STUDIES ON VEGETATION AND INSECT PREDATION

OF EUCALYPTS IN FOREST AND WOODLAND

AT RIDGEWAY, TASMANIA

by

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DECLARATION

Except as stated herein 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, this thesis contains no copy or paraphrase of material
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ABSTRACT

Studies on vegetation and insect predation were conducted during
the period 1982-84 at the Ridgeway Park Reserve, Tasmania. The vege-
tation of the area is eucalypt forest and woodland which varies in
composition, dominance and structure. Soil type, topography, the level
of grazing and incidence of fire also vary within the study area.

The influence of soil type on moisture availability was investigated
by comparing the vegetation on sites receiving the same incident solar
radiation. The majority of species experience a shift in distribution
over the three soil types such that with increasing radiation the species
reach their peak frequency first on the brown earth, then on the podzolic
soil and finally on the podsol. This pattern conformed to a model of
moisture availability devised for the three soils. Species that did not
conform to the model were either particularly vulnerable to the effects
of grazing or fire, opportunists or restricted to one or other of the
three soil types and hence a particular set of soil nutrient conditions.

The effects of insect grazing on sapling eucalypts on north and
south-facing slopes, which differed in geology, were assessed by monthly
monitoring of insect damage and by deterring insects from grazing certain
trees through the use of insecticide. On every tree percentage damage,
and the amount of different types of damage, leaf loss, mean shoot length,
the number of leaves per shoot and the percentage of damaged leaves,
were measured on the current season's shoots. A limited sample of the
same data was collected on leaves approximately one year old.

Overall, there were few significant differences in the level of
these variables between the different species and sites. Percentage
damage figures were comparatively low (7-12%) and there was no significant
difference between the species. However, damage was significantly higher
in the most mesic, least fertile site. Percentage damage, and leaf and
shoot loss were combined to derive a figure for the total damage to each
species (29-41%). This was significantly higher in *E. obliqua* compared

with the other species.

The patterns of insect defoliation may have been considerably
altered as a result of a drought experienced during the course of the
study. Insect activities may effect forest community composition, but
only as part of a web of inter-relationships whose effects vary, between
the species, in space and time.

ACKNOWLEDGEMENTS

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GLOSSARY OF TERMS

D	Dolerite bedrock
M	Mudstone bedrock
S	Sandstone bedrock
G_1 species	Those species with a % frequency of more than 10.0 in all three radiation periods
G_2 species	Those species with a % frequency of less than 10.0 in all three radiation periods
CPN	North-facing slope on Chimney Pot Hill
CPS	South-facing slope on Chimney Pot Hill
RWN	North-facing slope on Ridgeway
RWS	South-facing slope on Ridgeway
Actual Damage	Damage caused by insects
Hidden Damage	Missing leaves and shoots, that may or may not be of insect origin
Total Damage	Actual plus hidden damage
General Analysis	– Between-species analysis: comparison of one species with another over all the sites on which they jointly occur
	– Between-site analysis: comparison of all the species on one site with all the species on another
Species-site Analysis	– comparisons between species occurring on one site, and within one species occurring on different sites

Insect grazing on the leaves of
Eucalyptus viminalis

CHAPTER 1   INTRODUCTION

The structure, composition and distribution of forest communities in Australia have been shown to be controlled by a myriad of factors, including soil moisture availability (Walter 1973; Florence 1964), soil nutrient status (Moore 1959; Beadle 1962, 1966), disturbances such as fire (Mount 1964; Jackson 1968) and biotic factors such as grazing (Harper 1977; Springett 1978), inter and intra-specific competition and the origin of the seed pool. Due to the interactive nature of these factors, it is difficult to determine the extent to which each controls forest community patterns. The aim of this thesis was to isolate and investigate, as far as possible, three of these factors (soil moisture availability, soil nutrient status and insect grazing) in order to determine their individual influence on the vegetation patterns in the dry sclerophyll forests of south-east Tasmania.

There has been some debate in Australian literature as to whether the influence of soil moisture availability on forest community patterns is greater than the influence of soil nutrient status and vice versa (Florence 1968; Webb 1969). In Tasmania, both soil moisture availability and soil nutrient status have been shown to be important determinants of the vegetation patterns (Hogg and Kirkpatrick 1974). However, to date there has not been a comprehensive study to isolate and therefore establish the extent of their individual influences.

In order that the influence of soil moisture availability and soil nutrient status be effectively disentangled and the mechanism by which they control forest communities clearly understood, it was necessary that they be studied in such a way that one was subject to variation, independent of the other and then vice versa. This was accomplished by comparing the distribution of species over slopes differing in geology, pedology and aspect.

Some researchers have found the level of grazing in eucalypt forests to be very high (Burdon and Chilvers 1974b; Journet 1981) and on occasions this has led to tree death (Mazanec 1966). A series of experimental studies showed that repeated heavy defoliation could affect, amongst other things, tree height, radial growth and the ability of the tree to withstand future attacks (Greaves 1966; Readshaw and Mazanec 1969). As a consequence of these studies a number of hypotheses were developed to explain the possible regulating or control-ling effects of insects on forest community patterns (Chilvers and Brittain 1972; Burdon and Chilvers 1974; Mattson and Addy 1975; Springett 1978). However, more recent work has indicated that due to the concentration of the majority of research to forests in which insect defoliation is abnormally high, the extent of grazing and hence the influence of insects may have been overestimated (Ohmart, Stewart and Thomas 1983 a,b).

There is scanty information regarding the levels of insect defoliation in the dry sclerophyll forests of south-east Tasmania and much that is available has tended to concentrate on the outcome of atypical insect outbreaks (Greaves 1966; Kile 1974). Therefore, before the effects of insects on forest communities could be considered, it was necessary to undertake a comprehensive survey of the amount and types of defoliation among the different species of *Eucalyptus* in time and space.

Although many studies have sought to determine the level of grazing and its subsequent impact on forest communities, there have been few attempts to predict how insect activity may vary in space and time. Another purpose of this research then, was to detect and establish the nature of the relationship between the environmental gradients which control not only insect grazing but also soil moisture availability and soil nutrient status. By knowing how these gradients themselves change in space and time then subsequent changes in the individual or collective influence of soil moisture availability, soil nutrient status and insect grazing may also be predicted.

