
- Control — 68.2

Treatments

Leading shoot length (cm.)

Figure 17. Mean of the angle of the lateral shoot to the vertical of spur type 'Red Delicious' (Tas. Ag. no.5) on M2.

LSD (p=0.05) =12.3

☐ Angle of laterals

- Pinching — 50.31
- Deleaf 3 times — 66.8
- Deleaf once — 67.36
- Control — 67.71

Treatments

Angle of the lateral shoot to the vertical (°)

105

4.3.4. Removal of mature leaves, lower lateral shoots and buds

This experiment examined the removal of mature leaves, buds and the first-formed lateral shoots on the lower part of the trees. It has been reported that in some freely-branching cultivars, removal of first-formed lateral shoots resulted in the production of more and longer lateral shoots in the upper part of the nursery trees (Quinlan, 1981).

Methods:

In this trial, semi-spur type 'Red Delicious' (Tas. Ag. no.1), on seedling rootstock nursery trees, at Forest Home Nursery were used with 5 treatments:

1. Control

2. Removal of all mature leaves on the leading shoot by hand (on 11 December 1987).

3. The same as for treatment 2, but done 3 weeks later (on 1 January 1988).

4. Removal of already formed lateral shoots or buds by hand, from the 10 nodes from the node above the bud union upward (on 11 December 1987).

5. The same as for treatment 4, but done 3 weeks later (on 1 January 1988).

Each treatment contained 10 trees as single tree plots. The design was a randomized complete block. The data on the growth of the scion were collected and analysed as described in the General Materials and Methods section.

<u>Results:</u>

The growth of the scion, in terms of trunk diameter, showed no significant differences between the treatments. The growth of the leading shoot, from the trees in both mature leaf removal treatments produced significantly ($p \leq 0.05$) shorter leading shoots than the control and early disbudding treatment, as shown in Figure 18.

There were no new lateral shoots produced after the treatments were applied, for any treatment, consequently removal of lateral shoots in treatments 4 and 5 gave an apparent reduction in lateral shoot production.

Figure 18. Mean of leading shoot length of spur type 'Red Delicious' (Tas. Ag. no.5) on seedlings.
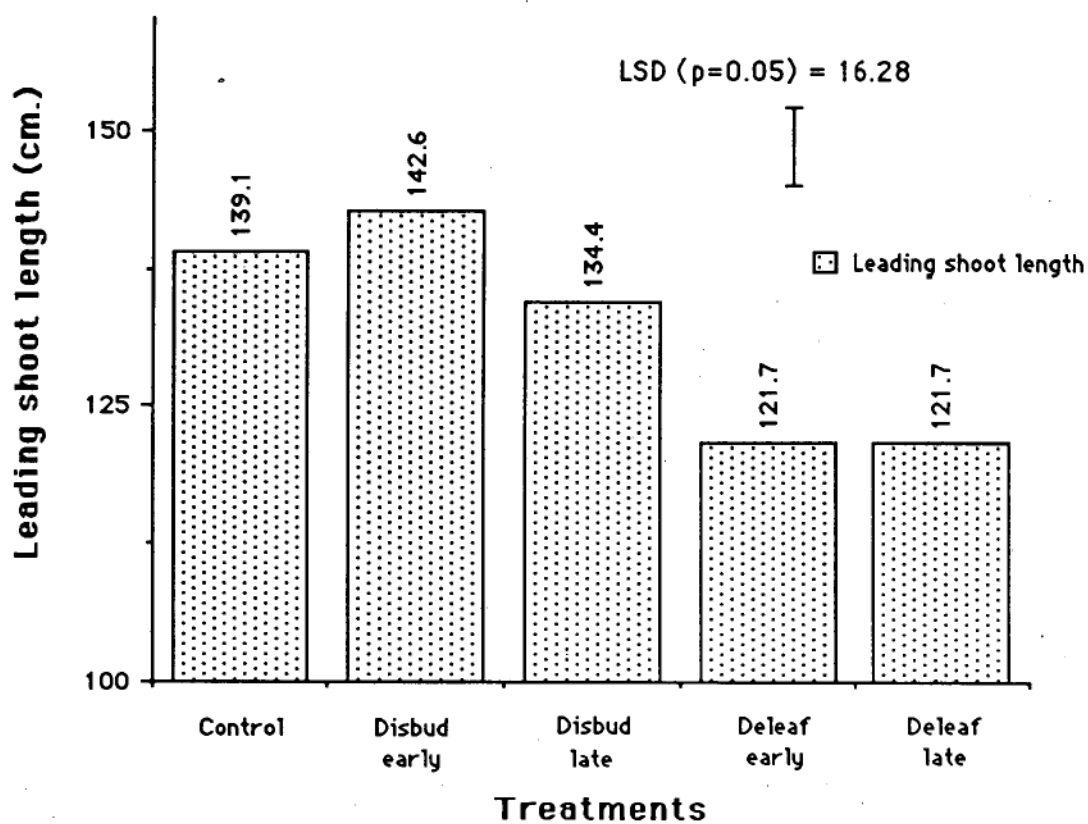
<u>Discussion:</u>

In experiment 4.3.3, the sequential removal of young leaves and the shoot tip significantly reduced the growth of the leading shoot ($p \leq 0.05$). The young unexpanded leaves, as well as the shoot tip, are believed to be the sites of auxin production (Sembdner et al., 1980), possibly controlling the inhibition of lateral buds. Generally, at the nursery stage, the main growing point is the leading shoot. The leading shoot tips will dominate the whole tree even though there may be lateral shoots formed. Removal of the source of auxin production, in order to reduce the apical dominance and induce the lateral shoot formation, was the main objective of this work. The results suggest that single or sequential removal of young leaves has no effects on lateral shoot formation. In addition, the sequential removal of young leaves also reduces the leading shoot growth.

The removal of whole shoot tips, did not significantly affect lateral shoot growth. This treatment also produced lateral shoots with narrow angles which is undesirable in nursery trees. The resultant trees were short and their induced lateral shoots formed at the top nodes. The topmost bud formed the shoot which took over from the old leader. The lateral shoots formed below this, had very narrow angles to the vertical. Sometimes, the topmost shoot did not completely dominate, and the lateral shoots grew almost at the same rate as the leading shoot, producing a multileader tree. For some planting systems (i.e., opened center), the multileader trees are suitable. For most new orchard plantings, however, trees with long leader shoots and many non-competing lateral shoots are required.

Inhibition of older buds is generally associated with leaf

abscisic acid (ABA) production (Theron et al.,1987). The results of mature leaf removal in experiment 4.3.4, suggest a more complex inhibition than a direct suppression mediated by ABA from the leaves, possibly involving stored ABA or an interaction with growth promoters. Overall, reduced photosynthetic area and assimilate production appears to be the dominant effect of leaf removal, resulting in a reduction of total growth. In contrast to the results reported for some apple varieties which produce lateral shoots freely (Quinlan, 1981), the early or late removal of low and early formed lateral shoots or buds, produced no effects on lateral growth.

4.4. Screening of synthetic plant growth regulators on branch induction

This section further examines the use of some growth regulators which have been reported to induce branching in some young apple trees cultivars. It contains three experiments. Each was conducted to determine the effects of various growth regulators on branch induction suitable for spur type 'Red Delicious' under Tasmanian conditions. While the main objectives related to the number of induced lateral shoots, the angles of the lateral shoots, and the growth of the leading shoot, phytotoxicity and other side effects of the chemicals on the trees were also considered.

M&B 25,105 has been used to achieve branch induction for young apple trees (Wertheim, 1978a. and 1978b.). It is understood to inhibit basipetal auxin transportation, which is believed to inhibit lateral shoot growth (Anon., 1976).

Williams and Billingsley (1970), suggested that cytokinin alone could induce bud break, but the shoot soon became a short flowering spur. When gibberellins (GA_{4+7}) were also present, the shoot continued to elongate and grow into a branch. GA_{4+7} alone, was relatively ineffective at stimulating branching, unless combined with a cytokinin.

Paclobutrazol (PP333) was found to inhibit gibberellin biosynthesis and reduce cell division and extension; the retardation effects can be reversed by GA application. (Lever et al., 1982). Wang et al. (1987a) also found that PP333 reduced the endogenous ABA levels of apple leaves.

Thidiazuron has been reported to have shoot proliferation

effects on apple in tissue culture (Van Nieuwkerk et al., 1986). Wang et al. (1986 and 1987b.), found that the chemical had the capacity to release lateral buds from dormancy and related the effect to ABA content in apple buds.

4.4.1. Branch induction effect of Cytolin, 6-benzyladenine (BA) and M&B 25,105 on apple nursery trees.

Methods:

Three chemicals were applied to the trees i.e., M&B 25,105, Cytolin, and BA. Cytolin is a commercial product containing a mixture of GA_{4+7} and BA. M&B 25,105 was applied as single applications at 400, 800, and 1600 ppm, or sequentially at 100, 200, or 400 ppm at 4 weekly intervals. Cytolin or BA was applied as single applications at 200, 400, and 800 ppm, or sequentially at 50, 100, and 200 ppm at 4 weekly intervals. All the chemicals were applied by hand sprayer to the growing tip of the leading shoot, as described in the General Materials and Methods section. The first application took place on 19 December 1986, when the new tree growth was 51-74 cm. above the graft union.

Spur type 'Red Delicious' (Tas. Ag. no.5) on M2 nursery trees were used in this trial. The experimental design consisted of 2 replicates of the 19 treatments (including the control and varying concentrations) in a randomized complete block design, with 5 tree plots. The growth was measured before and after the treatments, as described in the General Materials and Methods section.

<u>Results:</u>

All BA applications failed to produce any significant (p>0.05) effects on tree growth or lateral shoot induction.

M&B 25,105 applications produced some phytotoxicity first noticeable as deformed new leaves and the shoot tips stopped growing soon after the spray was applied. The higher the concentrations, the more severe were the phytotoxicity symptoms. The trees treated with lower concentrations, recovered from the effects of the chemical sooner than the ones treated with the higher concentrations and showed no significant growth reduction. The chemical at higher concentrations (400 or 800 ppm) and the sequential applications at 200 or 400 ppm, significantly reduced the growth of the leading shoot (p≤0.05), as shown in Figure 19.

In contrast, Cytolin applications did not affect the growth of the leading shoot. The angles of the lateral shoots to the vertical were significantly reduced by the sequential applications of Cytolin at 100 and 200 ppm (p≤0.05) as shown in Figures 20 and 21. In Figure 21, the mean angle of the lateral shoots to the vertical was calculated from all the lateral shoots on the trees which were produced after the experiment took place.

Both the control replicates failed to produce new lateral shoots after the period of chemical application, making statistical comparison with lateral shoot inducing chemicals impossible. Among the applications of Cytolin, the sequential applications at 200 ppm and the single application at 800 ppm produced significantly more lateral shoots than other Cytolin treatments (x^2 = 59.39). No M&B 25,105 applications produced significantly more lateral shoots than other treatments (x^2 = 1.3).
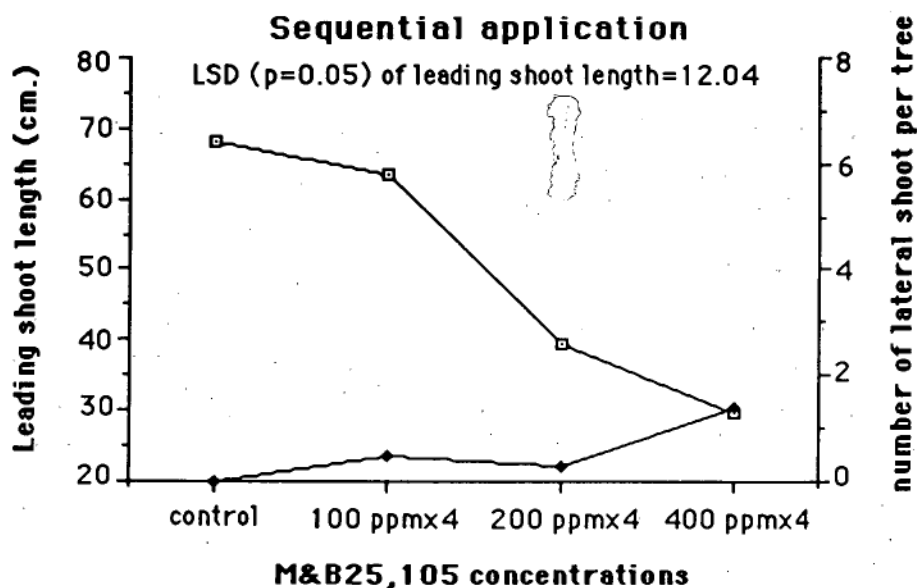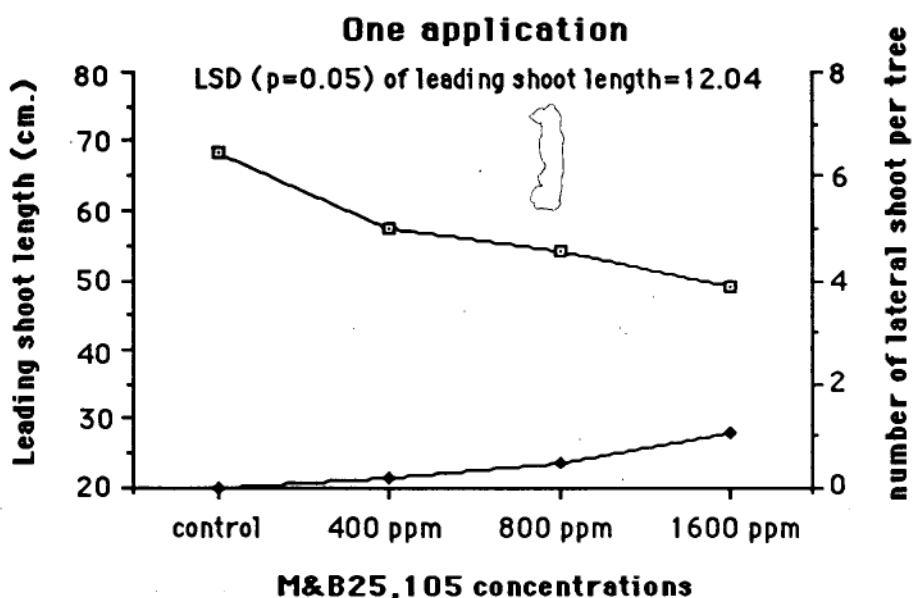
Figure 19. Mean length of leading shoot growth and number of new lateral shoots per tree of spur type 'Red Delicious' (Tas. Ag. no.5) on M2 after treatment of M&B25,105.

–□– shoot length , –◆– number of new lateral shoots

One application

LSD (p=0.05) of leading shoot length=12.04

M&B25,105 concentrations

Sequential application

LSD (p=0.05) of leading shoot length=12.04

M&B25,105 concentrations

Figure 20. Mean length of leading shoot growth and number of new lateral shoots per tree of spur type 'Red Delicious' (Tas. Ag. no.5) on M2 after treatment of Cytolin. ⊡ shoot length , ◆ number of new lateral shoots

One application
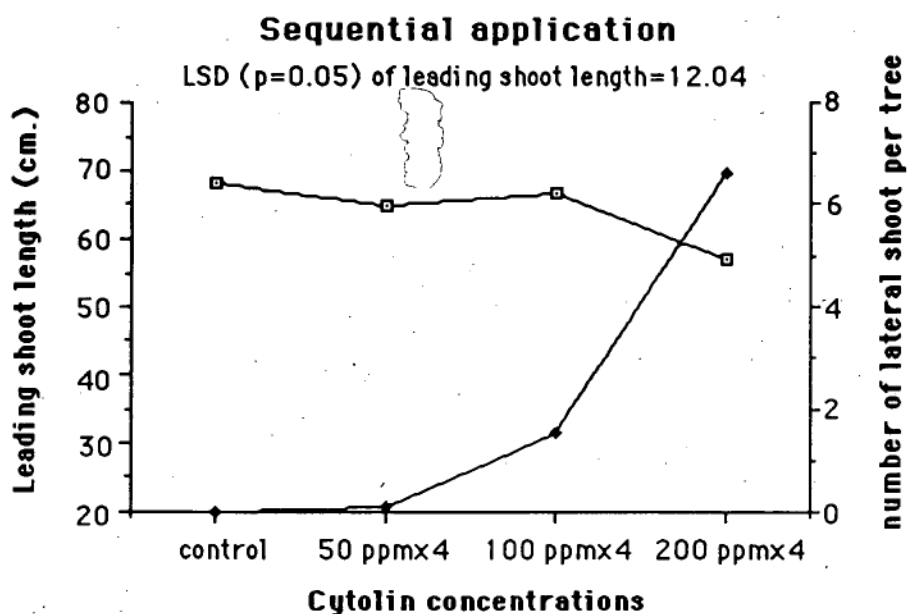
LSD (p=0.05) of leading shoot length=12.04

Sequential application

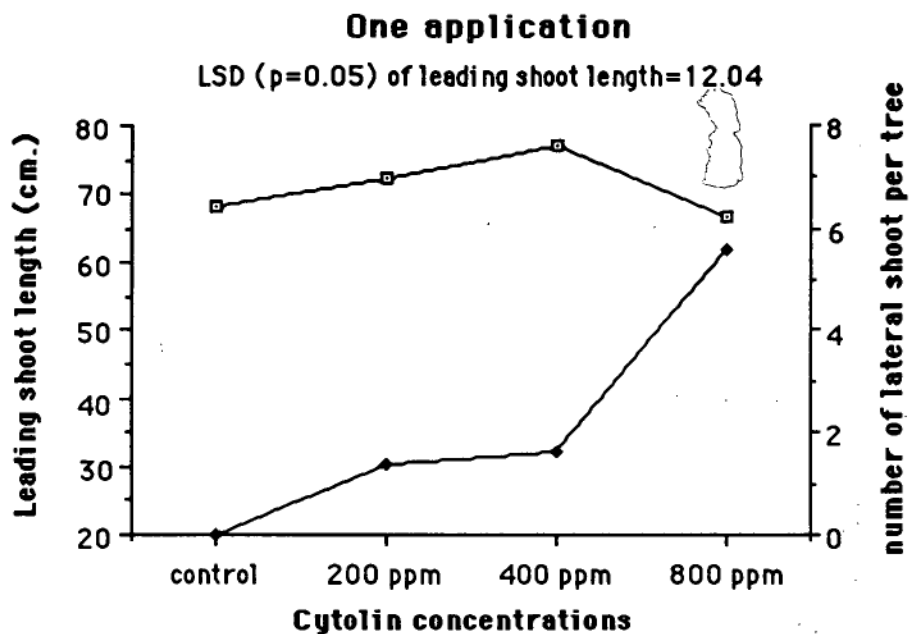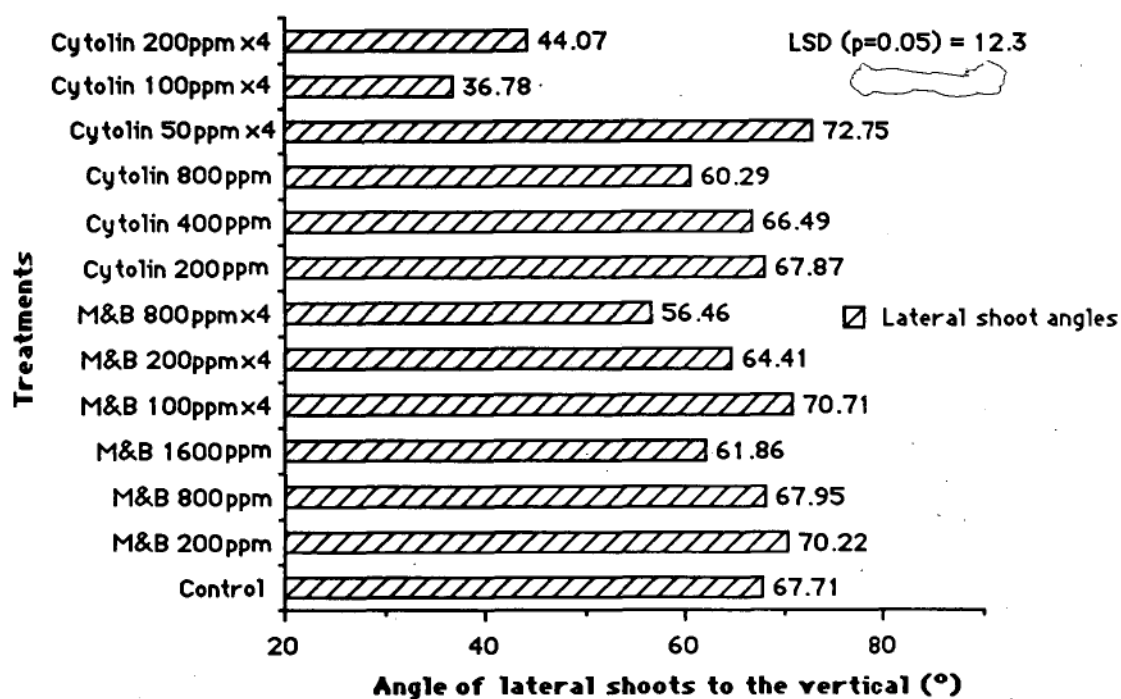LSD (p=0.05) of leading shoot length=12.04

Figure 21. Mean angle of lateral shoots to the vertical of spur type 'Red Delicious' (Tas. Ag. no.5) on M2

4.4.2. Branch induction effect of thidiazuron and Gibberellin 4 and 7 (GA$_{4+7}$) on apple nursery trees.

Methods:

Spur type 'Red Delicious' (Tas. Ag. no.5) on MM106 nursery trees, were used in this trial at Grove Research Station. The treatment design was a randomized complete block, replicated 8 times with single tree plots. The treatments were a control, single applications of thidiazuron at 100, 500, or 1000 ppm, or 4 sequential (weekly) applications of thidiazuron at 25, 125, or 250 ppm, single applications of GA$_{4+7}$ at 200, 400, or 800 ppm, or 4 sequential (weekly) applications of GA$_{4+7}$ at 50, 100, or 200 ppm. The first application took place on 29 December 1987. During the application period the new tree growth was 45-78 cm. above the graft union. The methods of application, data collection, and analysis are outlined in the General Materials and Methods section. In addition, the branch diameter at the branch base was also measured.

Results:

The trees sprayed with thidiazuron showed symptoms of phytotoxicity i.e., stem thickening, leaf curling, and production of multiple buds at some nodes.

The growth of the leading shoot was significantly reduced by thidiazuron applications, when compared to the control and all GA_{4+7} treatments ($p \leq 0.05$). None of the GA_{4+7} applications significantly influenced leading shoot growth compared to the control, as shown in Figure 22.

The average lateral shoot length per tree among the treatments and the control showed no significant differences.

Sequential GA_{4+7} application at 200 ppm induced a significant increase in number of new lateral shoots (3.6) per tree, when compared to the control and all other treatments ($p \leq 0.05$). All applications of thidiazuron and other applications of GA_{4+7} showed no significant lateral shoot induction effects compared to the control, as shown in Figure 23.

The sequential applications of GA_{4+7} at 200 ppm induced narrower angles on lateral shoots, when compared to the control and all other treatments ($p < 0.05$), as shown in Figure 24.

There was a weak ($r = 0.31$) but highly significant ($p \leq 0.01$) correlation between mean branch crotch angle and mean diameter at branch base taken across all treatments.

119

Figure 22. Mean length of the leading shoot growth after treatments of spur type 'Red Delicious' (Tas. Ag. no.5) on MM106

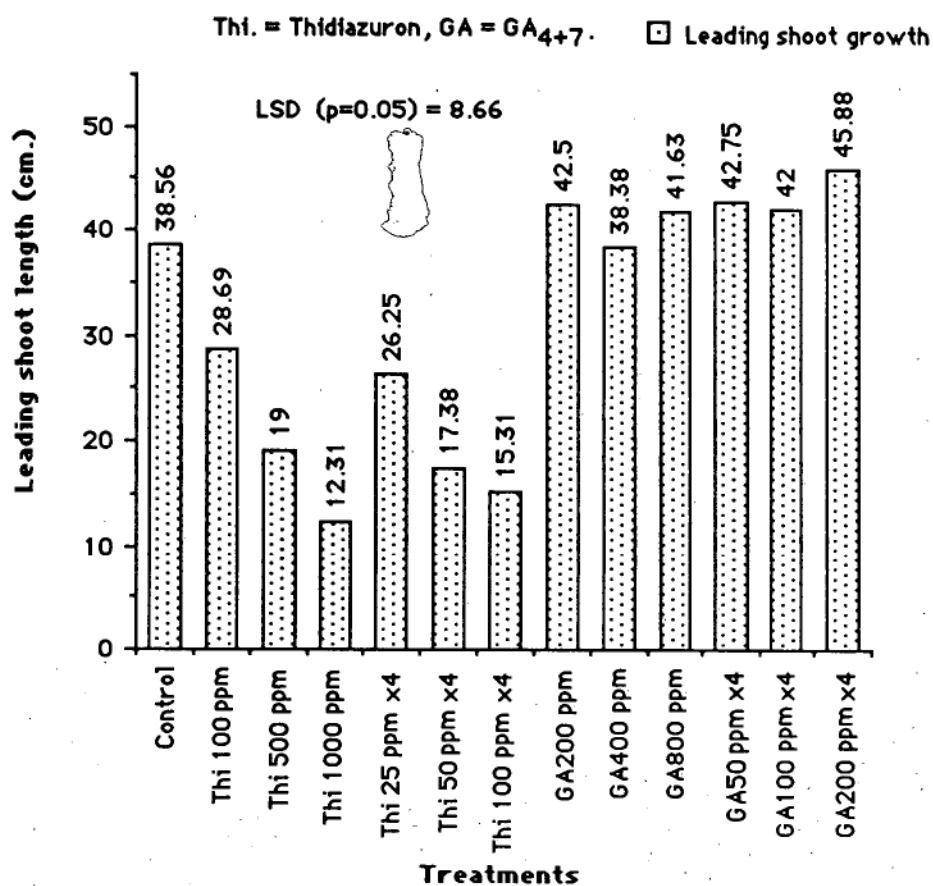Thi. = Thidiazuron, GA = GA$_{4+7}$.   ⊡ Leading shoot growth

Figure 23. Mean number of new lateral shoots per tree after treatments of spur type 'Red Delicious'(Tas. Ag. no.5) on MM106
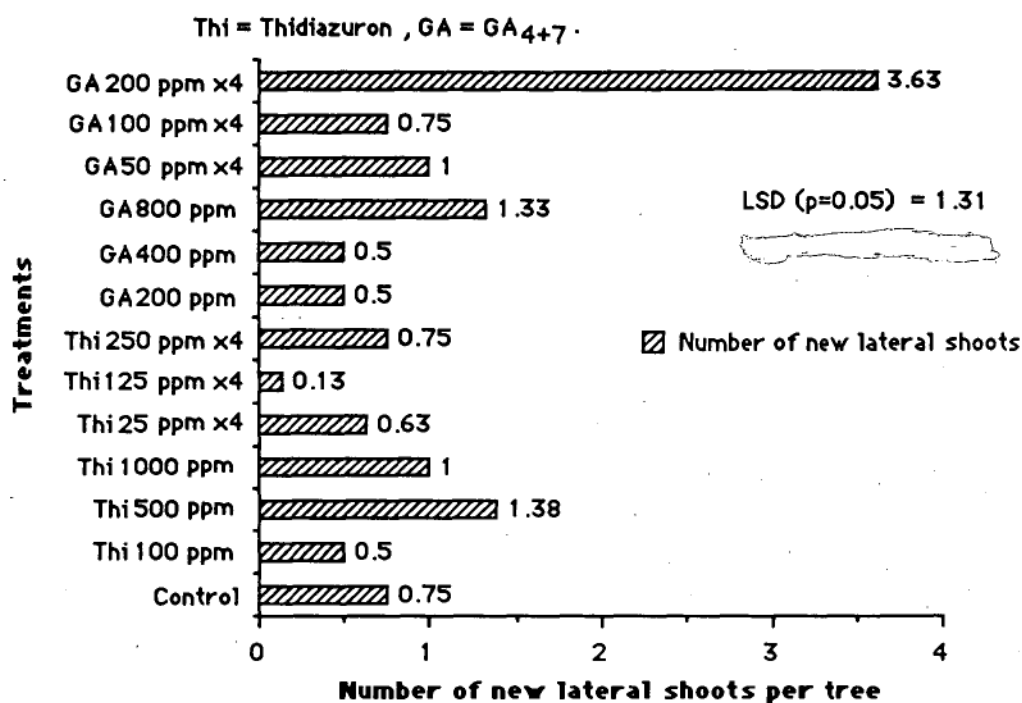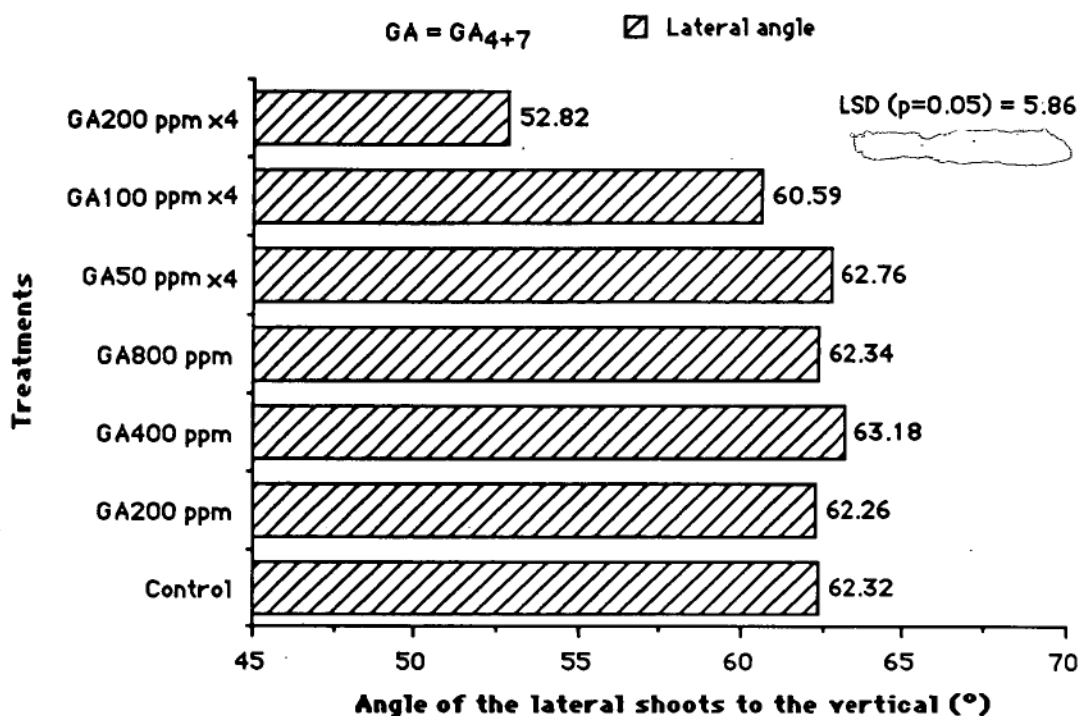
Figure 24. Mean angle of the lateral shoots to the vertical of spur type 'Red Delicious' (Tas Ag. no.5) on MM106.

4.4.3. Branch induction effect of paclobutrazol and Gibberellin 4 and 7 (GA_{4+7}) on apple nursery trees.

Methods:

Paclobutrazol (PP333) and GA_{4+7} were applied to spur type 'Red Delicious' (Tas. Ag. no.1), on seedling rootstocks. Before spraying, the ground beneath the trees along the planting strip, was covered by a 1 metre wide plastic sheet to prevent chemical uptake (in particular of PP333), by the roots.

The treatment design was a randomized complete block, replicated 12 times with single tree plots. The treatments used were:

1. Control

2. PP333 at 500 ppm

3. PP333 at 125 ppm (4 applications)

4. PP333 at 500 ppm and GA_{4+7} at 800 ppm

5. PP333 at 500 ppm and GA_{4+7} at 200 ppm (4 applications)

6. PP333 at 125 ppm (4 applications) and GA_{4+7} at 800 ppm

7. PP333 at 125 ppm (4 applications) and GA_{4+7} at 200 ppm (4 applications)

8. GA_{4+7} at 800 ppm

9. GA_{4+7} at 200 ppm (4 applications)

The four applications were applied sequentially at weekly intervals. The first application took place on 18 December 1987. During this application period, the new tree growth was 51-69 cm. above the graft union.

The increased length of the leading shoot during the growing season was measured sequentially (14 day intervals). The growth

parameters, before and after treatment were measured as described in the General Materials and Methods section.

Results:

The growth patterns of the leading shoot in each treatment during the growing season are shown in Figure 25. The leading shoot growth of the all of the treatments which received PP333 started slowing down, two weeks after the initial application, except when applied once with a sequential application of GA_{4+7}, at 200 ppm. The shoot tips of two trees in treatment 4 and seven trees in the treatment 7 were killed by the chemicals. GA_{4+7} applied alone produced no significant differences in the final leading shoot growth.

Figure 26 shows the overall leading shoot growth in response to the PP333 treatments.

There were significantly more lateral shoots on the trees which received GA_{4+7} sequentially, and received PP333 once with GA_{4+7} sequential applications ($p \leq 0.05$), as shown in Figure 27.

The angle of the lateral shoots to the vertical, induced by the sequential applications of GA_{4+7} alone at 200 ppm, as well as by the combined application of the sequential application of GA_{4+7} with PP333 (single application), was significantly narrower than the Control ($p \leq 0.05$) as shown in Figure 28.

Figure 25. Growth patterns of the leading shoot during the 1987-1988 growing season of spur type 'Red Delicious' (Tas. Ag. no.1) on seedlings
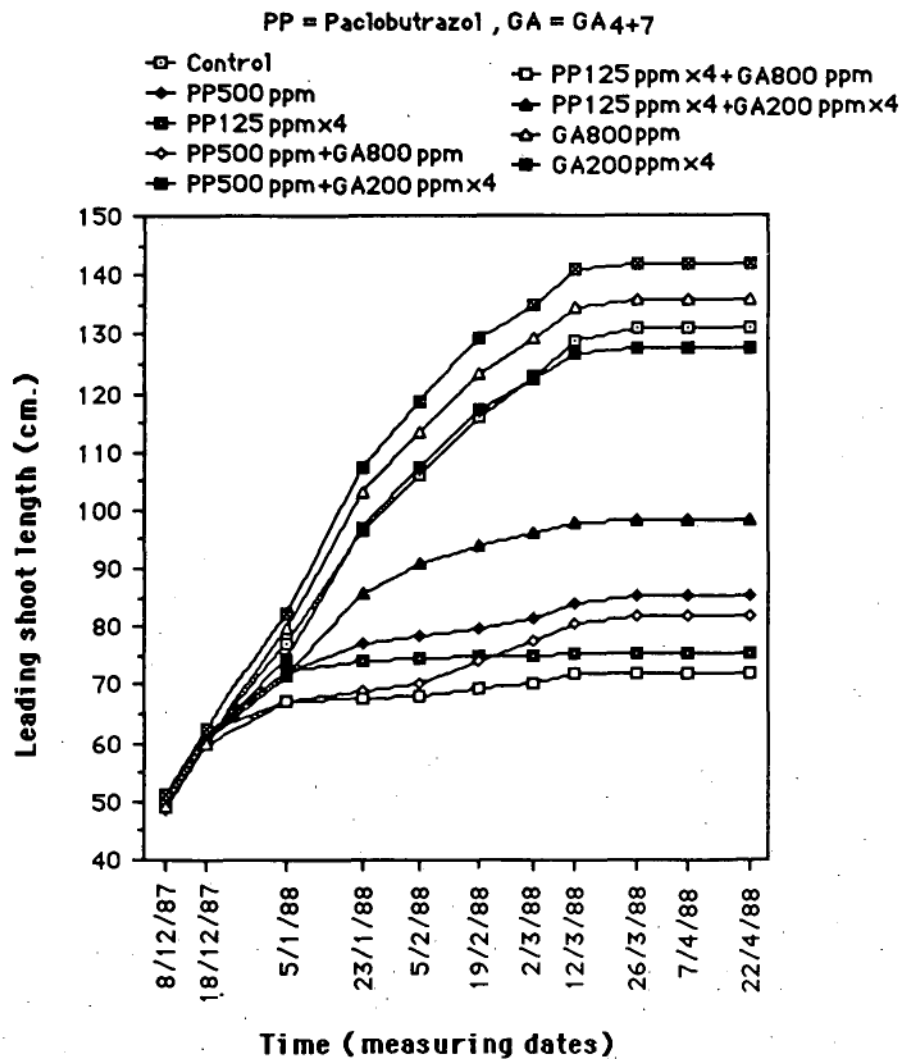

PP = Paclobutrazol , GA = GA4+7

- Control
- PP500 ppm
- PP125 ppm×4
- PP500 ppm+GA800 ppm
- PP500 ppm+GA200 ppm×4
- PP125 ppm×4+GA800 ppm
- PP125 ppm×4 +GA200 ppm×4
- GA800 ppm
- GA200 ppm×4

Figure 26. Mean length of the leading shoot growth after treatments of spur type 'Red Delicious' (Tas. Ag. no. 1) on seedlings