The manner in which incident radiation controls soil moisture availability and hence species distribution patterns has been well documented in Australia (Kirkpatrick and Nunez 1980: Harris and Kirkpatrick 1982). How the subtle differences between soil types modify the pattern of available soil moisture determined primarily by the level of solar radiation, is less well understood in the dry sclerophyll forests of south-east Tasmania.

Very little is known of how insects react to topographically-induced variations in solar radiation receipt or to the collective or individual influences of the many environmental gradients that may occur in the forest (i.e. humidity, wind speed and subtle changes in foliar nitrogen or allelochemic content as caused by changes in the amount of available moisture). By examining the defoliation levels of trees on slopes varying in microclimate, soil type and geology it was hoped to gain some useful information regarding the nature of the environmental gradients controlling insect grazing.

The thesis is divided into four chapters. The remainder of this chapter reviews the literature on the manner in which topography (aspect) influences the receipt of solar radiation and the general effect of this interaction on soil moisture, and vegetation and insect community patterns.

Chapter two examines; (1) the way in which soil moisture availability and soil nutrient status influences the composition, distribution and structure of plant communities in relation to changes in incident radiation over north and south-facing slopes and (2) how the inherent characteristics of the different soils may modify forest community patterns still further.

Chapter three investigates;(1) the levels of grazing by insects among different eucalypt species, (2) the effect of insects on forest community patterns, and (3) the influence of various environmental gradients on the amount and type of grazing.

Chapter four discusses the extent of the influence of soil
moisture availability, soil nutrient status and insect grazing on
forest community patterns and how these influences may change in time
and space.

1.1   THE EFFECT OF ASPECT

The effects of the variations in soil moisture availability,
soil nutrient status and insect grazing upon the composition, distribution
and abundance of forest flora is best examined using the topographic
extremes of north and south-facing slopes. These slopes vary maximally
in microclimate which in turn affects the nature of the soils, flora
and insect fauna. The influence of aspect is discussed below in order
that the effects of the differences in geology and pedology between the
three hillslopes may be understood in the context of these topographic-
ally induced variations.

1.1.1   The Influence of Aspect on Microclimate

Radiation Receipt:

Incoming radiation is made up of direct-beam and diffuse-beam
short wave radiation and long wave radiation. It is the extra-terrestrial
short wave radiation that forms the energy input into the 'earth-
atmosphere system' (Oke 1978). The amount of direct-beam short wave
radiation received at a point upon the earth's surface depends on slope
angle, aspect, latitude, time of day, season and topographic shading
(Geiger 1965).

The direct-beam short wave radiation receipt on a slope (S_{slope})
is a function of the incident radiation received perpendicular to the
beam (S_i) and the angle (θ) between S_i and the normal to the slope.

The total radiation input on a slope may be described as follows:

$$S_{slope} = S_i \cos \theta + D$$

where D is the diffuse-beam short wave radiation. Inherent in the angle θ are the effects of azimuth angle (aspect) and elevation. The above expression describes the instantaneous radiation receipt; the total radiation load per slope is obtained by summing the radiation receipt per day ($MJm^{-2}day^{-1}$). One of the results of this interaction is that slopes facing the equator receive more direct insolation than those facing the poles, a relationship which is mirrored on the north- and south-facing slopes of a hill.

Tasmania is an ideal location in which to undertake research involving an aspect component since at middle latitudes the modification of short wave radiation input by slope angle and aspect is at a maximum (Holland and Steyn 1975).

Nunez (1980, 1983) developed a model of the expected solar radiation receipt on slopes of different elevations and aspects in Tasmania. On north-facing slopes in winter the maximum mean daily solar radiation occurred at slope elevations of 60 - 65°, while in summer the maximum mean daily solar radiation was recorded on the horizontal. On south-facing slopes the maximum mean daily solar radiation was recorded on the horizontal in both winter and summer.

These aspect-induced inequalities in the receipt of radiation set up very distinct differences in the microclimate of the two slopes such that they differ with respect to temperature, light, moisture availability (ie evaporation and humidity) and other inter-related factors (see below).

Temperature and Light:

As a result of the differences in the radiant energy received on north and south-facing slopes air and soil temperatures are generally cooler and the amount of direct light received less on the latter slopes.

Differences in;   (1) the quality, intensity and duration of
light and in (2) the seasonal and extreme temperatures, experienced on
the slopes affects the distribution and composition of plant and insect
communities.

Moisture:

Of the environmental factors influencing plant survival,
development and productivity, moisture availability is probably the
most important (Rosenberg 1974).

The amount of water available to all organisms depends on a
number of interacting factors: solar radiation receipt, precipitation,
the vapour pressure gradient (which is in turn affected by temperature
and humidity), edaphic factors (i.e. field capacity of the soil, soil
texture and structure), runoff, ground water movement, canopy inter-
ception, and wind and air turbulence (Ayyad and Dix 1965; Jackson 1977;
Kirkpatrick and Nunez 1980).

(a) Precipitation

The amount of precipitation received at a point on the earth's
surface depends on its frequency, duration, intensity, type and temper-
ature (Lowry 1967). North and south-facing slopes do not receive equal
amounts of precipitation, but there is no distinct temporal pattern of
difference.

(b) Evapotranspiration

Evapotranspiration is the loss of water to the air from soil and
water surfaces (evaporation) and from plants (transpiration). The
energy sources for these processes come from the radiant energy of the
sun and the latent heat energy of the leaves. A number of factors can
therefore influence the rate of evapotranspiration including (air, soil,

plant) temperature, humidity, soil type, soil moisture availability and stomatal opening (Sabath and Quinnell 1981). It also follows that the trends in evapotranspiration are similar to those described for temperature, with maximum values occurring on the mid-upper portions of north-west facing slopes (Ashton 1976; Kirkpatrick and Nunez 1980).

(c) Humidity

Humidity is a measure of the moisture content of the atmosphere (Barry and Chorley 1971). Moisture content varies with temperature and pressure (Odum 1959), the highest values occurring at night and the lowest during the day.

There is conflicting evidence as to whether any differences in the humidity can be detected between slopes of different aspect (Ayyad and Dix 1965).

(d) Canopy Interception

Generally the trees on south-facing slopes are taller and the forest canopy is more dense. As a result of the increasing dense canopy cover on this slope, wind speed, temperature and light at the forest floor are reduced and relative humidity is increased.