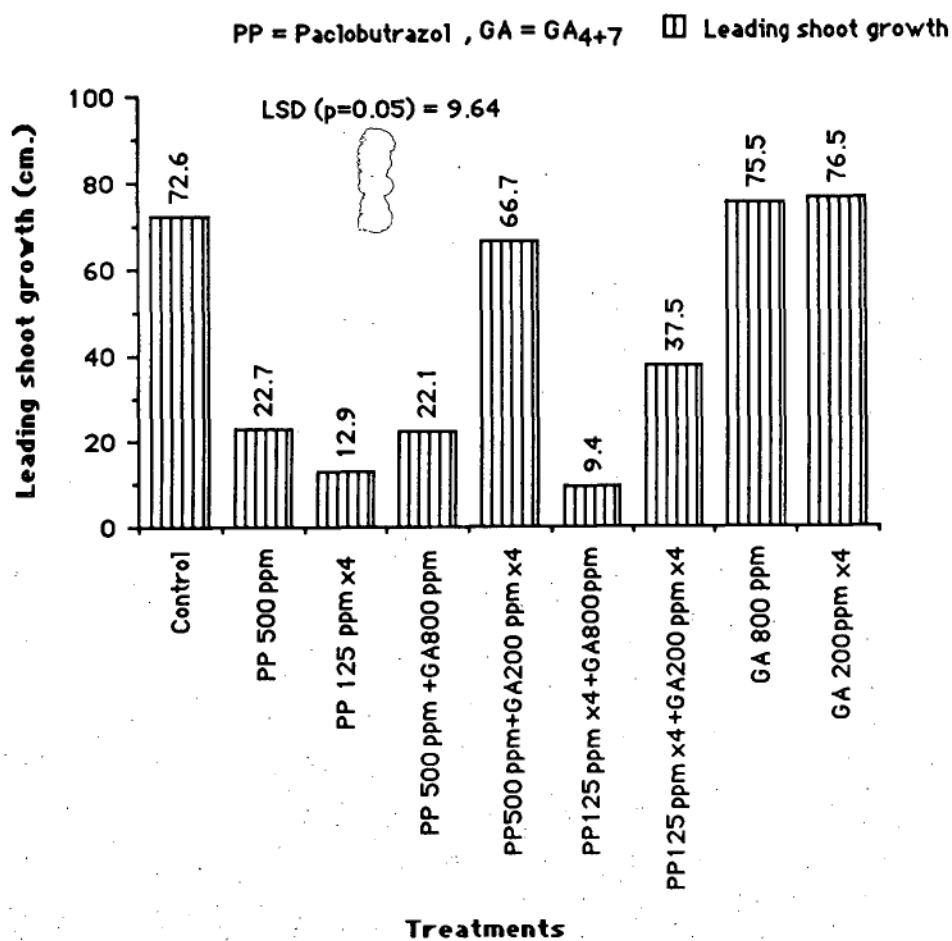PP = Paclobutrazol , GA = GA$_{4+7}$ ⊞ Leading shoot growth

Figure 27. Mean number of new lateral shoots per trees of spur type 'Red Delicious' (Tas. Ag. no.1) on seedlings

PP = Paclobutrazol , GA = GA$_{4+7}$ ☑ Number of new laterals
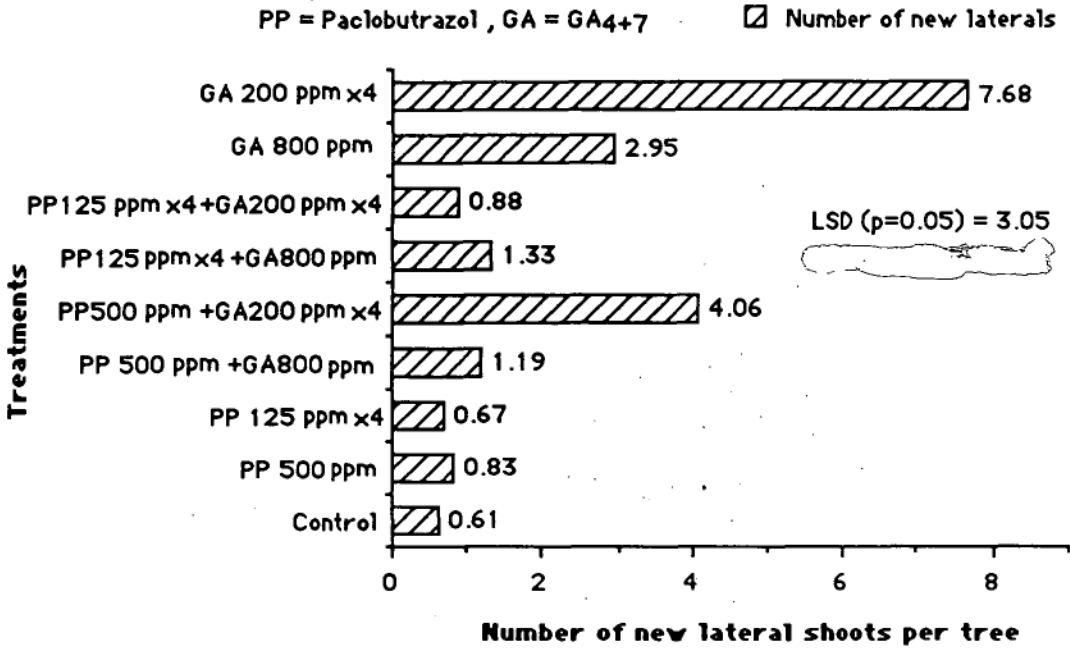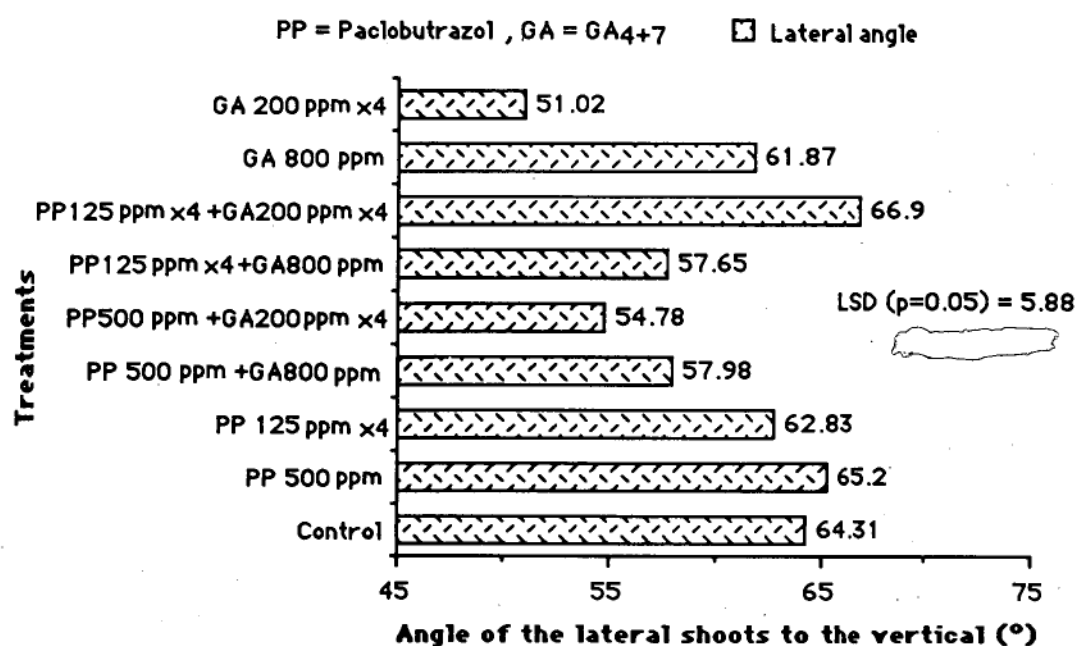

Number of new lateral shoots per tree

Figure 28. Mean angle of the lateral shoots to the vertical of spur type 'Red Delicious' (Tas. Ag. no.1) on seedlings

PP = Paclobutrazol , GA = GA₄₊₇   ▢ Lateral angle

Treatments:

Treatment	Value
GA 200 ppm x4	51.02
GA 800 ppm	61.87
PP125 ppm x4 +GA200 ppm x4	66.9
PP125 ppm x4 +GA800 ppm	57.65
PP500 ppm +GA200 ppm x4	54.78
PP 500 ppm +GA800 ppm	57.98
PP 125 ppm x4	62.83
PP 500 ppm	65.2
Control	64.31

LSD (p=0.05) = 5.88

Angle of the lateral shoots to the vertical (°)

128

Discussion:

Cytolin, at 800 ppm as well as the sequential applications at 200 ppm, to spur type 'Red Delicious', produced a substantial number of lateral shoots. The lateral shoots induced by the application of Cytolin, M&B 25,105, and GA_{4+7} arose from new buds formed after the first treatment. The sequential application of Cytolin produced lateral shoots with a very narrow angle to the vertical, considered undesirable in commercial practice. Although, lateral shoot growth was increased by Cytolin, there was no effect on the leading shoot growth. In addition, the position of the induced lateral shoots was at an optimum height for future production. In contrast, M&B 25,105 and thidiazuron did not induce useful lateral shoot growth and also produced some phytotoxicity effects and reduced leading shoot growth.

BA application has been found to be effective in lateral shoot induction in some varieties of nursery apple trees (Cody, et al.,1985). The results from the experiment 4.4.1, however, showed that BA applications failed to produce any effects on growth or lateral shoot induction. GA_{4+7}, the other component of Cytolin, has been reported to have no effect on lateral shoot induction (Elfving, 1984). The results indicate that concentrations up to 800 ppm GA_{4+7} (single application), did not have an effect on lateral shoot induction. The same amount of GA_{4+7} divided and applied 4 times (weekly intervals) at 200 ppm, produced a substantial number of lateral shoots. It is possible that the total dosage of GA_{4+7}, must be applied sequentially to get the continuous stimulation or induction of lateral shoot growth. Chrispeels and Varner (1967), suggested that GAs must be present continuously to be effective. The inductive effects of GA_{4+7}, unfortunately produced narrow crotch angles in the

induced lateral shoots. As the induced lateral shoots with narrow crotch angle were also seen in the sequential applications of Cytolin, the undesirable effects may be caused by the GA_{4+7} in the mixture.

ABA has been suggested to be a factor of lateral shoot inhibition in nursery apple trees (Theron et al., 1987). The results from Experiment 4.4.3, suggest that ABA may not be the main factor in lateral shoot inhibition (PP333 has been reported to have ABA inhibition effects (Wang et al., 1987a)). The results also suggest that GA, may be the main factor of lateral shoot production at the nursery stage. The lateral shoots can be induced by the sequential application of GAs, as indicated by the application of GA_{4+7} at 200 ppm 4 times. Sequential applications of GA_{4+7} may completely override the effects of a single application (but not sequential applications), of PP333 on shoot growth. This suggests that to overcome the effects of PP333, GA_{4+7} needs to be present over a period of time.

4.5. Effect of BA and GA_{4+7} on branch induction in nursery and one-year-old apple trees.

Results from Experiment 4.4.1, indicate that Cytolin has some effect on lateral shoot induction in the nursery apple trees of spur type 'Red Delicious'. In addition, it has been shown that Cytolin at 100 ppm, can induce lateral shoot growth on one-year-old spur type apple trees, without affecting the growth of the leading shoot and the crotch angle of the lateral shoots (Koen et al., in press). The first trial in this section, was to investigate the branch induction effect of the Cytolin mixture in a detailed concentration range, on one-year-old spur type 'Red Delicious' apple trees.

Commercial Cytolin contains BA and GA_{4+7} in equal proportions each in a concentration of 2% active ingredient. The mixture showed its effectiveness in lateral shoot induction on spur type 'Red Delicious' nursery trees, as described above. The second trial in this section aimed to determine whether BA or GA_{4+7} affected lateral shoot induction, and whether different concentrations of both growth substances in the combination gave any different effects on growth and branch induction.

4.5.1. Effect of Cytolin on branch induction in one-year-old apple trees.

Methods:

One-year-old trees of spur type 'Red Delicious' (Tas. Ag. no.2) on seedling, were used in this trial. The trees were planted at a spacing of 5 x 2.5 m. in the orchard at Rookwood. On 19th November, 1987, during the first season, when the length of the new growth was between 5-10 cm. in length, the trees were sprayed with Cytolin on the tip of the main shoot. Before treatment, the tree size was established by measuring the tree height, the trunk diameter (immediately above the graft union), and the number and length of the branches. The treatments were a control, and Cytolin applications at 20, 40, 60, 80, 100, 120, 140, 160, 180, and 200 ppm. The experimental design was a randomized complete block, with 2 replicates of 5 tree plots. At the end of the growing season, the growth of the main stem was measured, as well as the increase in trunk diameter, number of branches, branch length and the branch angle to the vertical.

Results:

Figures 29 and 30 show significant linear regressions between Cytolin concentrations and number of new branches (positive) and average branch length (negative). Leading shoot growth and average branch angle were not affected by Cytolin treatment.

132

Figure 29. Mean length of induced branches with various concentrations of Cytolin on one-year-old spur type 'Red Delicious' (Tas. Ag. no.2) on seedlings

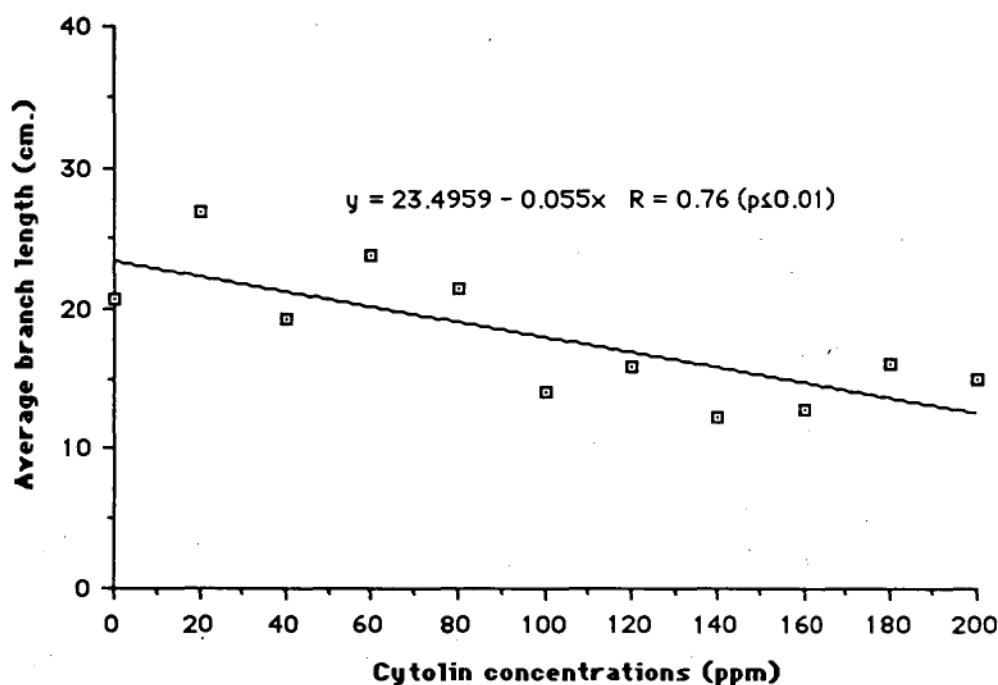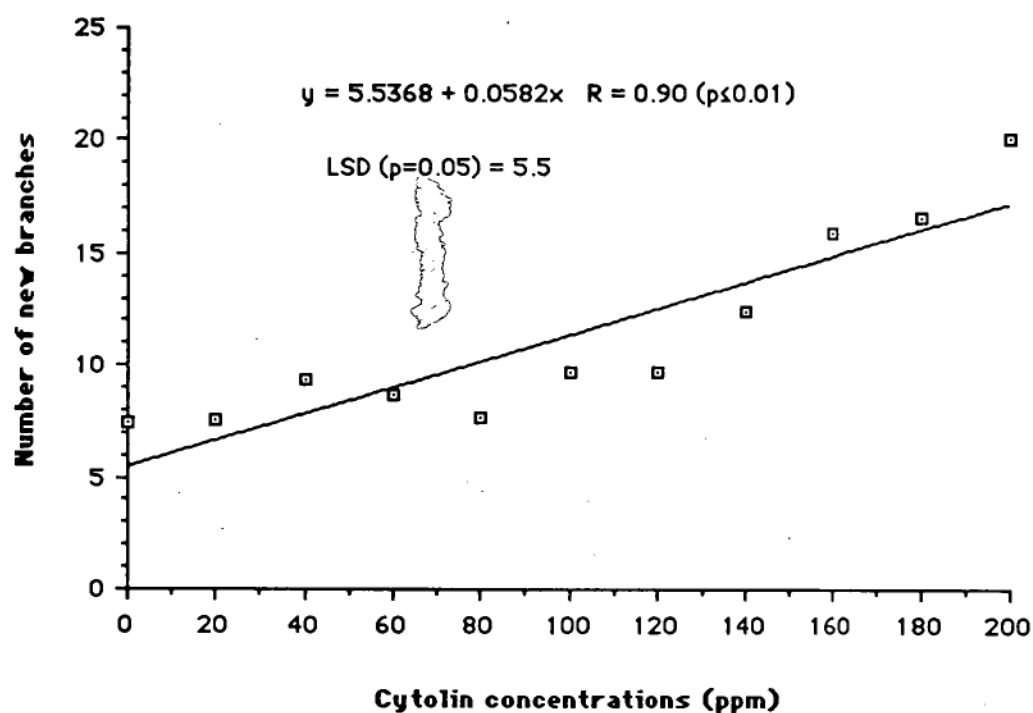$y = 23.4959 - 0.055x$ $R = 0.76 (p \leq 0.01)$

Figure 30. Mean number of induced branches by various
concentrations of Cytolin on one-year-old spur type
'Red Delicious' (Tas. Ag. no.2) on seedlings

$y = 5.5368 + 0.0582x$ $R = 0.90$ (p≤0.01)

LSD (p=0.05) = 5.5

Cytolin concentrations (ppm)

Discussion:

The concentrations of Cytolin, which elicited effective response in the trees already in the orchard were lower than those needed for a similar response in nursery trees. The branches which were induced on the one-year-old and the nursery trees originated differently. The branches on the one-year-old trees were induced from the dormant buds formed in the previous growing season. The lateral shoots induced on the nursery trees were induced from the current growing buds. It is therefore possible that different growth induction mechanisms operated in these two different types of buds.

The additional branches induced by Cytolin appeared to substantially influence the growth of other parts of the trees. That is if there was a high number of induced branches, their length was reduced. In practical terms this only became a difficulty when the number of branches induced was unnecessarily high.

Plate 1. Responses to Cytolin applications on one-year-old 'Red Delicious' (Tas. Ag. no. 2) apple trees. A. No spray; B. 60 ppm; C. 100 ppm; D. 200 ppm.

A. No spray

B. Cytolin 60 ppm

C. Cytolin 100 ppm

D. Cytolin 200 ppm

4.5.2 .Effect of different BA and GA_{4+7} ratios on branch induction in apple nursery trees

Methods:

Spur type 'Red Delicious' (Tas. Ag. no.5) on seedling nursery trees were used in this trial at the Grove Research Station. The experimental design was factorial with BA and GA_{4+7} at 5 different concentration combinations. The concentrations of BA and GA_{4+7} were 0, 300, 600, 900, or 1200 ppm giving 25 treatments. There were 10 replicates with single tree plots. The applications took place on 15 December 1987, and the new tree growth at that time was 37-66 cm. above the graft union. The application of chemicals and the data collection are described in the General Materials and Methods section.

Results:

The application of BA at high concentrations (900 or 1200 ppm) combined with GA_{4+7}, produced some phytotoxicity. The symptoms were yellowing of young leaves, stunting of growth, and damage of lateral or leading shoot tips. The number of damaged tips increased with increased concentrations of both BA and GA_{4+7}. The treatments and the number of the trees in which the leading shoot tip was killed, are presented in Table 10.

Figure 31 shows the means of the number of induced lateral shoots after treatment for all the concentrations of GA_{4+7}, with each concentration of BA. The application of different GA_{4+7} concentrations with the same concentration of BA, did not produce

138

significant differences in number of induced lateral shoots but this number increased significantly with an increasing concentration of BA ($p \leq 0.05$).

The angle of the lateral shoots to the vertical was affected by the treatments. Figure 32 shows that the lateral shoot angle to the vertical was significantly decreased by an increase in the concentration of BA ($p \leq 0.05$). GA_{4+7} did not significantly affect or interact with BA on lateral shoot angles.

The growth of the lateral shoots was affected by BA. As shown in Figure 33, the lateral shoot growth was stimulated by increasing the BA concentration up to 600 ppm. At 900 and 1200 ppm however, lateral shoot growth was reduced.

GA_{4+7} and BA produced some interactive effects on the leading shoot growth, as shown in Figure 34. The leading shoot growth decreased significantly as the concentration of BA was increased ($p \leq 0.05$). There were some significant differences in the leading shoot growth with different concentrations of GA_{4+7} applied in combination with BA ($p \leq 0.05$), as seen in the treatments of BA at 900 and 1200 ppm (Figure 34). There were no significant differences in leading shoot growth when GA_{4+7} was applied alone.

Table 10. Treatments which produced damage to the leading shoot tips and number of trees on which the leading shoot tip was killed, in spur type 'Red Delicious' (Tas. Ag. no.5) on seedlings.

Treatments	Number of trees with dead shoot tips
BA 900 ppm + GA_{4+7} 300 ppm	1
BA 900 ppm + GA_{4+7} 600 ppm	4
BA 900 ppm + GA_{4+7} 900 ppm	6
BA 900 ppm + GA_{4+7} 1200 ppm	6
BA 1200 ppm + GA_{4+7} 300 ppm	8
BA 1200 ppm + GA_{4+7} 600 ppm	10
BA 1200 ppm + GA_{4+7} 900 ppm	10
BA 1200 ppm + GA_{4+7} 1200 ppm	8

Figure 31. Means and standard errors of the induced lateral shoots by BA application (including GA $_{4+7}$) of spur type 'Red Delicious' (Tas. Ag. no.5) on seedlings
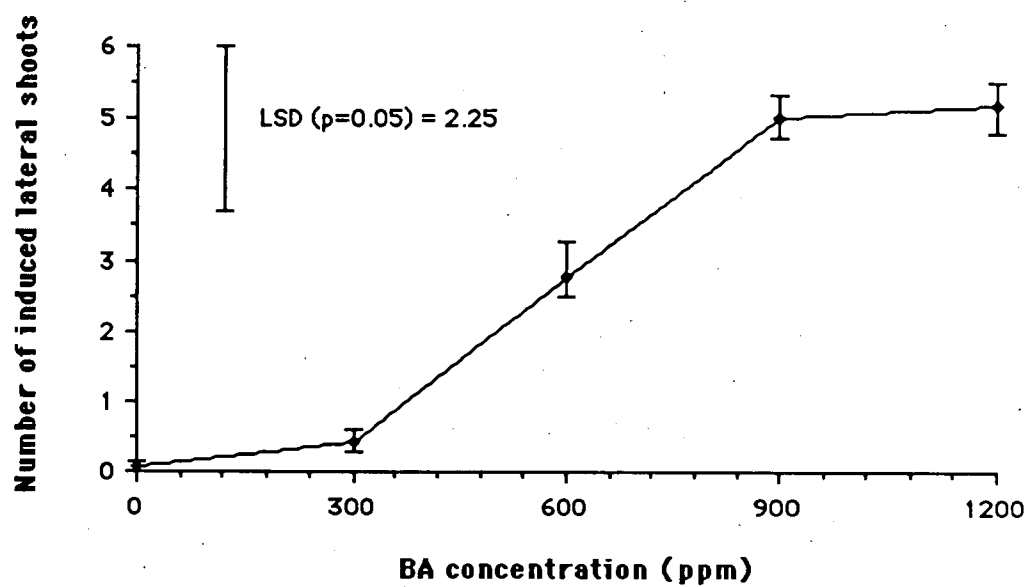
Figure 32. Mean angle of the lateral shoots to the vertical of spur type 'Red Delicious' (Tas. Ag. no.5) on seedlings applied with various concentrations of BA (including GA $_{4+7}$)
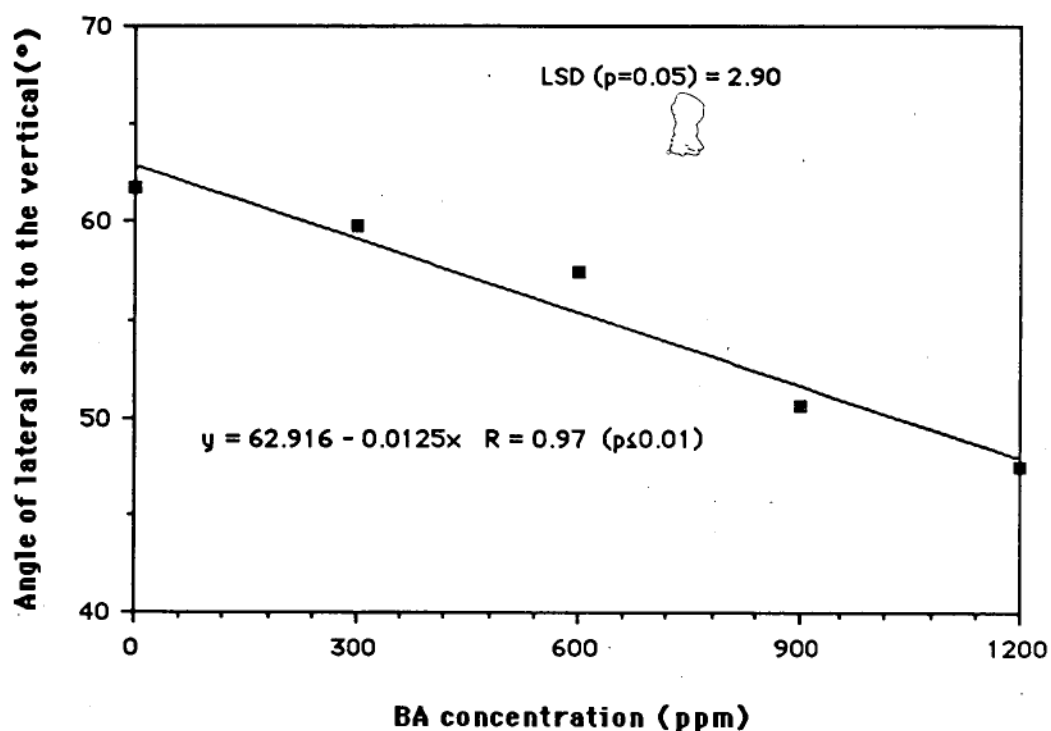
Figure 33. Means and standard errors of lateral shoot growth after treatment by BA application (including GA $_{4+7}$) of spur type 'Red Delicious' (Tas. Ag. no.5) on seedlings
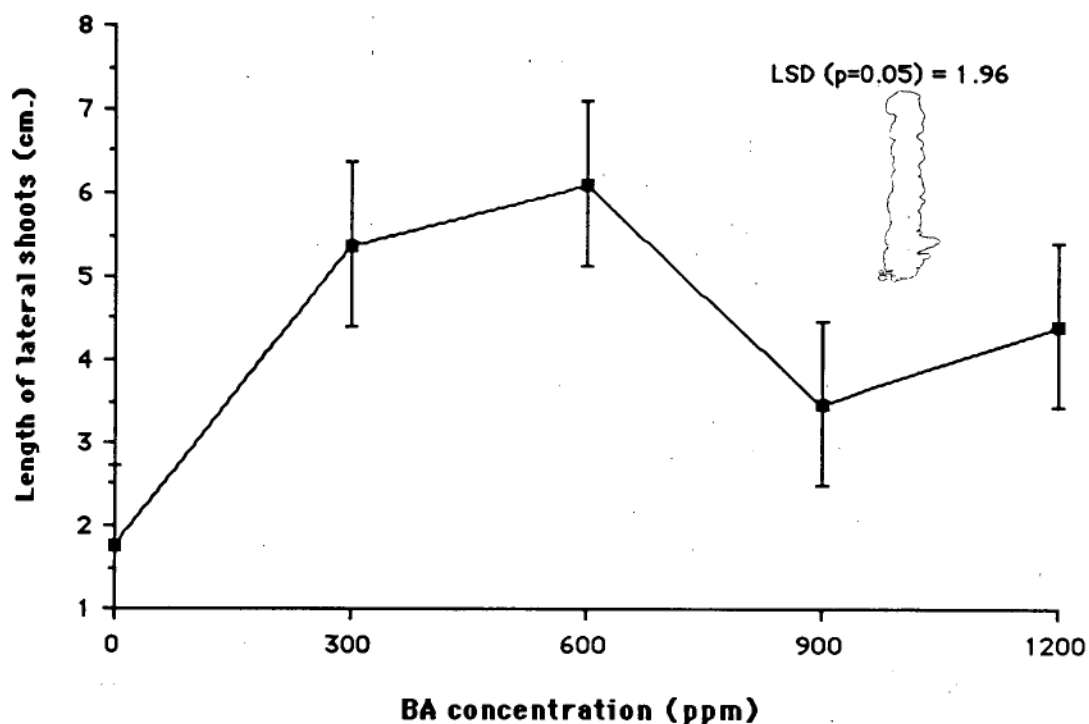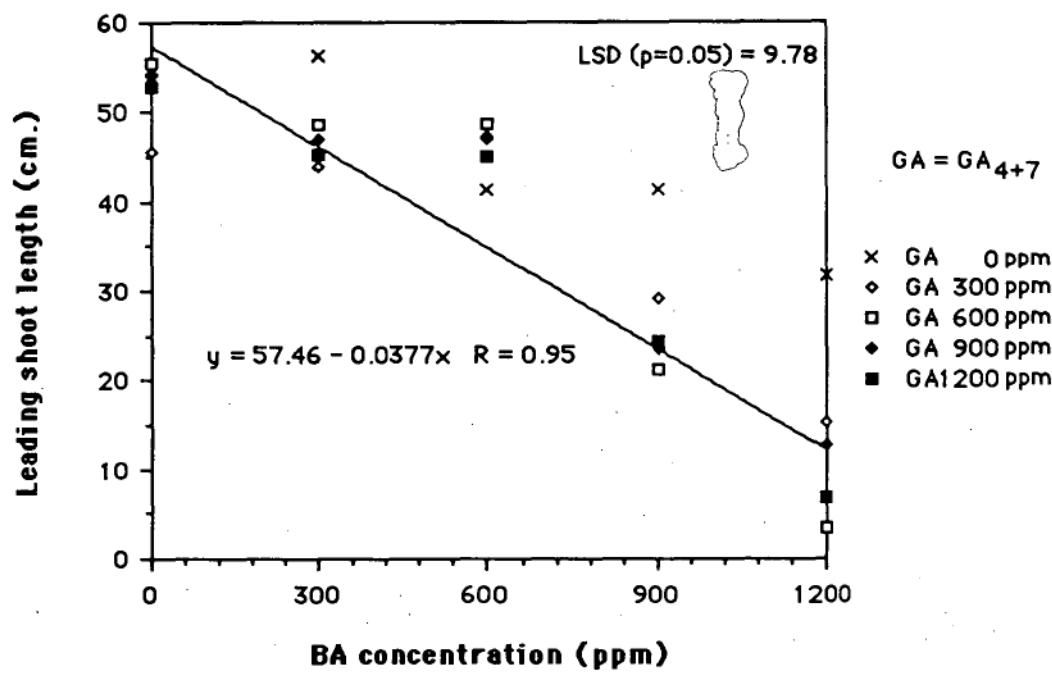
Figure 34. Mean length of leading shoot growth after treatment by BA application (including GA_{4+7}) of spur type 'Red Delicious' (Tas. Ag. no.5) on seedlings

144

Discussion:

The results suggest that the lateral shoot induction effect is caused by BA rather than GA_{4+7}. The only interactive effects of BA and GA_{4+7} were on the leading shoot growth. Increasing the concentration of BA and GA_{4+7} caused a reduction in the growth of the leading shoot. The presence of phytotoxic symptoms and the reduction of the angles of the lateral shoots to the vertical, at high concentrations of BA, suggest that 900 and 1200 ppm are too high concentrations to be used on the spur type 'Red Delicious'.

The reduction of the leading shoot growth and the angles of the lateral shoots to the vertical, with increased concentrations of BA and GA_{4+7}, is probably mainly be due to the damage to shoot tips by the high concentrations of the chemicals, the effect of which was similar to mechanical shoot tip removal (seen in experiment 4.3.3).

The results also suggest that the concentration of BA must be between 600 ppm and 900 ppm, in order to achieve the lateral shoot induction effects without undesirable side effects. GA_{4+7}, in comparison, produced a limited effect with a single application (with or without BA). However, similar to results in earlier experiments, when applied sequentially, it did induce an increase in shoot number and importantly increased the growth of lateral shoots.

4.6. Branch inducing effects of Cytolin and GA_{4+7} with NAA (1-naphthaleneacetic acid) in apple nursery trees

In previous experiments 4.4.2 and 4.4.3, it was noted that the branches which were induced by GA_{4+7} produced a very narrow angles to the vertical. It has been reported that auxin was involved in the formation of branch crotch angle (Jankiewicz, 1970) but Popenoe and Barritt (1988) found that NAA at 10 ppm applied to BA-induced branches of apple nursery trees produced shorter branches without affecting crotch angle. This experiment was therefore designed to determine the effect of timing of NAA application on the crotch angle of the Cytolin or GA_{4+7} induced branches.

It was also noted in the earlier experiments that while GA_{4+7}-induced branches were growing, their angles to the vertical were apparently getting wider. This observation was not quantified however. Consequently this experiment was also designed to measure both the rate of growth and the rate of changing angle of the GA_{4+7}-induced branches.

Methods:

Spur type 'Red Delicious' (Tas. Ag. no.8) on seedling nursery trees were used in this trial at Forest Home Nursery. The experimental design was a split plot with 3 main plot, and 8 sub plot treatments. The main plot treatments were control, single application of Cytolin at 800 ppm, and four weekly sequential applications of GA_{4+7} at 200 ppm. The sub plot treatments were single applications of NAA at 10 ppm applied at weekly intervals from 0 to 6 weeks after the main plot treatments were started, giving seven NAA treatments, plus a nil NAA giving a total of 8 sub plot treatments. There were 4 replicates with single tree plots. The applications started on 14 December 1988, when the new tree growth was 38-56 cm. above the graft union. The application of the chemicals and the data collection were as described in the General Materials and Methods section. The node numbers on the branches was also counted to calculate the internode length. As there were some missing data, estimation for statistical analysis was performed by using the formula from Steel and Torrie (1981).

In addition, a treatment of GA_{4+7}, as four weekly sequential applications, was applied to seven more trees to measure the growth and crotch angles of the induced branches at weekly intervals from when the first induced branch was noticeable. These were not part of the main trial and were statistically analysed separately.

Results and Discussion:

Both main treatments of GA_{4+7} and Cytolin produced trees with significantly ($p \leq 0.05$) more branches than the control. The leading shoot growth of the trees treated with Cytolin, both expressed as total growth or increment in growth after treatment, was significantly ($p \leq 0.05$) lower than the rest, as shown in Figure 35. There was no significant differences ($p \geq 0.05$) in mean branch length or internode length between the three main plot treatments, but the mean number of nodes per tree treated with GA_{4+7} was significantly ($p \leq 0.05$) lower than the rest, as shown in Figure 36. Cytolin reduced leading shoot growth while GA_{4+7} reduced the number of nodes per branch. The leading shoot growth was possibly reduced in this case as the more active growing lateral shoots, induced by Cytolin, competing for limited nutrients and other growth factors. As cytokinin promotes cell division (Salisbury and Ross, 1985), the BA (cytokinin) in the Cytolin could produce the same effect by inducing more nodes in the lateral shoots. The increase in node number would subsequently required more nutrients and other growth promoting factors.

In contrast, the lateral shoot growth induced by GA_{4+7}, without decreasing the leading shoot growth, might be due to the reduction in number of nodes per branch, as GA_{4+7} induces growth in terms of cell elongation. This is seen in internode extension without an increase in number of internodes formed (Sachs and Lang, 1961). The nodes of the GA_{4+7}-induced branches may have been formed before the promotion of cell elongation took place with the competition for nutrients and other growth factors being less than in the Cytolin-induced trees. GA_{4+7} would also promote cell elongation in the growing leading

148

shoot tip. Thus the affect of increased lateral growth on leading shoot growth could have been minimal.

The branches of the trees treated by GA_{4+7} were produced at significantly ($p \leq 0.05$) higher positions compared to the other treatments, as shown in Figure 38. The GA_{4+7} applied sequentially may therefore have continued to affect the young growing points of the induced branches and the leading shoot.

The final angle of the lateral shoots to the vertical was also reduced significantly ($p \leq 0.05$) by the applications of both GA_{4+7} and Cytolin, compared to the Control, as shown in Figure 37. This may be due to the plant growth regulators interacting with the natural hormone system as suggested by Ferree (1981).

There was no significant difference ($p \geq 0.05$) among the sub plot treatments for all measured parameters. It is possible that exogenous application of auxin (NAA) did not affect growth on the induced branches because auxin produced in the trees was sufficient and the concentration of applied NAA may have been too low to produce responses.

Where sequential sprays of GA_{4+7} were applied to the seven additional trees, the results are presented by showing both average branch length and average branch angle on a time basis and a branch age basis. More branches were induced for a period of time after the first branches were noticed as shown in Figure 39. The number of induced branches increased sharply in the first five weeks with the length of the induced branches also increasing sharply. There was however very little change in branch number after 6 weeks of measurement, as shown in Figure 40A. However, Figure 40B. shows that the mean branch length slowed down but still increased steadily as the branches grew older. The mean branch length based on the age of the branches (Figure 40B.)

increased in a pattern which is different from the branch length plotted against the time of measurement (Figure 40A.). The length of the induced branches (Figure 40A.) shows an initial rapid rate of elongation followed by a period of no significant elongation after 5 weeks. This could be due to the length of the newly formed branches reducing the average. On the other hand, the growth pattern in relation to the age of the branches (Figure 40B.) suggests that there is a bimodal pattern of growth in young branches.

Figure 41A. shows the induced mean branch crotch angle widened steadily then stabilized slightly in week 7th. Figure 41B., on the other hand, shows that the branch crotch angles widened sharply in the first five weeks before stabilizing. This suggests that crotch angles in the individual newly formed branches widened rapidly in the first five weeks of development (Figure 41B.). This effect was less obvious when crotch angle was plotted against time (Figure 41A.).