Mount (1972) from a study of the interception rates measured in several catchments throughout Australia determined interception rates for different densities of forest and woodland taking into account the density of the shrub layer as well. He proposed that the proportion of the total rainfall intercepted by: (1) woodlands was 3%; (2) light forests was 4%; and (3) moderately dense forests was 5%.

1.1.2   The Influence of Aspect on Soils

Microclimate affects a whole range of inter-related pedogenic processes including weathering, microbial activity and nutrient cycling. As a result of this soils on north and south-facing slopes differ with respect to depth, texture, pH and horizon formation. Kirkpatrick and Nunez (1980), for example, found the mudstone soils on the north-facing slopes at Risdon, south-east Tasmania, to be thinner, less well defined, immature, of a courser texture and more acidic than those on the south-facing slopes.

As a consequence of these micro-climatically induced differences in the properties of the soils, the water holding capacity of the soil on the north-facing slope is lower than that on the south-facing slope.

The amount of water available for plant growth at any one point in time depends on the interplay between a number of variables including solar radiation receipt, evapotranspiration, air and soil temperature, precipitation, soil texture and structure and the soil water holding capacity.

Soil texture (determined by measuring the size of the soil particles) and soil structure (determined by the shape or form of the aggregates comprising the soil) influence the amount and movement of water in the soil. For example, the larger the surface area to volume ratio of the soil aggregates, the larger the surface area available to bind water. Also particle size and aggregate shape influence the permeability and therefore infiltration rate of surface water.

As a consequence of the interaction of all these factors, north and north-westerly facing slopes have a lower soil moisture content than those that are south and south-easterly facing.

1.1.3   The Influence of Aspect on Flora

The topographically induced microclimatic variations between the north and south-facing slopes affects the flora to the extent that the vegetation on the slopes may differ with respect to:(1) community composition (Cantlon 1953; Shaw 1961 cited in Ayyad and Dix 1965); (2) species distribution (Hogg and Kirkpatrick 1974);   (3) species density (Ashton 1976);   (4) species richness (Kirkpatrick and Nunez 1980);   (5) the time of shoot growth, flowering (Pook and Moore 1966); and (6) community structure (Pook and Moore 1966; Ashton 1976; Hogg and Kirkpatrick 1974).

1.1.4   The Influence of Aspect on Insect Fauna

Very little research has been undertaken to establish whether insect fauna varies between slopes of different aspect; instead, studies have tended to concentrate upon the density of insects or the level of defoliation within different parts of the tree crown (White 1970a; Lowman 1982a),the distribution of species around tree trunks (Schimitscheck 1931 cited in Geiger) or the location of insect dwellings with respect to microclimate (Hesse 1924; Wellenstein 1929 both cited in Geiger). Slack, Nauman and Tilley (1980) reported that the distribution and composition of insect communities had been found to vary between sunny and shaded slopes.

Also Hawkins and Cross (1982) found that (1) the number of arthropod species increased on north-facing compared with south-facing slopes on coalmine spoils in Alabama, U.S.A. and (2) that insect density was negatively correlated with temperatures on south-facing slopes. Similarly, Cox et al. (1973) noted that some insects were more abundant on slopes facing the equator.

CHAPTER 2   TOPOGRAPHIC AND EDAPHIC EFFECTS ON HIGHER PLANT SPECIES DISTRIBUTION

The effects of incident radiation on soil moisture have been shown to be strongly related to species distribution patterns within areas of varying lithology in the forests of eastern Australia (e.g. Hogg and Kirkpatrick 1974; Kirkpatrick and Nunez 1980; Harris and Kirkpatrick 1982; Austin *et al.* 1984). The close juxtaposition of different soil types in hilly terrain at the Ridgeway Park Reserve, provided the opportunity for an investigation of the degree to which the soil type could influence the composition and structural diversity of the vegetation, and shift species distributions, in a situation where precipitation and incident radiation could be held constant.

2.1 THE STUDY AREA

The Ridgeway Park Reserve lies in the foothills of Mount Wellington, some 7 km south-west of Hobart (Figure 2.1). The field area fulfilled the two main requirements of the study: (1) that the three geologies outcropped in close proximity ensuring the climatic regime experienced by each was similar (Figure 2.2); and (2) that the area provided a wide range of topographic environments. The entire area was burnt during the bush fires of 1967.