The GA_{4+7} applied sequentially showed increasing branch crotch angles as the branches grew older. This could be due to the effects of GA initiating cell division rather than accelerating division in cells already mitotically active (Evans, 1984). GA normally stimulates growth by cell elongation following increased cell wall plasticity (Jones, 1973). Thus increased cell wall plasticity could facilitate changes in branch angle due to growth discussed later. As GA_{4+7} was applied sequentially for a period of four weeks, the young growing shoot could be induced to grow longer, mainly by increased cell elongation. Jankiewicz et al. (1973) suggests that the mechanical effect of tissue forming in the crotch may push the base of young shoot to increase the angle from the axis, and this might be the reason for the increasing crotch angle. The effect of GA_{4+7} increasing cell wall plasticity may synergize this effect.

Figure 35. Total and increment after treatment of both leading shoot growth and number of branches of spur type 'Red Delicious' (Tas. Ag. no.8) nursery apple trees
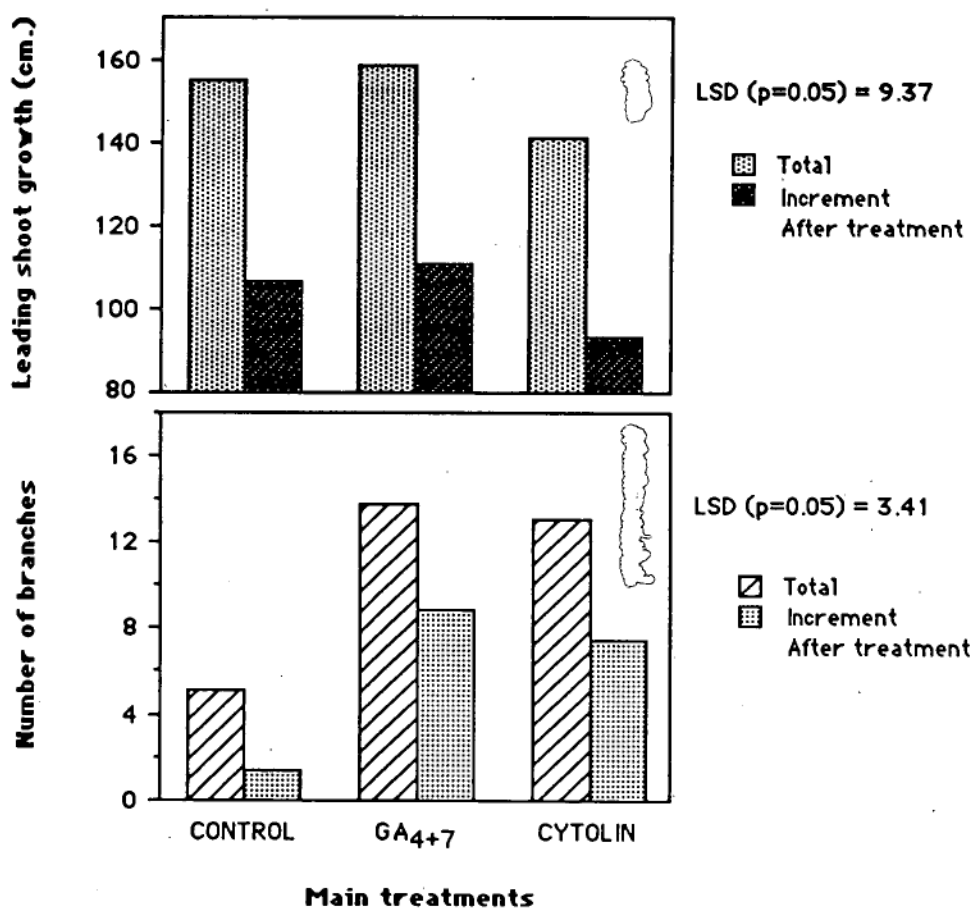
Figure 36. Number of nodes per tree, mean branch length and internode length of spur type 'Red Delicious' (Tas. Ag. no.8) apple nursery trees
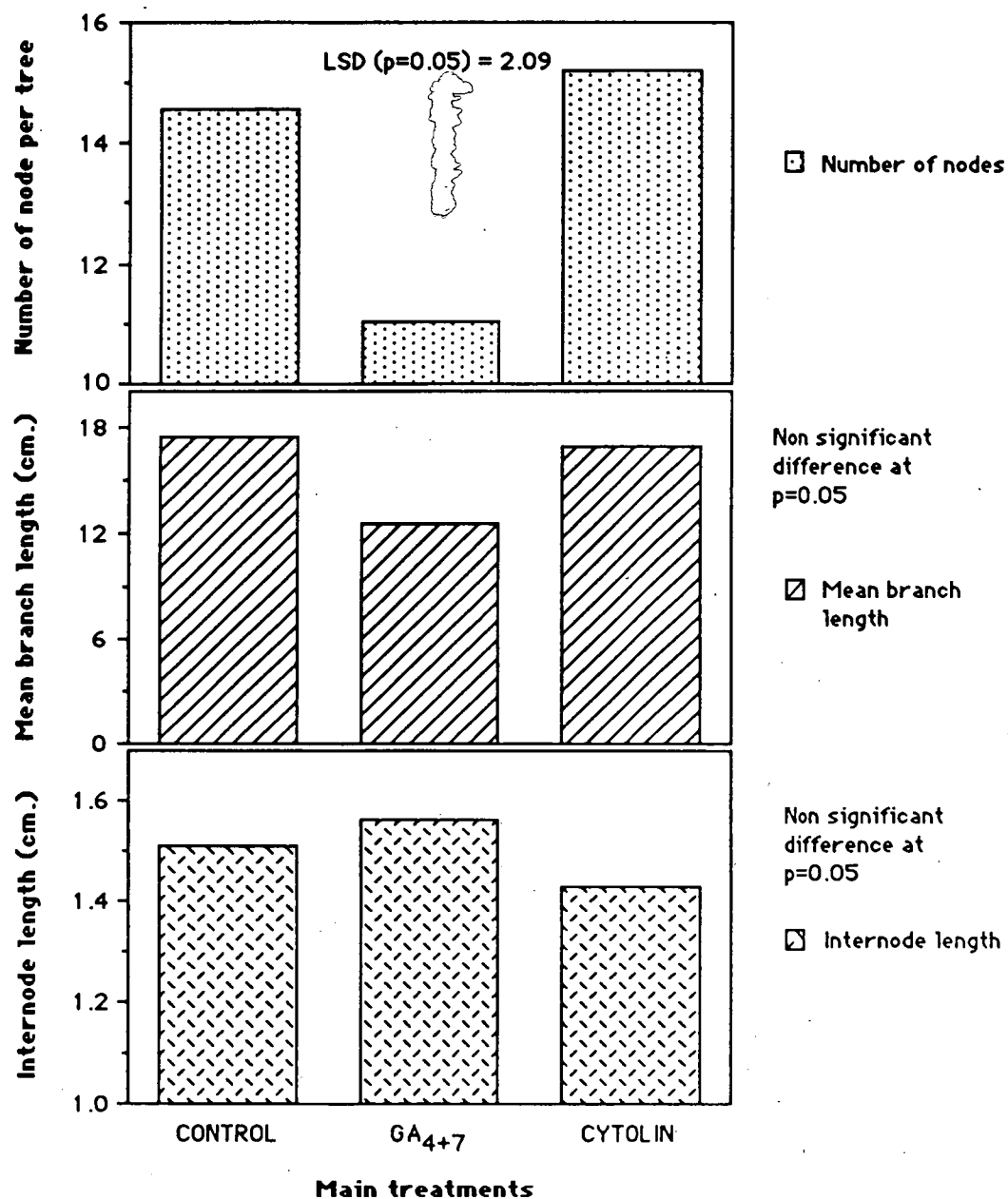
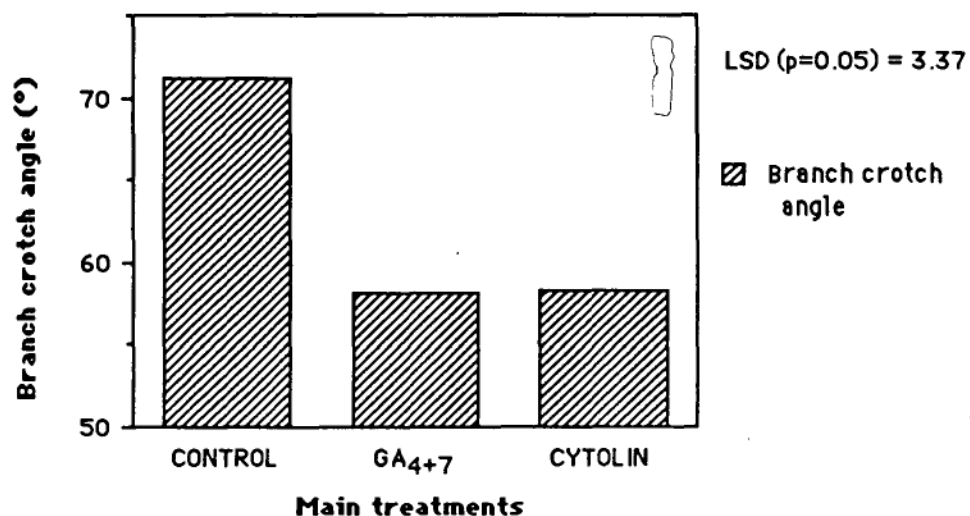**Figure 37.** Mean branch crotch angle of spur type 'Red Delicious' (Tas. Ag. no.8) apple nursery trees

LSD (p=0.05) = 3.37

▨ Branch crotch angle

Figure 38. Mean branching height of spur type 'Red Delicious' (Tas. Ag. no.8) apple nursery trees
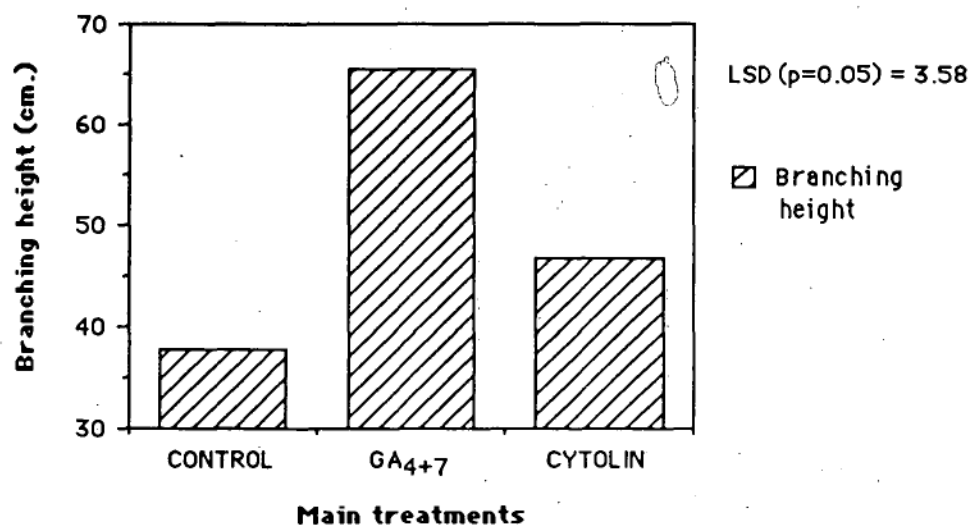

LSD (p=0.05) = 3.58

▨ Branching height

Figure 39. Number of induced branches of spur type 'Red Delicious' (Tas. Ag. no.8) nursery apple trees by sequential applications of GA_{4+7} measured since first branch was noticed
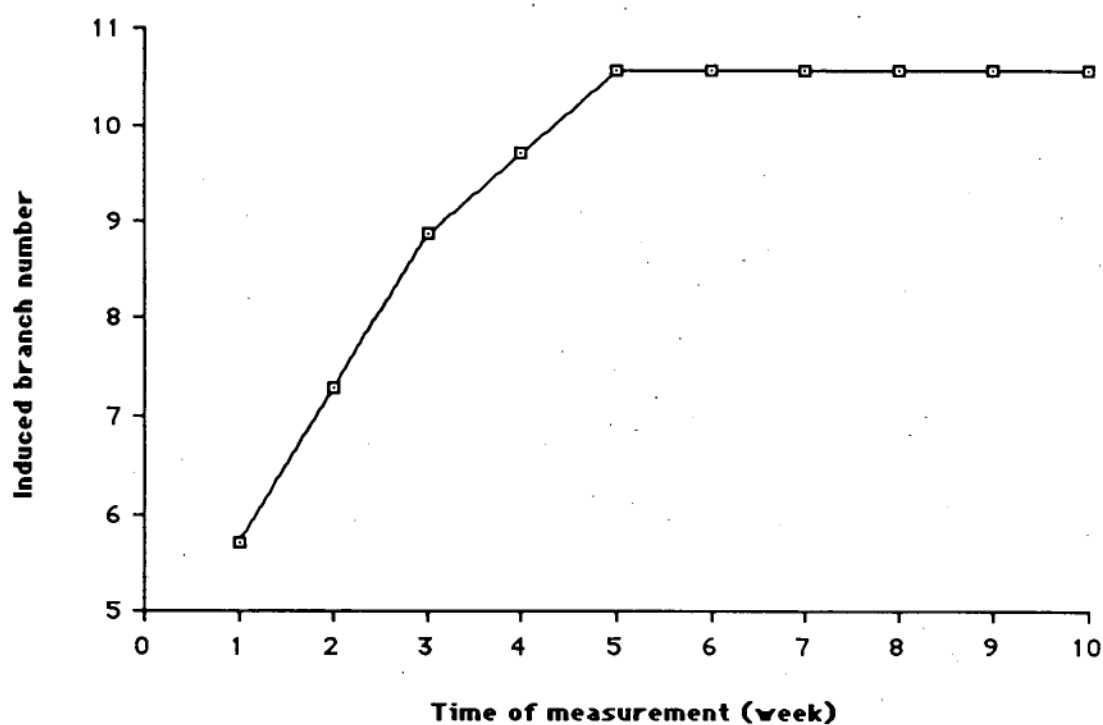
Figure 40. Mean length of induced branches of spur type 'Red Delicious' (Tas. Ag. no.8) nursery trees in response to sequential applications of GA_{4+7}; A). plot against time (week) from emergence of first branch, B). Mean length of branches at the same age (week) plotted against age.
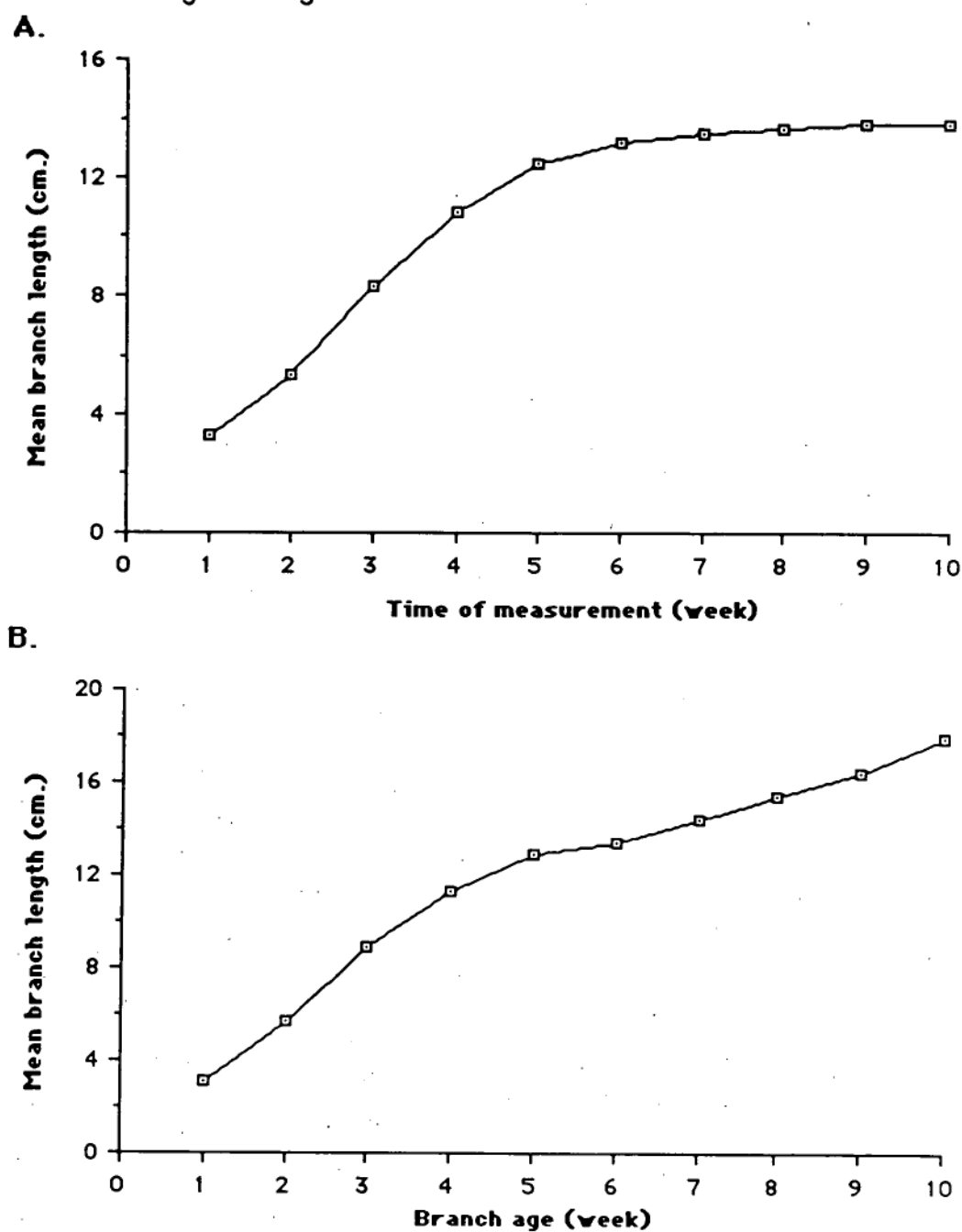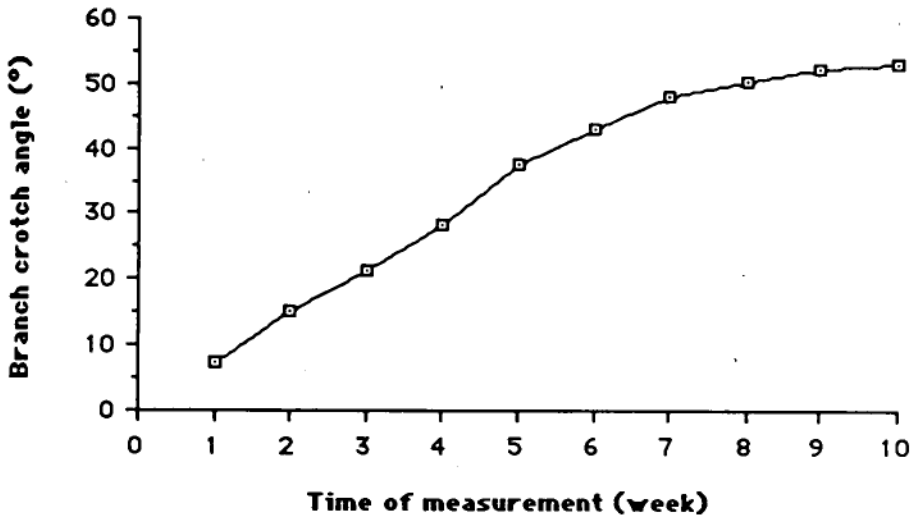
Figure 41. Mean branch crotch angle of the induced branches of spur type 'Red Delicious' (Tas. Ag. no.8) nursery apple trees response to sequential applications of GA_{4+7}; A). plot against time (week) from emergence of first branch, B). Mean branch crotch angle of branches at the same age (week) plotted against age.
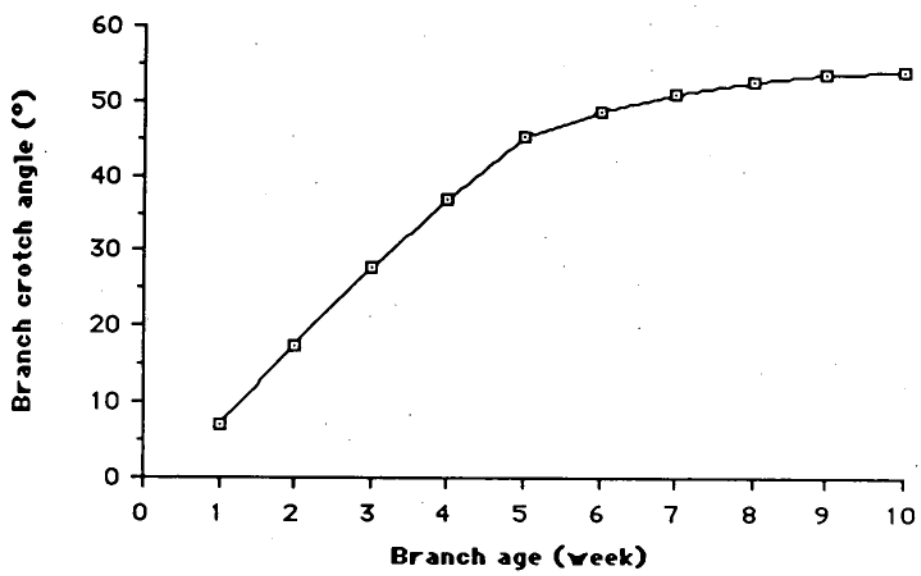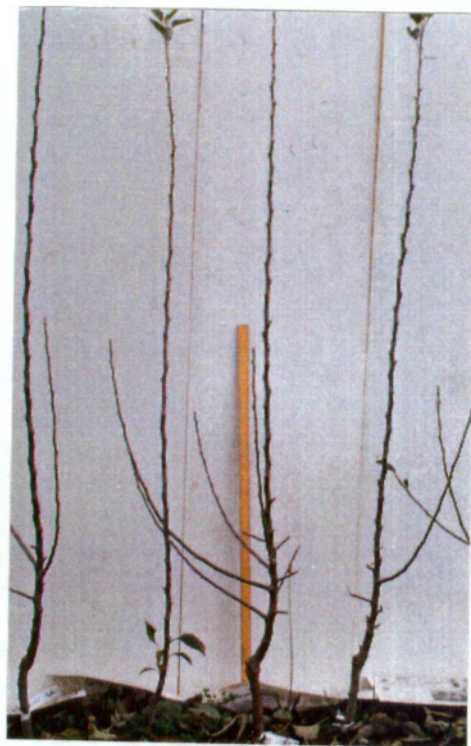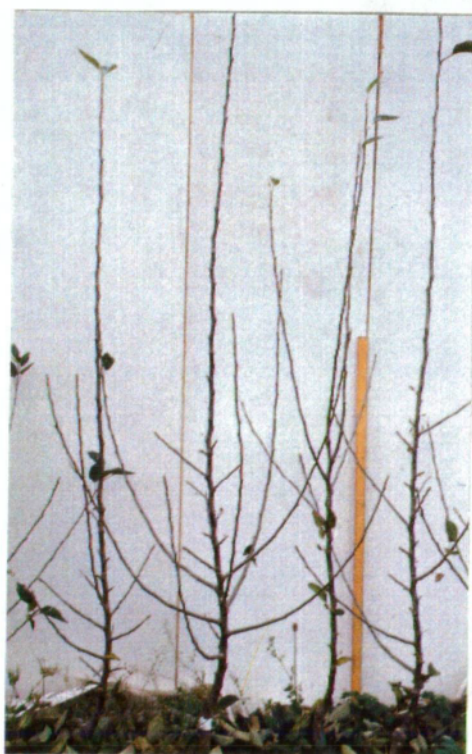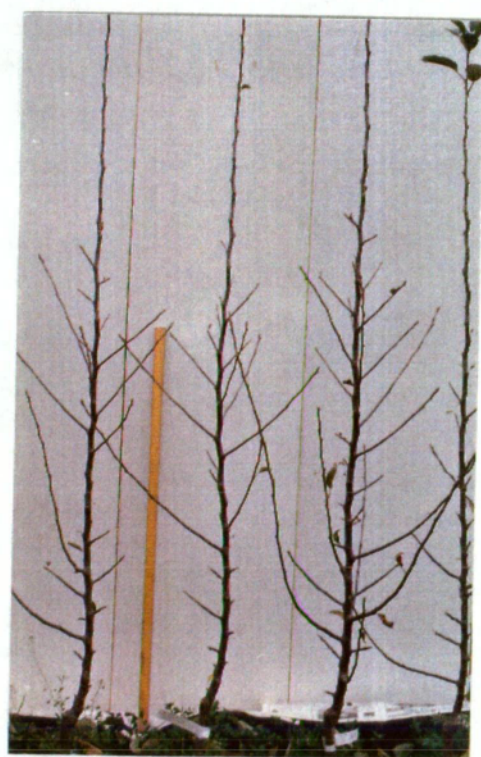
A.

B.

Plate 2. Branch induction responses to exogenous growth applications on spur type 'Red Delicious' (Tas. Ag. no.8) nursery trees. A. Control; B. Single application of Cytolin at 800 ppm; C. Four-weekly sequential applications of GA_{4+7} at 200 ppm.

A. Control

B. Cytolin

C. GA₄₊₇

5. General Discussion

Tree quality

To establish an apple orchard, it is important to start with high quality nursery trees. It is well documented that nursery apple trees which are considered of high quality are well branched. These trees have been found to have a better growth form and produce crops earlier than non-branched trees (Preston, 1968; van Oosten, 1978). There are also other important characteristics to be considered, including both the length and the crotch angle of the lateral shoots. Lateral shoot length is an important determinant of the area of future fruit production. Wider branch crotch angles ensure that the branches are not susceptible to branch splitting under heavy crop load conditions and they are also more productive than upright branches.

There are many factors influencing branch production. Because of the complexity and the interaction of these factors on growth and branch production, this series of experiments has been undertaken to identify the influence of these factors. In addition, the results could lead to practical methods of manipulation of apple tree form to achieve early cropping.

The scion/rootstock relationships

Some apple cultivars produce lateral shoots readily in the nursery, but some do not. The scion variety trial (4.2.1) showed that on the same clonal rootstocks, Red Fuji and Golden Delicious readily produced lateral shoots at the nursery stage of growth but three strains of

Red Delicious did not. Rootstocks also have some well known influences on the scion, including tree size control and change of tree shape (Barlow, 1970; Tukey, 1981). The influence of the rootstock on the scion can be seen in the first year of growth where the number of lateral shoots produced were different on the various rootstocks, as shown in experiment 4.2.2.

The results of the preliminary observations (4.1.1) on seedling and MM106 rootstocks suggest that lateral shoot production was directly correlated with the size of the rootstocks. The effect of roots on shoot growth is not limited to supplying water and nutrients, but also includes provision of growth substances which control shoot growth. The main substances involved are cytokinins which are synthesized primarily in the roots and are translocated through the xylem to the shoot tip where they influence shoot growth (Lockard and Schneider, 1981). Young (1989) found that the endogenous cytokinin levels of apple rootstocks reached a peak prior to budbreak, but after budbreak the levels dropped dramatically. Grochowska et al. (1984) reported that GAs found in the xylem were also very high at the beginning of the growing season. In addition, GAs which are shoot-synthesized may be converted to another kind of GA in the root and then recirculated to the shoot, to be active in shoot metabolism, but the root conversion may also alter the effectiveness of the hormone (Crozier and Reid, 1971). It is possible that the production of cytokinin and GAs from root system could be different for different rootstock varieties. Ibrahim and Dana (1971) suggested that in apple trees, the dwarfing response of some rootstocks may be due to a lower production of GA-like substances than that produced by vigorous rootstocks. These influences were seen where spur type Red Delicious (Tas. Ag. no.5) nursery trees on clonal rootstocks varied in growth and lateral shoot production.

The relationship between the rootstock and scion, produces a specific ratio of top to root growth, by which the growth pattern of the tree is established after union, even if the two parts have different growth rate before combination (Barlow, 1960). Lockard and Schneider (1981) suggested that the response of changing growth pattern of both scion and rootstock after union requires communication between them. Such communication could be hormonal with the main signal from the root to the shoot being cytokinin, and that from the shoot to the root being auxin.

As the scions of the budded trees were grown from single buds, the auxin production was limited to that produced at the terminal bud. The balance of auxin, cytokinin and GAs, acting on the lateral buds, should influence the subsequent development of these buds. In the experiments where the nursery trees used were grown as rootstocks in the nursery for one growing season, the root system was well established before budding. In the beginning of the growing season after budding, cytokinin and GAs from the root should play a major role on the top growth during the period in which the growth ratio between top and root is re-established. The small top/big roots combination could give advantages to the roots with large amounts of hormones being upwardly transported by the xylem with little coming back in the phloem. In addition, cytokinins are also known as the growth hormones which stimulate lateral growth with the differentiation of buds being regulated by cytokinin (Williams and Stahly, 1968). The GAs are involved in extension growth e.g. stem extension (Barlow, 1970). GAs may be more effective in initiating cell division than in accelerating division in cells already mitotically active (Evans, 1984), which is supported by the occurrence of internode extension without increase in the number of internodes formed (Sachs and Lang, 1961). The exogenous applications of

cytokinin (BA) and/or GA_{4+7} (which induced lateral shoot growth on the growing leading shoot) may increase the endogenous levels of effective cytokinin and/or GA to the levels which can produce physiological influence on lateral bud growth. The same phenomenon occurs as natural growth during the early stages of leading shoot growth. Enrichment of cytokinin and GAs supply induced the growth of the lateral shoots with auxin promoting further growth. As the leading shoot grows longer, increasing auxin from the shoot tip interrupts the balance with cytokinin and GAs from the roots causing inhibition of the later formed lateral buds.

Growth regulator applications and other treatments

Auxin is well known as the main factor contributing to maintenance of apical dominance, with the well documented inhibitory influences on lateral bud outgrowth (Phillips, 1975). Duckworth et al. (1979) suggested that M&B 25,105 temporarily checks apical dominance by inhibiting the basipetal movement of auxin in treated shoots. This chemical has successfully been used to induce lateral shoots in some apple cultivars (Anon., 1976), but it failed to induce lateral shoots in others e.g., Topred (Strydom and Honeyborne, 1980) and Crispin (Mutsu) (Anon., 1976). The results in experiment 4.4.1 suggest that spur type 'Red Delicious' (Tas. Ag. no. 5) is another cultivar in which M&B 25,105 failed to induced lateral shoots.

The most active production sites of auxin are in the young expanding leaves in the growing shoot tips (Sembdner et al., 1980). Induction of lateral shoots by reducing auxin production sites have been successfully achieved in some apple cultivars by removal of young leaves

(Wertheim, 1978a and 1978b). The results of experiment 4.3.3 show that lateral bud growth in spur type 'Red Delicious' (Tas. Ag. no. 5) did not respond to removal of young leaves. Sequential removal of young leaves also had an unwanted inhibitory effect on tree growth. Wertheim (1978a and 1978b) found that removal of the shoot tip gave unsatisfactory results because the highest lateral shoot grew so rapidly that apical dominance was quickly restored, or the induced lateral shoots grew too upright. The complete removal of the leading shoot tip in experiment 4.3.3 also gave similar unfavorable effects. The cluster of lateral shoots, induced just below the place where the tipping was done, formed very narrow crotch angles giving unsatisfactory nursery trees.

The conclusive results following the removal of auxin production sites (young leaves or shoot tip) and the inhibition of auxin translocation (application of M&B 25,105) suggest that other factors, operate in lateral shoot production or inhibition.

Theron et al. (1987) suggested that in nursery apple trees, the inhibition of buds could also be related to abscisic acid (ABA). ABA, primarily synthesized in mature leaves, could inhibit lateral bud outgrowth or prevent the buds from using endogenous cytokinins (Phillips, 1975; Tucker and Mansfield, 1973). Removal of mature leaves and applications of paclobutrazol, which has been reported to reduce endogenous ABA level in apple leaves (Wang et al., 1987a), could result in increased induction of lateral bud outgrowth. It has also been shown that GA suppression is the commonly accepted mode of action of paclobutrazol (Richardson and Quinlan, 1986) and experiment 4.4.3 tried to manipulate ABA synthesis and replace GA. It is also worth noting that it is extremely difficult to manipulate ABA. Few people have reported success with foliar application of ABA, and there are no other known

chemicals which specifically target either ABA synthesis storage or activity. Experiments 4.3.4 and 4.4.3 do not support the ABA inhibition hypothesis but imply that ABA may not be the main factor in lateral shoot inhibition, or conversely that ABA which has been already stored in buds well before the treatment may cause the inhibition. While it is possible to suggest hormone mediated controls, it is important not to dismiss the role of photosynthesis and assimilate distribution as a possible controlling influence. Reduced carbohydrate transfer to the roots could for example reduce cytokinin production and consequently influence budbreak. A more direct effect was evident in experiment 4.3.3 and 4.3.4 in which leaf removal reduced growth.

Experiments 4.4.1 and 4.5.1 confirm that exogenous application of the BA and GA_{4+7} mixture induced lateral shoots, without suppression of leading shoot growth, in one-year-old trees in the orchard, but also showed that this could happen in the first year in the nursery. It has been reported that $BA+GA_{4+7}$ was used successfully to induce lateral shoots in young apple trees for many apple cultivars (Basak and Soczek, 1986; Cody et al., 1985; Miller, 1985; Wertheim, 1987). It also has been suggested that the cytokinin (BA) is the main factor influencing lateral bud outgrowth rather than GA_{4+7} (Elfving, 1984). The results of experiment 4.5.2, in which BA and GA_{4+7} were applied in varying concentrations and proportions, confirmed that BA is the main influence on lateral shoot induction, as there was no response to changing $BA:GA_{4+7}$ ratio and no direct GA effect.

Experiments 4.4.2 and 4.4.3 show that single applications of GA_{4+7} did not induce lateral shoots, but the sequential applications of GA_{4+7} significantly increased them, and also increased the leading shoot growth. This agrees with Evans (1984) who postulated that GA initiated cell division, and Chrispeels and Varner (1967) who found that GAs must

be present continuously for the regulatory action to be successful.

The possible effects of hormonal control of lateral shoot induction, discussed above, are explained by some observations, some experimental results and the known effects of various plant hormones. The lack of information on comparative endogenous hormone levels is one of the difficulties in achieving a better picture. It is not possible to separate all the effects of hormones on the functions of plant organs and other essential functions. For instance the root system has the main functions of supplying nutrients and water, but it also produces hormones and is itself hormonally controlled. The leaves produce photosynthates and hormones, leaf removal would alter the hormone balance as well as a reduction in photosynthesis both of which could be the limiting factors of growth.

The plant growth substances used in the experiments 4.4, 4.5, and 4.6 were all foliar applications. Bukovac (1973) suggested some extraneous factors, including leaf structure, the concentration of the applied spray, the wetting agent used and other environmental factors, could influence the mechanism of foliar penetration of the plant by growth regulators. Hall (1973) also suggested that the exogenous plant growth regulators producing significant responses might only reflect the capacity of the tissue to utilize the agent in its applied chemical composition.

The result of the experiment 4.4.2 suggested that thidiazuron gave no lateral shoot induction effects as a foliar application. This does not agree with reports on thidiazuron, where it has been shown to have a very high cytokinin-like effect, releasing lateral apple buds from dormancy (Wang et al., 1986 and 1987b). Single applications of GA_{4+7} (in experiments 4.4.2 and 4.4.3) did not give any response, contrasting sharply

with the response to sequential application at the same total dosage. This evidence suggests that the timing and dosage of exogenous GA_{4+7} application are critical in evoking a response. The NAA applications (in experiment 4.6) did not produce any effects on induced-branch crotch angles, suggesting that the NAA concentration used may be too low to produce any response as there was sufficient auxin already in the trees.

Kim et al. (1984) suggested that, in nursery apple trees, only the lateral shoots developing from positions at least, 65 cm. above ground were considered suitable for permanent branches. Application of exogenous plant growth regulators to induce lateral shoots in nursery apple trees, seen in experiments 4.4.1, 4.4.2, 4.4.3, and 4.5.3, show that the lateral shoots were induced from the newly formed buds. The heights of the induced lateral shoots were above the height of the trees at the first application. Natural lateral shoot induction in all experiments occurred very early after bud burst supporting the view that the hormonal balance at that stage of growth is responsible for release of lateral bud inhibition. As lateral shoot induction in the nursery trees only occurred in the new growth, useful lateral shoots can be achieved by applying the growth regulators to the trees at the appropriate tree height for useful branches to develop.

The stage of growth was also important. The response to the application of plant growth regulators, was different during the rapidly growing early part of the season compared with the slower growing period at the end of the season.

The right branching height (normally at 50 cm.) was achieved by $BA+GA_{4+7}$ treatment when the trees had reached 50 cm. At this time, there was still a further 6 weeks of rapid extension growth before it started to slow down (Figure 13). The induced lateral shoots

therefore had a period of 6 weeks of rapid extension growth thus ensuring a useful branch length. In contrast, branch induction caused by GA_{4+7} alone needed sequential treatment to induce an equivalent bud break response. However slower emergence of the induced lateral shoots, as the increased time necessary to apply the sequential sprays meant that they had only 2-3 more weeks of rapid extension growth before overall growth started to slow down. That is in practice, for the production of branched trees, one spray of BA+GA_{4+7} at the right concentration would be better than four sprays of GA_{4+7}.

The height of budding has been reported to have some effects on yield and tree vigor in some apple varieties on dwarfing rootstocks (Parry, 1986). In the U.K., in order to produce high quality maiden apple trees with many lateral shoots at a height where they can be retained as main production branches and obtain early cropping, Cox's Orange Pipin on MM106 apple trees are commonly budded as high as 60 cm. above ground level (Parry, 1986). Experiment 4.3.1 showed that in spur type 'Red Delicious' (Tas. Ag. no.5) on MM106, varying the height of budding did not affect lateral shoot production. However when higher budded trees did produce lateral shoots they were at a height suitable for retention as branches, whereas some of the branches from lower budding were too low to be useful. Thus the rootstock height effects are clearly physical and not physiological.