2.2 CLIMATE

Hobart experiences a temperate climate. Table 2.1 shows the mean monthly daily maximum and minimum temperatures for Grove, the station recording temperature whose climate most closely approximates that of the study area. Differences in altitude influence the temperature range, with temperatures falling $0.65^{\circ}C$ for every 100 metre rise (M. Nunez, unpub. data). Elevational differences between the transects
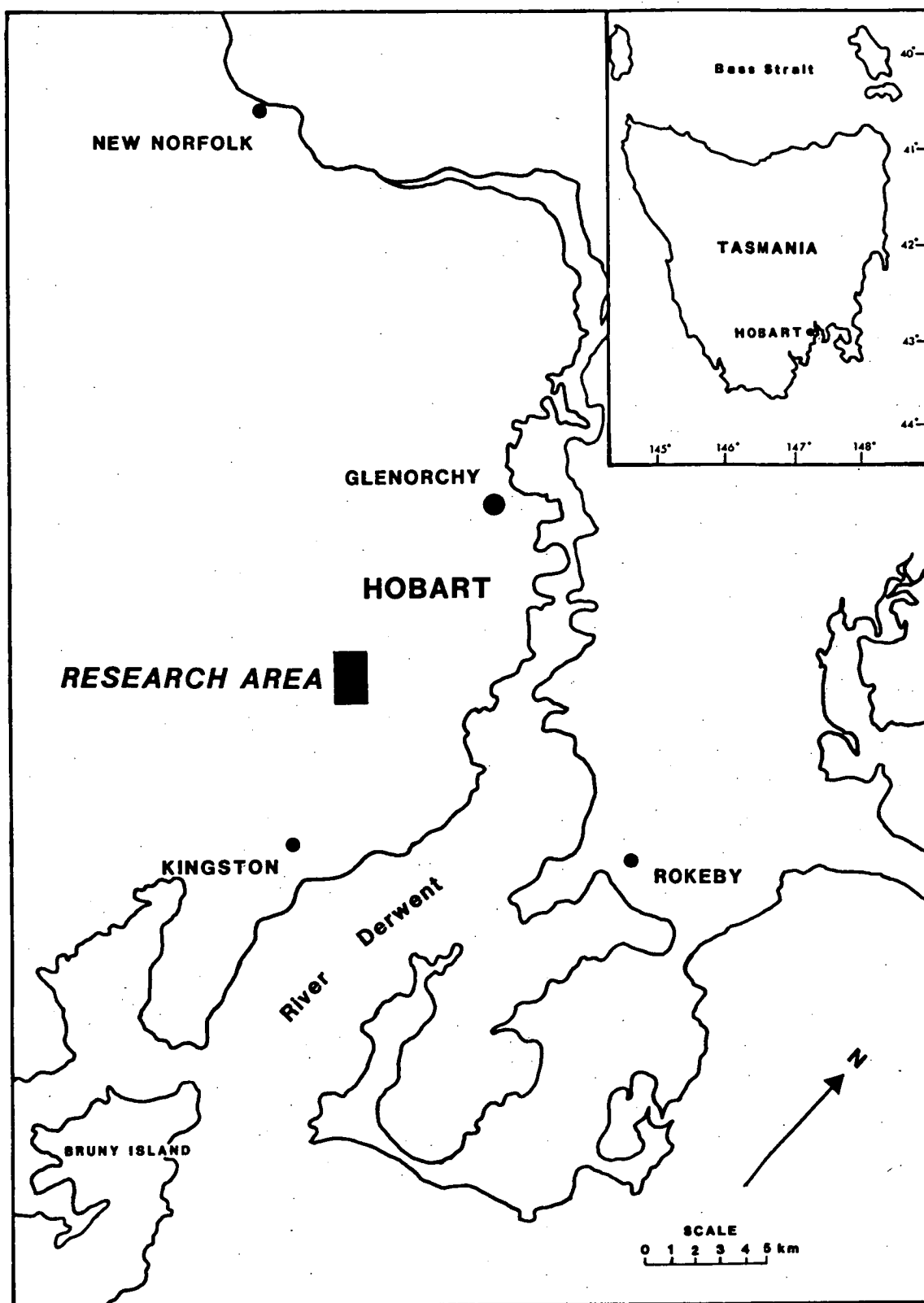
FIGURE 2.1: Map of Hobart and its environs showing the location of the research area (Ridgeway Park Reserve).
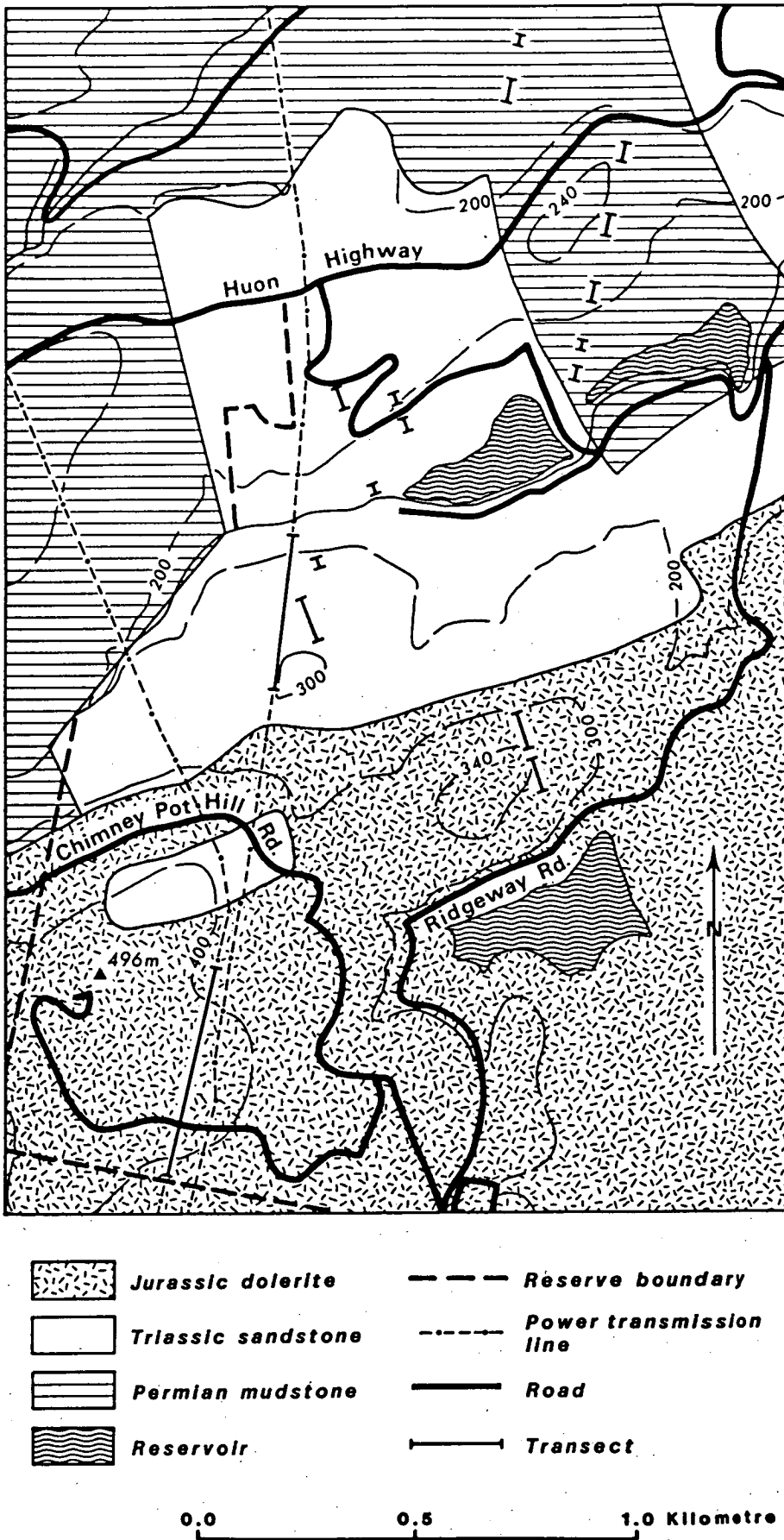
FIGURE 2.2: Map showing the topography, geology and location of the transects in the research area. The transects along the power transmission lines are part of the studies described in Chapter 3.

in the study area were not enough to cause large variations in temperature between the sites.