As tree growth was restricted by planting distance, in experiment 4.3.2, branching was limited. For the closer planting spaces, the growth restrictions could have occurred in both above and under ground parts of the trees. Above ground, closer planting spaces produced less leaf area and then less total growth, as shown in Figure 14 and Table 9. As the trees in the closer planting spaces competed for light, the resultant strong upright growth was expected. However both the

sequential and final leading shoot growth was similar in both wider or closer planting spaces as shown in Figure 13 and Table 14. Restriction of root space may have resulted in less growth, as a result of the lower rootstock volume available. This in turn would limit cytokinin production from these roots. Lower cytokinin production by the roots could lead to less induction of lateral shoots. It is however not possible to separate competition for root space and above ground competition for light and these factors could be operating alone or in competition.

Branch crotch angles

The branch crotch angle is the angle between the main trunk and the lateral shoot. This angle is important because the branches produced in the nursery or in the early stages of growth are the primary branches remaining as the scaffold limbs on the trees throughout the entire life of the tree. Narrow angles are subject to breakage, when the crop load is heavy, and also by winter injury (Verner, 1938).

The exogenous application of growth regulators and other treatments to induce lateral growth have direct effects on the branch crotch angle. For example, one of the mechanical treatments used to induce lateral shoot production was found to have direct effects on the crotch angle. That is the removal of the leading shoot tip induced lateral shoots immediately below the tip with very narrow crotch angles (see experiment 4.3.3). This agrees with the work of Werthiem (1978a.). It has also been found that sequential applications of GA_{4+7} alone (experiments 4.4.2, 4.4.3, and 4.6) or with BA (experiment 4.4.1) induced branches with very narrow final crotch angles.

The observed change in branch angle with time

(Experiment 4.6) has not been previously reported and it was assumed that branch angle was fixed at the time extension growth was initiated. While the experiments described do not give any indication of the physiology or mechanics of the change it is possible to speculate on possible processes.

The weak relationship between branch thickness and angle obtained in experiment 4.4.2 suggests a possible link between radial growth and branch angle. Radial growth of both the main stem and the side shoot will lead to an accumulation of tissue in the acute angle between leader and side shoot, thus forcing an increase in the angle if the junction remains plastic enough. It seems reasonable to suggest that this only occurs where growth is relatively slow. Strong growing side shoots would rapidly lose plasticity and little change would be expected in diameter.

The change in branch angle may be related to radial growth of the branch as it develops after extension growth is initiated.
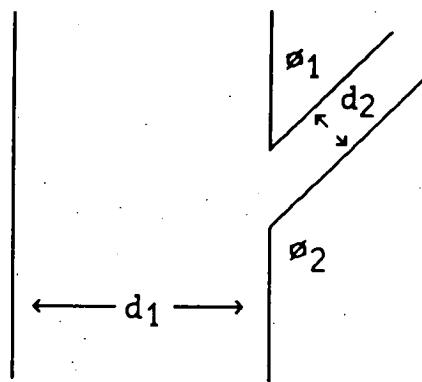
If branch diameter (d_2) does not change as main stem radial growth occurs (i.e. trunk diameter (d_1) increases) then branch angle would not be expected to change. If however both d_1 and d_2 change, then

the additional tissue formed in the acute angle ($\varnothing_1$) will tend to force the branch outward thus increasing $\varnothing_1$. Additional tissue formed in the obtuse angle ($\varnothing_2$) is unlikely to influence branch angle. Consequently while the branch/trunk junction remains moderately plastic changes in angle can be forced simply by radial growth of branch and trunk.

One-year-old trees

The lateral shoot induction properties of $BA+GA_{4+7}$ on one-year-old apple trees, was more marked and at lower concentrations than for nursery trees, in both cases without any suppressive effects on leading shoot growth. The lateral shoots induced in the one-year-old trees grew from buds of last season. In the nursery trees they grew from buds of the current season. The results of the experiment 4.5.1 show, that in one-year-old 'Red Delicious' apple trees, there is a negative correlation between the number of the induced lateral shoots and the length. The results suggest that, as the trees were transplanted the root system was damaged reducing the production of cytokinins and GAs, and the ability to supply nutrients and water to the top. When $BA+GA_{4+7}$ was applied to these trees, the already formed buds were induced to grow but with the amount of total growth was still being limited by the restricted supply of nutrients and water from the root.

Conclusion

Well branched nursery trees are considered to be of the required quality for new plantings. The correct choice of apple varieties and rootstocks should be the most convenient way of achieving this

quality as shown in experiments 4.2.1 and 4.2.2. However, scion/rootstock combinations which branch freely during the nursery stage may not always be suitable for the desired planting systems in terms of orchard productivity and management.

In Tasmania, Red Delicious is one of the most important fresh market varieties which have some spur type mutants. The spur types produce flower buds and few branches at a very early stage of growth. In order to exploit the early cropping potential of these trees, branches need to be induced on the trees at the nursery stage. Experiment 4.5.1 also shows that it is possible to induce branch growth by exogenous application of $BA+GA_{4+7}$ on one-year-old spur type 'Red Delicious' apple trees.

The quality of young trees includes good leading shoot growth and a sufficient number of wide angle, long branches to be retained at a useful height for future crop production.

Increase in the number of branches, as discussed above, has been achieved by applying plant growth regulators, but there are possibilities of a few undesirable side effects on the quality of the trees and/or the induced branches i.e., reduced leading shoot growth, narrower crotch angles, or shorter branches. The branch crotch angle is an important factor in quality as the effects of plant growth regulators demonstrated, but the relationship between growth and branch crotch angle is not clear and needs further study. Thus the right approach in using growth regulators is to select the appropriate type, concentration, timing of application and application technique for the chemical. It is important to use the one with the least undesirable side effects.

Long lateral shoots on a given scion/rootstock combination can be achieved in the nursery by planting them further

apart as shown in experiment 4.3.2. In most nursery practices, the use and productivity of the ground area in terms of number of trees grown per hectare should not be the only consideration at planting. If the spacing is too close it can have a negative effect on the quality of nursery trees. The use of some growth regulators to induce lateral shoots also adversely affected lateral shoot length as shown in experiments 4.5.1 and 4.5.2. There is an optimum number of shoots needed to produce a satisfactory tree. Increasing the branch number beyond this is wasteful as well as reducing the length of the useful branches. Reduction in the branch length can also delay the onset of cropping.

Integrated techniques have to be used to produce high quality trees from an early stage of growth, particularly in the nursery and the very early years in the orchard. Although successful apple crop production still requires good management before and during the productive period in the orchard, it is important to get the best foundation. As an ancient proverb says 'Well begun is half done'.

6. References

Abbas, M. F. (1978). Association between branching in maiden apple trees and levels of endogenous auxin. Acta Hort. 80: 59-62.

Abbott, D. L. (1970). The role of budscales in the morphogenesis and dormancy of the apple fruit bud. p.65-82. *In*: L. C. Luckwill and C. V. Cutting (eds.) Physiology of tree crops. Academic Press.

Anon. (1976). Technical information on M&B25,105 plant growth regulator. May and Baker Ltd. England. 16 pp.

Arney, S. E. and Mitchell, D. L. (1969). The effect of abscisic acid on stem elongation and correlative inhibition. New Phytol. 68: 1001-1015.

Avery, D. J. (1969). Comparisons of fruiting and deblossomed maiden apple trees, and of non-fruiting trees on a dwarfing and an invigorating rootstock. New Phytol. 68: 323-336.

Baldini, E., Sansavini, S. and Zocca, A. (1973). Induction of feathers by growth regulators on maiden trees of apple and pear. J. Hort. Sci. 48: 327-337.

Barlow, H. W. B. (1960). Root/shoot relationships in fruit trees. Scientia Hort. 14: 35-41.

Barlow, H. W. B. (1970). Some aspects of morphogenesis in fruit trees. p.25-43. *In*: Luckwill, L. C. and Cutting, C. V. (eds.) Physiology of tree crops. Academic Press.

Barritt, B. H. (1988). Influence of strain of 'Delicious' apple on root development of 1-year-old trees. HortSci. 23(2): 316-317.

Basak, A. and Soczek, Z. (1986). The influence of Promalin on one-year-old apple nursery trees. Acta Hort. 179: 279-280.

Baxter, P. (1981). Growing fruit in Australia. Thomas Nelson Australia. 200 pp.

Bearder, J. R. (1980). Plant hormones and other growth substances - their background, structures and occurrence. p.9-112. *In*: MacMillan, J. (ed.) Hormonal regulation of development I. Molecular aspects of plant hormones. Encyclopedia of plant physiology new series, vol. 9. Springer-Verlag.

Brenner, M. L., Wolley, D. J., Sjut, V., and Salerno, D. (1987). Analysis of apical dominance in relation to IAA transport. HortSci. 22(5): 833-835.

Brown, A. G. (1975). Apple. p.3-37. *In*: Janick, J. and Moore, J. N. (eds.). Advances in fruit breeding. Purdue University Press.

Bukovac, M. J. (1973). Foliar penetration of plant growth substances with special reference to tree fruits. Acta Hort. 34: 69-78.

Bukovac, M. J. (1981). Interrelationships between vegetative and reproductive development of fruit trees. p.78-89. *In*: Tukey, R. B. and Williams, M. W. (eds.) Tree fruit growth regulators and chemical thinning, the proceedings of 1981 Pacific northwest tree fruit short course. Washington State University.

Capelle, S. C., Mok, D. W. S., Kirchner, S. C. and Mok, M. C. (1983). Effects of thidiazuron on cytokinin autonomy and the metabolism of N^6-(Δ^2-isopentenyl)[8-^{14}C] adenosine in callus tissues of *Phaseolus lunatus* L. Plant Physiol. 73: 796-802.

Chrispeels, M. J. and Verner, J. E. (1967). Gibberellic acid enhanced synthesis and release of amylase and ribonuclease by isolated barley aleurone layers. Plant Physiol. 42: 398-406.

Cody, C. A., Larsen, F. E. and Fritts, R. (1985). Stimulation of lateral branch development in tree fruit nursery stock with GA_{4+7} + BA. HortSci. 20(4): 758-759.

Crabbé, J. J. (1984). Morphogenetical ways towards vigor restriction in spontaneous and man-made dwarf trees. Acta Hort. 146: 113-120.

Crozier, A. and Reid, D. M. (1971). Do roots synthesize gibberellins? Can. J. Bot. 49: 967-975.

Digby, J. and Wareing, P. F. (1966). The effect of applied growth hormones on cambial division and the differentiation of cambial derivatives. Ann. Bot. 30: 539-548.

Duckworth, S. J., Abbas, M. F. and Quinlan, J. D. (1979). Influence of endogenous growth regulators on branching. Rep. E. Malling Res. Stn. for 1978. p.39.

Edgerton, L. J. (1983). Effects of some growth regulators on branching and flowering of young apple trees. Acta Hort. 137: 87-94.

Elfving, D. C. (1984). Factors affecting apple-tree response to chemical branch-induction treatments. J. Amer. Soc. Hort. Sci. 109(4): 476-481.

Elfving, D. C. (1985). Comparison of cytokinin and apical-dominance-inhibiting growth regulators for lateral-branch induction in nursery and orchard apple trees. J. Hort. Sci. 60(4): 447-454.

Evans, M. L. (1984). Functions of hormones at the cellular level of organization. p.23-79. *In*: Scott, T. K. (ed.) Hormonal regulation of development II. The functions of hormones from the level of the cell to the whole plant. Encyclopedia of plant physiology new series, vol. 10. Springer-Verlag.

Faust, M. and Zagaja, S. W. (1984). Prospects for developing low vigor fruit tree cultivars. Acta Hort. 146: 21-27.

Fellman, C. D., Read, P. E. and Hosier, M. A. (1987). Effects of thidiazuron and CPPU on meristem formation and shoot proliferation. HortSci. 22(6): 1197-1200.

Ferree, D. C. (1976). Effect of rootstocks, propagation method, and transplanting on growth and flowering of young apple trees. J. Amer. Soc. Hort. Sci. 101(6): 676-678.

Ferree, D. C. (1981). Physiological aspects of pruning and training. p.90-104. *In*: Tukey, R. B. and Williams, M. W. (eds.) Tree fruit growth regulators and chemical thinning, the proceedings of 1981 Pacific northwest tree fruit short course. Washington State University.

Ferree, D. C., Schmid, J. C. and Morris, C. A. (1982). An evaluation over 16 years of Delicious strains and other cultivars on several rootstocks and hardy interstems. Fruit Variety Journal. 36(2): 37-45.

Ferree, D. C. (1988). Role of rootstocks and spur-type scions for controlling vegetative growth of apple and peach trees. HortSci. 23(3): 464-467.

Filipovich, S. D. (1976). Increasing the crotch angle of young apple trees by using growth hormones or plastic discs. Aust. J. of Exp. Agric. and Ani. Husb. 16: 286-288.

Fisher, D. V. and Ketchie, D. O. (1981). Survey of literature on red strains of 'Delicious'. Washington State University., College of Agriculture Research Center. Bull. no. 0898, 17 pp.

Forshey, C. G. (1977). Chemical training of young apple trees. Proc. N. Y. State Hort. Soc. 122: 157-159.

Fulford, R. M. (1966). The morphogenesis of apple buds. IV. The effect of fruit. Ann. Bot. 30: 597-606.

Goldsmith, M. H. M. (1977). The polar transport of auxin. Ann. Rev. Plant Physiol. 28: 439-478.

Greene, D. W. (1981). Growth regulator application and cultural techniques to promote early fruiting of apples. p.117-146. *In*: Tukey, R. B. and Williams, M. W. (eds.) Tree fruit growth regulators and chemical thinning, the proceedings of 1981 Pacific northwest tree fruit short course. Washington State University.

Greene, D. W. and Miller, P. (1988). Effects of growth regulator sprays and notching on growth and branching of 'Starkrimson Delicious' apple trees. J. Amer. Soc. Hort. Sci. 113(1): 18-23.

Grochowska, M. J., Buta G. J., Steffens, G. L. and Faust, M. (1984). Endogenous auxin and gibberellin levels in low and high vigor apple seedlings. Acta Hort. 146: 125-134.

Hall, R. H. (1973). Cytokinins as a probe of developmental processes. Ann. Rev. Plant Physiol. 24: 415-444.

Hall, W. C. (1952). Evidence on the auxin-ethylene balance hypothesis of foliar abscission. Bot. Gaz. 113: 310-322.

Harrison, M. A. and Kaufman, P. B. (1984). The role of hormone transport and metabolism in apical dominance in oats. Bot. Gaz. 145: 239-297.

Hartmann, H. T. and Kester, D. E. (1983). Plant propagation principles and practices. 4th ed. Prentice-Hall, Inc. 727 pp.

Head, G. C. (1966). Estimating seasonal changes in the quantity of white unsuberized root on fruit trees. J. Hort. Sci. 41: 197-206.

Head, G. C. (1969). The effects of fruiting and defoliation on seasonal trends in new root production on apple trees. J. Hort. Sci. 44: 175-181.

Howard, B. H., Skene, D. S. and Coles J. S. (1974). The effects of different grafting methods upon the development of one-year-old nursery apple trees. J. Hort. Sci. 49: 287-295.

Ibrahim, I. M. and Dana, M. N. (1971). Gibberellin-like activity in apple rootstocks. HortSci. 6(6): 541-542.

Jackson, J. E. (1970). Aspects of light climate within apple orchards. J. Appl. Ecol. 7: 207-216.

Jackson, J. E. (1981). Pomology. Ann. Rep. E. Malling Res. Stn. for 1980. p. 25-42.

Jackson, J. E., Harrison-Murray, R. S. and Hicks, S. (1984). Reducing staking costs and improving tree establishment. Rept. E. Malling Res. Stn. for 1983. p.31-32.

Jacobs, W. P. (1984). Functions of hormones at tissue level of organization. p.149-171.In: Scott, T. K. (ed.) Hormonal regulation of development II. The functions of hormones from the level of the cell to the whole plant. Encyclopedia of plant physiology new series, vol. 10. Springer-Verlag.

Jankiewicz, L. S. (1970). Mechanism of crotch angle formation in apple trees. II. Studies on the role of auxin. Acta Agrobot. 23: 171-181.

Jankiewicz, L. S., Plich, H., Borkowska, B. and Moraszczyk, A. (1973). Growth correlations and the shape of young trees and shrubs. Acta Hort. 34: 107-116.

Jarassamrit, N. (1989). Branch induction of spur type Red Delicious apple nursery trees. Acta Hort. 240: 155-158.

Johann, G. (1983). Effect of growth regulators on branching habit of some apple cultivars in the nursery. Acta Hort. 137: 77-82.

Jones, O. P. (1973). Effects of cytokinins in xylem sap from apple trees on apple shoot growth. J. Hort. Sci. 48: 181-188.

Jones, O. P. (1984). Mode-of-action of rootstock/scion interactions in apple and cherry trees. Acta Hort. 146: 175-182.

Jones, O. P. (1986). Endogenous growth regulators and rootstock/scion interactions in apple and cherry trees. Acta Hort. 179: 177-184.

Jones, O. P. and Lacey, H. J. (1968). Gibberellin-like substances in the transpiration stream of apple and pear trees. J. Exp. Bot. 19(60): 526-531.

Jones, R. L. (1973). Gibberellins: Their physiological role. Ann. Rev. Plant Physiol. 24: 571-598.

Jotic, P. (1985). Modern apple orchards planning, design and development. Tasmanian Dept. of Agric., Fruit and Ornamental Branch Bulletin. 12 pp.

Kender, W. J. and Carpenter, S. (1972). Stimulation of lateral bud growth of apple trees by 6-benzylamino purine. J. Amer. Soc. Hort. Sci. 97(3): 377-380.

Kerns, H. R. and Meyer, M. M. (1986). Tissue culture propagation of *Acer* x *freemanii* using thidiazuron to stimulate shoot tip proliferation. HortSci. 21(5): 1209-1210.

Kim, Y., Howard, B. H. and Quinlan, J. D. (1984). Growth responses to different grafting and manipulating treatments in one-year-old fruit trees. J. Hort. Sci. 59(1): 23-33.

Knox, J. P. and Wareing, P. F. (1984). Apical dominance in *Phaseolus vulgaris* L. : The possible roles of abscisic and indole-3-acetic acid. J. Exp. Bot. 35(151): 239-244.

Koen, T. B., Jones, K. M. and Oakford, M. Promoting branching in Red Delicious trees using growth regulators. (in press).

Kohstall, H. and Schmähling, P. (1985). Effect of planting distances on the quality of budded maiden apple trees. *Baumschulpraxis*. 15(3): 106-109. (Hort. Abstr. 55:4116).

Kviklis, A. M. (1986). Rationalization of budding methods. *Sadovodstvo* 3: 13-15 (Hort. Abstr. 56: 8511.).

Lapins, K. O. (1976). Inheritance of compact growth type in apple. J. Amer. Soc. Hort. Sci. 101(2): 133-135.

Leopold, A. C. and Kriedemann, P. E. (1975). Plant growth and development. 2nd ed. McGraw-Hill, Inc. 545 pp.