The mean annual precipitation at The Waterworks (in the Ridgeway Park Reserve) is 834 mm, distributed fairly evenly throughout the year (Table 2.2). The fieldwork was undertaken during the period 1982-83, at which time the south-east of the State had received less than average rainfall for many years (Figure 2.3).

2.3 GEOLOGY AND SOILS

The rocks that outcrop in the Hobart area belong to three main groups, viz; igneous (dolerite) rocks of Jurassic age, and mudstone and sandstone sediments of Permian and Triassic age respectively. The soils that have formed upon these bedrocks are classified as the brown earths, podzolic soils and podzols (Nicholls and Dimmock 1964).

2.3.1 Dolerite and the Brown Earths

Dolerite is a crystalline igneous rock that has relatively few joints. It is particularly susceptible to chemical weathering, which causes the disintegration of the rock matrix around corestones.

The brown earth that has developed at Ridgeway has a sand-loam A horizon overlying a clay B horizon (Robinson 1979). The B horizon when dry is firm to hard, and when wet is plastic (Nicholls 1958). Below the soil is a layer of weathered bedrock, of variable depth into which plant roots penetrate.

Boulders are scattered throughout, and over the surface of the soil. The soil occurs on gentle to steep slopes (Loveday 1955) and a major outcrop occurs in the midsection of the north-facing slope.

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Max Temp (°C) Mean = 16.9	22.4*	22.2	20.3	17.5	14.2	11.9	11.5*	12.6	14.6	16.7	18.2	20.1
Min Temp (°C) Mean = 5.8	9.3	9.4*	8.0	6.9	4.2	2.4	2.0*	2.4	3.9	5.5	6.9	8.6

TABLE 2.1   Mean monthly daily maximum and minimum temperatures for Grove at an elevation of 60m. Asterisk denotes the hottest and coldest months.

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Rainfall (m)	58	54*	60	75	67	74	73	68	71	88*	73	73

TABLE 2.2   Mean monthly rainfall for The Waterworks at an elevation of 160.6 metres. Asterisk denotes the wettest and driest months.
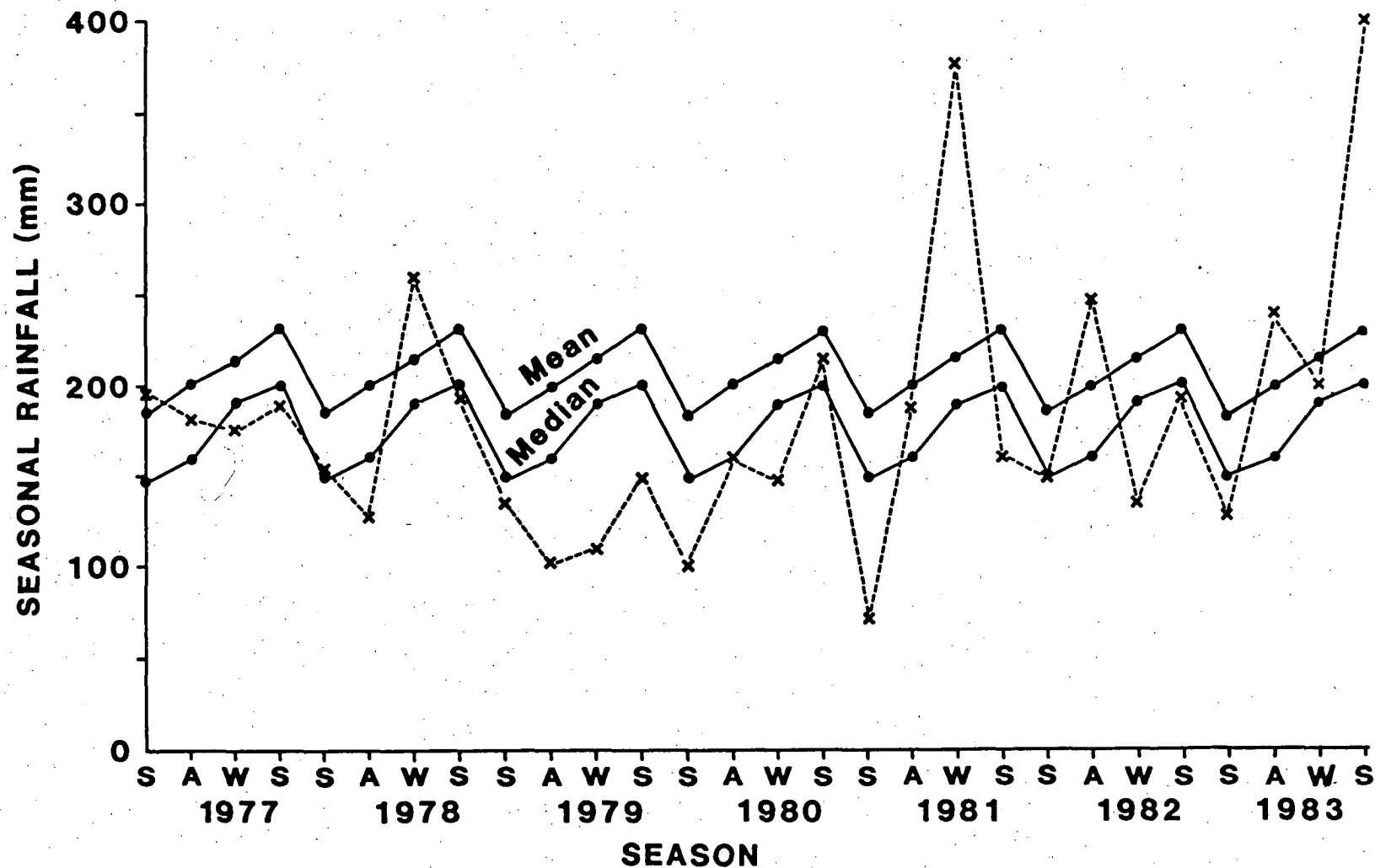
FIGURE 2.3: Mean and median seasonal rainfall for the period 1897-1984 for the Hobart Waterworks (42°55'S 147°17'E, 160 m above sealevel, mean annual rainfall 834 mm, median annual rainfall 819 mm), compared with seasonal precipitation from the summer of 1976/77 to the summer of 1983/84 (X---X).