Leopold, A. C. and Noodén, L. D. (1984). Hormonal regulatory systems in plants. p.4-22. *In*: Scott, T. K. (ed.) Hormonal regulation of development II. The functions of hormones from the level of the cell to the whole plant. Encyclopedia of plant physiology new series, vol. 10. Springer-Verlag.

Lever, B. G., Shearing, S. J. and Batch, J. J. (1982). PP333 - a new broad spectrum growth retardant. Proceedings 1982 British Crop Protection Conference - Weeds. 1: 3-10.

Lockard, R. G. and Schneider, G. W. (1981). Stock and scion growth relationships and the dwarfing mechanism in apple. Hort. Rev. 3: 315-375.

Looney, N. E. and Lane, W. D. (1984). Spur-type growth mutants of McIntosh apple: A review of their genetics, physiology and field performance. Acta Hort. 146: 31-46.

Looney, N. E., Taylor, J. S. and Pharis, R. P. (1988). Relationship of endogenous gibberellin and cytokinin levels in shoot tips to apical form in four strains of 'McIntosh' apple. J. Amer. Soc. Hort. Sci. 113(3): 395-398.

Luckwill, L. C. (1968). The effect of certain growth regulators on growth and apical dominance of young apple trees. J. Hort. Sci. 43: 91-101.

Luckwill, L. C. (1970). The control of growth and fruitfulness of apple trees. p.237-254. *In*: Luckwill, L. C. and Cutting, C. V. (eds.) Physiology of tree crops. Academic Press.

Luckwill, L. C. (1972). Growth regulators - their potential and limitations. Scientific Hort. 24: 153-157.

Marth, P. C., Audia, W. V., and Mitchell, J. W. (1956). Effects of gibberellic acid on growth and development of plants of various genera and species. Bot. Gaz. 118: 106-111.

Martin, G. C. (1987). Apical dominance. HortSci. 22(5): 824-833.

Matthysse, A. C. and Scott, T. K. (1984). Functions of hormones at the whole plant level of organization. p.219-243. *In*: Scott, T. K. (ed.) Hormonal regulation of development II. The functions of hormones from the level of the cell to the whole plant. Encyclopedia of plant physiology new series, vol. 10. Springer-Verlag.

McCullagh, P. and Nelder, J. A. (1983). Generalized linear models. Chapman and Hall, London. 261 pp.

Miller, S. S. (1985). Low-volume sprays of BA and Promalin increase branching in apple trees. HortSci. 20(4): 730-732.

Miller, S. S. and Eldridge, B. J. (1986). Use of 6-benzylamino purine and Promalin for improved canopy development in selected apple cultivars. Scientia Hort. 28: 355-368.

Mok, M. C., Mok, D. W. S., Armstrong, D. J., Shudo, K., Isogai, Y. and Okamoto, T. (1982). Cytokinin activity of N-phenyl-N'-1,2,3-thiadiazol-5-yl urea (thidiazuron). Phytochemistry 21(7): 1509-1511.

Mosse, B. and Labern, M. V. (1960). The structure and development of vascular nodules in apple bud-unions. Ann. Bot. 24(96): 500-509.

Mullins, M. G. (1965). The gravitational response of young apple trees. J. Hort. Sci. 40: 237-247.

Mullins, M. G. (1967). Gravity and the apple tree. J. Aust. Inst. Agric. Sci. p.167-171.

Naylor, A. W. (1984). Functions of hormones at the organ level of organization. p.172-218. *In*: Scott, T. K. (ed.) Hormonal regulation of development II. The functions of hormones from the level of the cell to the whole plant. Encyclopedia of plant physiology new series, vol. 10. Springer-Verlag.

Newman, I. A. (1970). Auxin transport in *Avena* I. Indoleacetic acid-^{14}C distributions and speeds. Plant Physiol. 46: 263-272.

Nickell, L. G. (1983). Plant growth regulating chemicals vol. I. CRC Press Inc. 280 pp.

Ogata, R., Kikuchi, H., Hatayama, T. and Komatsu, H. (1986). Growth and productivity of vigorous 'Fuji' apple trees on M.26 as affected by summer pruning. Acta Hort. 160: 157-165.

Parry, M. S. (1986). The effects of budding height on field performance of two apple cultivars on three rootstocks. J. Hort. Sci. 61(1): 1-7.

Patrick, J. W. and Wareing, P. F. (1972). Experiments on the mechanism of hormone-directed transport. p.695-700. *In*: Carr, D. J. (ed.) Plant growth substances 1970. Springer-Verlag.

Phillips, I. D. J. (1975). Apical dominance. Ann. Rev. Plant Physiol. 26: 341-367.

Poovaiah, B. W. (1981). The role of naturally occurring plant hormones in the growth and development of tree fruit crops. p.63-77. *In*: Tukey, R. B. and Williams, M. W. (eds.) Tree fruit growth regulators and chemical thinning, the proceedings of 1981 Pacific northwest tree fruit short course. Washington State University.

Popenoe, J. and Barritt, B. H. (1988). Branch induction by growth regulators and leaf removal in 'Delicious' apple nursery stock. HortSci. 23(5): 859-862.

Powell, L. E. (1973). Naturally occurring plant growth regulators and their physiological roles in fruit trees. Acta Hort. 34: 33-40.

Preston, A. P. (1967). Apple rootstock studies: Fifteen years' results with some M.IX crosses. J. Hort. Sci. 42: 41-50.

Preston, A. P. (1968). Pruning and rootstock as factors in the production of primary branches on apple trees. J. Hort. Sci. 43: 17-22.

Quinlan, J. D. (1978). Chemical induction of lateral branches (feathers). Acta Hort. 65: 129-138.

Quinlan, J. D. (1980). Recent developments in the chemical control of tree growth. Acta Hort. 114: 144-151.

Quinlan, J. D. (1981). New chemical approaches to the control of fruit tree form and size. Acta Hort. 120: 95-105.

Quinlan, J. D. and Preston, A. P. (1978). The use of branching agents to replace hand pruning of young trees of Bramley's Seedling apple. J. Hort. Sci. 53: 39-43.

Raese, J. T. and Looney, N. E. (1981). Other growth regulators uses on apple and pear. p.192-212. *In*: Tukey, R. B. and Williams, M. W. (eds.) Tree fruit growth regulators and chemical thinning, the proceedings of 1981 Pacific northwest tree fruit short course. Washington State University.

Ramirez, H., Rumayor, A. and Martinez, V. (1983). Induction of feathers by growth substances in nursery apple trees. Acta Hort. 137: 83-85.

Richardson, P. J. and Quinlan, J. D. (1986). Uptake and translocation of paclobutrazol by shoots of M26 apple rootstock. Plant Growth Regulation 4: 347-356.

Robinson, J. B. D. (1975). The influence of some growth-regulating compounds on the uptake, translocation and concentration of mineral nutrients in plants. Hort. Abstr. 45(10): 611-618.

Rogers, W. S. and Beakbane, A. B. (1957). Stock and scion relations. Ann. Rev. Plant Physiol. 8: 217-236.

Rogers, W. S. and Parry, M. S. (1968). Effects of deep planting on anchorage and performance of apple trees. J. Hort. Sci. 43: 103-106.

Rom, R. C. and Motichek, G. R. (1987). Cultivar effect on adventitious root development of clonal apple rootstocks. HortSci. 22(1): 57-58.

Rubinstein, B. and Nagao, M. A. (1976). Lateral bud outgrowth and its control by the apex. Bot. Rev. 42(1): 83-113.

Sachs, R. M. and Lang, A. (1961). Shoot histogenesis and the subapical meristem: the action of gibberellic acid, Amo-1618, and maleic hydrazide. p.567-578. *In*: Plant growth regulation. Iowa State University Press.

Sachs, T. and Thimann, K. V. (1964). Release of lateral buds from apical dominance. Nature. 201: 939-940.

Salisbury, F. B. and Ross, C. W. (1985). Plant physiology. 3rd ed. Wadsworth Publishing Company Inc. USA. 540 pp.

Saure, M. C. (1985). Dormancy release in deciduous fruit trees. Hort. Rev. 7: 239-300.

Seeley, E. J. and Tukey, R. B. (1981). Plant growth regulators and fruit tree physiology. p.46-62. *In*: Tukey, R. B. and Williams, M. W. (eds.) Tree fruit growth regulators and chemical thinning, the proceedings of 1981 Pacific northwest tree fruit short course. Washington State University.

Sembdner, G., Gross, D., Liebisch, H. W. and Schneider, G. (1980). Biosynthesis and metabolism of plant hormones. p.281-444. *In*: MacMillan, J. (ed.) Hormonal regulation of development I. Molecular aspects of plant hormones. Encyclopedia of plant physiology new series, vol. 9. Springer-Verlag.

Sheldrake, A. R. and Northcote, D. H. (1968). The production of auxin by tobacco internode tissues. New Phytol. 67: 1-13.

Simons, R. K. (1986). Graft-union characteristics as related to dwarfing in apple (*Malus domestica* Borkh.). Acta Hort. 160: 57-66.

Simons, R. K. and Chu, M. C. (1983). Growth characteristics of apple graft unions of stock/scion combinations in relation to dwarfing. Acta Hort. 140: 79-86.

Simons, R. K. and Chu, M. C. (1984). Tissue development within the graft union as related to dwarfing in apple. Acta Hort. 146: 203-210.

Simons, R. K. and Chu, M. C. (1985). Graft union characteristics of M.26 apple rootstock combined with 'Red Delicious' strains-morphological and anatomical development. Scientia Hort. 25: 49-59.

Sistrunk, W. A. and Moore, J. N. (1983). Quality. p.274-293. *In*: Moore, J. N. and Janick, J. (eds.) Methods in fruit breeding. Purdue University Press.

Smith, N. G. and Rogers, W. S. (1961). Higher budding of apple rootstocks. Rep. E. Malling Res. Stn. for 1960. p. 49-51.

Stebbins, R. L. (1980). Training and pruning apple and pear trees. Nortwest Ext. Pub. no.156. 18pp.

Steel, R. G. D. and Torrie, J. H. (1981). Principles and procedures of statistics a biometrical approach. 2nd ed. McGraw-Hill Inc. 633 pp.

Stoddart, J. L. and Venis, M. A. (1980). Molecular and subcellular aspects of hormone action. p.445-510. *In*: MacMillan, J. (ed.) Hormonal regulation of development I. Molecular aspects of plant hormones. Encyclopedia of plant physiology new series, vol. 9. Springer-Verlag.

Strydom, D. K. and Honeyborne, G. E. (1980). Chemically induced feathers on nursery, topworked and maiden apple and pear trees. The Deciduous Fruit Grower. p. 412-420.

Taylor, J. K. and Stephens, C. G. (1935). The apple growing soils in Tasmania. Part 2 - A soil survey of part of Huonville district. C.S.I.R.O. Bull. no. 92, 32 pp.

Temple-Smith, M. G. (1984). Nutritional status of Tasmanian Red Delicious orchards. Liaison note supplement edition no. 31. Tasmanian Department of Agriculture, Soil and Chemistry section. 4 pp.

Teskey, B. J. E. and Shoemaker, J. S. (1972). Tree fruit production. 2nd ed. The AVI Publishing Co., Inc. 336 pp.

Theron, K. I., Jacobs, G., and Strydom, D. K. (1987). Correlative inhibition of axillary buds in apple nursery trees in relation to node position, defoliation, and Promalin application. J. Amer. Soc. Hort. Sci. 112(5): 732-734.

Tromp, J. (1976). Flower-bud formation and shoot growth in apple as affected by temperature. Scientia Hort. 5: 331-338.

Tromp, J. (1987). Growth and flower-bud formation in apple as affected by paclobutrazol, daminozide, and tree orientation in combination with various gibberellins. J. Hort. Sci. 62(4): 433-440.

Tubbs, F. R. (1973). Research fields in the interaction of rootstocks and scions in woody perennials - part 1. Hort. Abstr. 43(5): 247-253.

Tubbs, F. R. (1973). Research fields in the interaction of rootstocks and scions in woody perennials - part 2. Hort. Abstr. 43(6): 325-335.

Tubbs, F. R. (1980). Growth relations of rootstock and scion in apples. J. Hort. Sci. 55(2): 181-189.

Tucker, D. J. and Mansfield, T. A. (1973). Apical dominance in *Xanthium strumarium* a discussion in relation to current hypothesis of correlative inhibition. J. Exp. Bot. 24(81): 731-740.

Tukey, H. B. (1964). Dwarfed fruit trees. Cornell University Press. 562 pp.

Tukey, L. D. (1981). Growth and development in tree fruits. p.1-45. *In*: Tukey, R. B. and Williams, M. W. (eds.) Tree fruit growth regulators and chemical thinning, the proceedings of 1981 Pacific northwest tree fruit short course. Washington State University.

Unrath, C. R. and Shaltout, A. D. (1985). Branch induction on young 'Delicious' apple trees by application of growth regulators. HortSci. 20(2): 230-231.

Van Nieuwkerk, J. P., Zimmerman R. H. and Fordham, I. (1986). Thidiazuron stimulation of apple shoot proliferation in vitro. HortSci. 21(3): 516-518.

Van Oosten, H. J. (1978). Effect of initial tree quality on yield. Acta Hort. 65: 123-127.

Van Oosten, H. J. (1986). Effects of some new rootstocks on orchard behaviour of apple trees. Acta Hort. 160: 39-46.

Verner, L. (1938). The effect of a plant growth substance on crotch angles in young apple trees. Proc. Amer. Soc. Hort. Sci. 36: 415-422.

Verner, L. (1955). Hormone relations in the growth and training of apple trees. Ida. Agric. Exp. Sta. Res. Bul. 28; 31pp.

Vyvyan, M. C. (1955). Interrelation of scion and rootstock in fruit trees: I. Weights and relative weights of young trees formed by the reciprocal unions as scion and rootstock, of three apple rootstock varieties: M.IX, M.IV, and M.XII. Ann. Bot. 19: 401-423.

Vyvyan, M. C. (1957). An analysis of growth and of form in young apple trees: I. Relative growth and net assimilation rates in 1- and 2-year-old trees of apple rootstock-variety M.XIII. Ann. Bot. 21(83): 479-497.

Walsh, C. S. (1979). The effects of node position, shoot vigor, and strain on 'Delicious' apple spur development. J. Amer. Soc. Hort. Sci. 104(6): 825-828.

Walsh, C. S. and Miller, A. N. (1984). Observations of the growth and vigor of spur and non-spur-type apple trees. Acta Hort. 146: 211-214b.

Walton, D. C. (1980). Biochemistry and physiology of abscisic acid. Ann. Rev. Plant Physiol. 31: 453-489.

Wang, S. Y., Steffens, G. L. and Faust, M. (1986). Breaking bud dormancy in apple with a plant bioregulator, thidiazuron. Phytochemistry 25(2): 311-317.

Wang, S. Y. and Faust, M. (1987). The relationship of internode length to carbohydrate content in genetic dwarf apple trees. Scientia Hort. 33: 197-203.

Wang, S. Y., Sun, T., Ji, Z. L. and Faust, M. (1987a.). Effect of paclobutrazol on water stress-induced abscisic acid, in apple seedling leaves. Plant Physiol. 84: 1051-1054.

Wang, S. Y., Ji, Z. L., Sun, T. and Faust, M. (1987b.). Effect of thidiazuron on abscisic acid content in apple bud relative to dormancy. Physiol. Plant. 71: 105-109.

Wareing, P. F., Hanney, C. E. A. and Digby, J. (1964). The role of endogenous hormones in cambial activity and xylem differentiation. p.323-334. *In*: Zimmermann, M. H. (ed.) The formation of wood in forest trees. Academic Press.

Wareing, P. F. (1970). Growth and its co-ordination in trees. p.1-21. *In*: Luckwill, L. C. and Cutting, C. V. (eds.). Physiology of tree crops. Academic Press.

Wareing, P. F. and Phillips, I. D. J. (1981). Growth and differentiation in plants. 3rd ed. Pergamon Press. 343 pp.

Weaver, R. J. (1972). Plant growth substances in agriculture. W. H. Freeman and Company. 428 pp.

Went, F. W. (1928). Wuchsstoff und Wachstum. Recl. Trav. Bot. Neerl. 25: 1-116.

Wertheim, S. J. (1978a.). Induction of side-shoot formation in the fruit-tree nursery. Acta Hort. 80: 49-54.

Wertheim, S. J. (1978b.). Manual and chemical induction of side-shoot formation in apple trees in the nursery. Scientia Hort. 9: 337-345.

Wertheim, S. J. (1987). The branching promoters Promalin and M&B25,105. The results of trials in 1983-1985. *Fruitteelt* (1986) 76(22): 665-667 (Hort. Abstr. 57: 3152.)

Westwood, M. N. and Zielinski, Q. B. (1966). Comparative growth habit and leaf composition of a compact mutant and standard Delicious apple. Proc. Amer. Soc. Hort. Sci. 88: 9-13.

Westwood, M. N. (1978). Temperate-zone pomology. W. H. Freeman and Company. 428 pp.

Williams, M. W. and Billingsley, H. D. (1970). Increasing the number and crotch angles of primary branches of apple trees with cytokinins and gibberellic acid. J. Amer. Soc. Hort. Sci. 95(5): 649-651.

Williams, M. W. and Stahly, E. A. (1968). Effect of cytokinins on apple shoot development from axillary buds. HortScience. 3: 68-69.

Woolley, D. J. and Wareing, P. F. (1972a.). The interaction between growth promoters in apical dominance. I. Hormonal interaction, movement, and metabolism of a cytokinin in rootless cuttings. New Phytol. 71: 781-793.

Woolley, D. J. and Wareing, P. F. (1972b.). The interaction between growth promoters in apical dominance. II. Environmental effects on endogenous cytokinin and gibberellin levels in *Solanum andigena* New Phytol. 71: 1015-1025.

Woolley, D. J. and Wareing, P. F. (1972c.). The role of roots, cytokinins and apical dominance in the control of lateral shoot form in *Solanum andigena*. Planta (Berl.) 105: 33-42.

Young, E. (1989). Cytokinin and soluble carbohydrate concentrations in xylem sap of apple during dormancy and budbreak. J. Amer. Soc. Hort. Sci. 114(2): 297-300.

Young, E. and Werner, D. J. (1986) 6-BA applied after shoot and/or root chilling and its effect on growth resumption in apple and peach. HortSci. 21(2): 280-281.

Zagaja, S. W. and Faust, M. (1983). Population analysis of vigor and growth pattern of apple seedlings with short internode parentage. J. Amer. Soc. Hort. Sci. 108(6): 939-944.

Zajaczkowski, S., Wodzicki, T. J. and Romberger, J. A. (1984). Auxin waves and plant morphogenesis. p.244-262. *In*: Scott, T. K. (ed.) Hormonal regulation of development II. The functions of hormones from the level of the cell to the whole plant. Encyclopedia of plant physiology new series, vol. 10. Springer-Verlag.

Zeroni, M. and Hall, M. A. (1980). Molecular effects of hormone treatment on tissue. p.511-586. *In*: MacMillan, J. (ed.) Hormonal regulation of development I. Molecular aspects of plant hormones. Encyclopedia of plant physiology new series, vol. 9. Springer-Verlag.