2.3.2 Mudstone and the Podzolic Soils

Mudstone is composed of fine sediments. The heavily jointed bedrock is highly fissile.

The podzolic soil which has formed on the mudstone consists of a grey rocky loam overlying the bedrock (Robinson 1979). The soil contains many fragments of porous rocks and stones, derived from the bedrock. This makes determination of the point where the stoney soil ends and weathered bedrock commences very difficult, especially as plant roots penetrate through the layers of weathered bedrock.

Rock outcrops occur occasionally on the gentle-steep slopes that form on this bedrock (Loveday 1955), and the north-facing slopes are covered by a layer of scree (Plate 2.5) that developed as a result of periglacial activity during the last ice age.

2.3.3 Sandstone and the Podzols

The sediments comprising the sandstone bedrock are coarse grained. The bedrock is highly jointed.

The podzols that have formed on this siliceous rock consist of a sandy surface horizon over a sandy-clay sub-surface (Robinson 1979). In the soil a hardpan has developed, at a depth of around 70-100 cm. Many porous rocks and stones were scattered throughout the soil.

The slopes on sandstone vary from gentle to steep (Loveday 1955) and rock outcrops range from small areas of exposed rocks to cliffs (Plate 2.1).

2.4 METHODS

2.4.1 Field Studies

Belt transects were located to include north-facing and south-

PLATE 2.1: A sandstone cliff on the north-facing slope, Ridgeway Park Reserve.

facing slopes on three parent materials. As previous studies had shown that in the southern hemisphere the most mesic vegetation was found on south-easterly facing slopes and the most xeric on north-westerly facing ones (Ashton 1976; Kirkpatrick and Nunez 1980), the transects were, as far as possible, located on NNW and SSE facing slopes, orthogonal to the contours. However some of the transects were adjusted from this location to ensure that the incident radiation values on each of the parent materials fell within the same range. The directions of the transects on the dolerite, mudstone and sandstone were placed at 17° west of north, 17° east of north and 21° west of north respectively, within relatively undisturbed bush (see Figure 2.2).

Following the procedure of Kirkpatrick and Nunez (1980), contiguous 1 m^2 quadrats were used to record the presence or absence of vascular plant taxa less than 2 m tall and 1 x 5 m quadrats were used to record the presence or absence of vascular plant taxa more than 2 m in height. The data were collected in the winter and early spring of 1983. Thus some annuals and geophytes may not have been recorded and other species had to be grouped because of the lack of suitable material for identification. Nomenclature follows Curtis (1963, 1967), Willis (1970), Curtis and Morris (1976).

The percentage frequency of each taxon within groups of five adjacent quadrats was determined. The slope angle of each quadrat within the groups was measured using a Sunto clinometer, and the mean slope angle for each group of quadrats was calculated. Slope angle and aspect were then used to establish the solar radiation receipt for each group along the transect using the insolation diagrams derived from the solar radiation model of Nunez (1980, 1983), which estimates solar and net radiation input for slopes in Tasmania. The model calculates direct and diffuse radiation taking into account direct and diffuse radiation from a clear sky, cloud cover, surface albedo and the sky view factor (see Equations 1 and 2).

$$G_c = I_o \tau \cos Z + D \qquad\qquad (1)$$

$$K_c\!\downarrow = \frac{I_o \tau \cos \gamma}{equ.\ 1} + \frac{D\ VF}{2} + \frac{G_c\ \alpha(1-VF)}{3} \qquad (2)$$

The model does not take into account shadow effects. However these were minimal on the slopes covered by the transects.

Estimates of global solar radiation derived from this equation were found to be within 5% of the mean monthly values of solar radiation monitored at Hobart airport (Nunez 1983).

Maximum:minimum thermometers were placed 10 cm above the surface by means of wooden supports, at approximately 20 m intervals along the transects. The maximum and minimum temperatures were recorded fortnightly during the autumn and winter of 1984.

Soil depth to 60 cm was recorded every 0.5 m along the transect. Soil pH was determined for each group of quadrats along the transect, using a CSIRO soil testing kit, accurate to half a unit. This allowed the soils to be analysed rapidly in the field, thus avoiding the problems associated with transportation and storage. The percentage of rock in the soils on each parent material was estimated after examining soil profiles exposed in quarries and road cuttings. Soil depth and rock content were used in deriving the water capacity of the three soils (see below).

2.4.2 The Soil Model

(a) *Introduction*

A model was devised to compare the daily water balance of the soils on the north-facing slopes on dolerite, mudstone and sandstone. The model was developed from the Soil Dryness Index (S.D.I.) of Mount (1972), which by definition indicates the amount of moisture needed to raise the soil to field capacity. Thus a soil with an S.D.I. of zero is at field capacity, and one at an S.D.I. of one hundred needs 100 points of water to reach field capacity (all equations are expressed in points).

(b) *Water Budget Relationships*

The model is based upon the following equations:-

$$EFF = R - IN - FR \qquad (3)$$

where the actual or effective rainfall (EFF) entering the soil is a function of the total rainfall (R), interception (IN) and flash runoff (FR).

$$AM = PM - EFF \qquad (4)$$

where AM is the S.D.I. in the morning of day 2 and PM the S.D.I. on the afternoon of the previous day (on day 1 this is equal to zero).

$$PM = AM + AE \qquad (5)$$

where PM is the S.D.I. on the afternoon of day 2 and AE the actual evaporation from each of the three soils.

$$SM = SWC - PM \qquad (6)$$

where SM is the actual amount of moisture in each of the soils and SWC their soil water capacity.

Thus equations 3 to 6 are solved on a daily basis and a daily S.D.I. in the afternoon (PM) is derived.

(c) *Definition of Variables*

RAINFALL:

Rainfall is recorded daily at The Waterworks. It was decided to focus upon the years 1970-74 since this time period included years of high and low rainfall.

The model assumes that all three soils are at field capacity

(S.D.I. = 0) upon day 1, for this reason day 1 is taken as 1st November, 1970, since October was a month of very high (Spring) rainfall.

INTERCEPTION (IN) and FLASH RUNOFF (FR):

Interception and Flash Runoff are derived from the following equations:-

$$IN = CD \times R \qquad (7)$$

$$FR = CID \times R \qquad (8)$$

where CD and CID are constants which are determined by soil type.

IN and FR differ in each site depending upon the density of the tree canopy and understorey. The density of the vegetation on the brown earths, podzolic soils and podzols determined the "Interception Loss Class" of each soil (C, D and E respectively) and therefore the magnitude of water loss by interception. Accordingly the values of 0.3, 0.4 and 0.5 were taken as the proportion of the total rainfall intercepted by the canopy (CD) on the dolerite, mudstone and sandstone parent materials. The maximum interception (MIN) by the canopy, at any one time, was taken as 8 points, 11 points and 14 points in these sites respectively.

The proportions of rainfall lost as flash runoff (CID) were 0.025 upon the dolerite parent material, 0.020 upon the mudstone parent material and 0.017 upon the sandstone parent material.

In this model it was assumed that evaporation from the canopy is such that it dries out totally between daily rainfall events (cf Mount's Model). On days of continuous heavy rainfall (R>MIN), this would not be the case. In such circumstances therefore, values of IN are artificially inflated and those of EFF underestimated. As IN is highest on the podzols, the model is most conservative in its estimates of S.D.I. on this soil type.

SOIL WATER CAPACITY:

The soil water capacity of each of the three soils was derived using Specht's model (1972);

$$SWC \ (S_{max}) = \frac{1}{100} \ x \ depth \ x \ \frac{vol. \ soil}{vol. \ soil + rock} \ x \ bulk \ density$$

$$x \ (field \ capacity \ \% - permanent \ wilting \ \%) \quad (9)$$

where S_{max} is the maximum amount of water which can be extracted from the soil moisture profile by a plant community.

The field capacity and soil bulk density for each soil were taken from the results of Robinson (1979). Based on this data, the browth earths, podzolic soils and podzols were given SWC values of 822, 922 and 1251 points respectively.

(d) *Estimating Evapotranspiration*

The actual evaporation from the soil (AE) is taken as a function of the potential evaporation (PE) multiplied by some factor (F), which takes into account the decreasing evaporative losses as soils dry. Thus actual evaporation is given as;

$$AE = F \ x \ PE \qquad\qquad (10)$$

The model assumes PE to be equal to the measurements of pan evaporation. This is in contrast to Mount's Model which uses maximum temperature to derive PE. Temperature is however, only one of the climatic variables affecting PE, others include solar radiation, wind speed and humidity. Pan evaporation is likewise effected by all these variables and so more closely resembles PE.

As pan evaporation data was not collected in the Waterwork's Reserve, figures from Hobart Bureau of Meteorology were used. It was felt that this would be a reasonable approximation, as data plotted from 1970 for two sites in areas around Hobart (Hobart Bureau of Meteorology and Grove) deviated on average by 8% from one another.

FIGURE 2.4: Species distribution and frequency across a dolerite hill
(see profile) in the Ridgeway Park Reserve.
--- = a gap in the sampling.

F takes the form:

$$F = 1.006 - 1.215(P) + 1.306(P^2) - 0.995(P^3) \qquad (11)$$

where P is the soil dryness index expressed as a percentage of the maximum possible for that soil type. P will vary depending upon the maximum SWC of the soils.

F was estimated by reworking Mount's data which describes the relationship between maximum air temperature, the soil dryness index and evapotranspiration. In this study the air temperature effect was neglected. Instead a mean evapotranspiration rate for a range of air temperatures was obtained. This simplification is most likely not critical as the use of pan evaporation data already partially accounts for the effects of air temperature. The model therefore makes the assumption that evaporation decreases, with a decline in soil moisture levels, in a linear manner, attaining a maximum potential value at field capacity (cf Specht 1972b).

Further investigations of this relationship would be the first priority in any future development of the model. Other modifications needed to improve the model's predictive ability include taking into account; (1) transpiration rates, (2) capillary losses and (3) the moisture holding capacity of the bedrock (see discussion).

2.5 RESULTS

2.5.1 Analysis of the Vegetation

The Dolerite Transect:

Figure 2.4 shows the distribution and relative abundance of taxa along the transect. The vegetation forms a continuum, with no perceptible break in species composition. The north-facing slope is covered by grassy woodland (Plate 2.2) dominated by *Eucalyptus pulchella*

PLATE 2.2: The north-facing slope on the dolerite hill, Ridgeway Park Reserve.

and *E. viminalis*, with a sparse tall shrub intermediate stratum
consisting of *Exocarpos cupressiformis*, *Banksia marginata*, and
Bedfordia linearis. Some shrubs emerge from the dense grass layer,
but have low total cover. *Acacia dealbata* forms a shrub, no more
than 1 m high, on this north-facing slope (cf south-facing slope).
The majority of shrubs however, are smaller than this species and
include *Hibbertia riparia*, *Eriostemon verrucosus*, and *Acacia
myrtifolia*, which are confined to the north-facing slope, and
Olearia ericoides, *Leucopogon virgatus*, *Tetratheca pilosa*, *Bossiaea
prostrata* and *Daviesia ulicifolia* which extend to the south-facing
slope.

Other species which are restricted to the north-facing slope
include the herbs *Linum marginale* and *Helichrysum apiculatum*, and the
sedges *Lepidosperma laterale* and *L. lineare var. inops*. The grass
Themeda australis and the sedge *Schoenus apogon* while being predominantly
found on this slope, also extend to the top of the south-facing slope.

The south-facing slope supports open forest consisting of
Eucalyptus pulchella, *E. viminalis* and *E. obliqua*, with *E. obliqua*
dominating the most mesic section. The dense understorey is composed of
tall shrubs (Plate 2.3) including *Bedfordia linearis*, *Leptospermum
scoparium*, *Banksia marginata* and *Acacia dealbata*. Gaps in the tall
shrub stratum have allowed the development of a dense cover of grass,
herb, graminoid and small shrub species; many are confined to this
slope, including *Epacris impressa*, *Viola hederacea*, *Laginifera
stipitata*, *Oxalis corniculata*, *Ranunculus lappaceus* and *Dianella
tasmanica*.

Figure 2.5 shows the percentage of bare ground along each of the
three transects. The south-facing slopes have a higher amount of ground
covered by vegetation than the north-facing slopes, while a comparison
of the north-facing slopes alone shows just as great a contrast between
the vegetation cover on the three rock types. The much lower amounts
of bare ground on the north-facing slope of the dolerite transect is
due to the dense covering of grasses. This predominance of grasses can
be attributed to several factors, including the higher fertility of the
brown earths (Specht 1972a; see section on 'soil fertility') and the

PLATE 2.3: The south-facing slope on the dolerite hill,
Ridgeway Park Reserve.
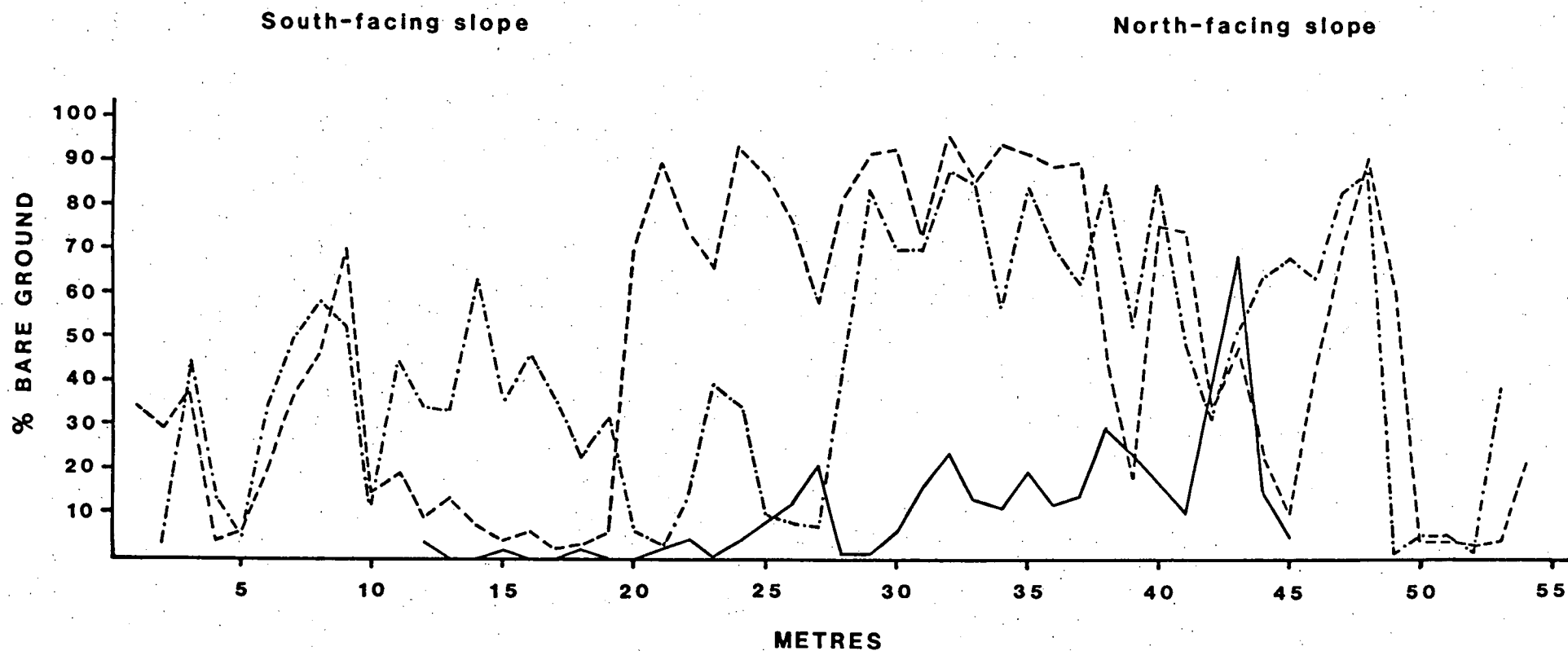
FIGURE 2.5: The percentage of bare ground across dolerite, mudstone and sandstone hills in the Ridgeway Park Reserve. ———— = dolerite hill; ----- = mudstone hill and -.-.-. = sandstone hill.

frequency and intensity of fire on the dolerite site. The dolerite is subject to frequent hazard reduction burns of low intensity. These burns destroy the aerial parts of grasses, but not their root stock. Consequently such a fire regime favours the regeneration of the predominantly grassy understorey (K.J.M. Dickinson, pers. comm.).

The openness of the tree stratum on the north-facing slope on dolerite is probably largely due to the interaction of fire with slow tree growth rates on shallow soils which favour grasses. The native grasses are highly flammable and can and often do burn at intervals of less than two years. This time period is insufficient to allow tree seedlings to become tall enough, and to develop thick enough bark to avoid being set back to ground level. General observation suggests that most trees up to 18 years old are set back to ground level on these sites, which can become forests rather than woodlands if there is a sufficient fire-free interval. Successful tree establishment may be partly related to the deeper soils formed on weathered joints in the bedrock, as the summer moisture deficit might not be as restrictive to growth in these sites than on shallower soils. For example Florence (1965), found that the tree species *Eucalyptus pilularis* (Blackbutt), was confined to niches of fractured rock and deeper soil on slopes in the Blackall Ranges, where the soil covering was immature.

Shrubs on the north-facing slope of the dolerite transect tend to be concentrated in areas where rock is exposed (Plate 2.4). Here the fibrous roots of the grasses are unable to become established, while the root system of shrubs (a tap root plus laterals) are able to penetrate the clefts between the rocks to the soil below (Walter 1973). It is probable that these clefts also tunnel water, increasing the moisture content of the soil immediately beneath them.

The Mudstone Transect:

The transect was made of sections sampled from the upper, middle and lower parts of the north and south-facing slopes (Figure 2.2). The brow of the hill was subject to hazard reduction burns in 1979 and 1984.

PLATE 2.4: The concentration of shrubs to areas where rock outcrops on the north-facing slope of the dolerite hill, Ridgeway Park Reserve.

The north-facing slope (Figure 2.6) is covered by low open-forest of *Eucalyptus tenuiramis, E. obliqua* and *E. viminalis* (Plate 2.5). There is a sparse layer of shrubs (*Acacia dealbata, A. genistifolia, A. verticillata, Exocarpos cupressiformis* and *Leptospermum scoparium*), underlain by grasses, sedges, herbs and small shrubs, both layers increasing in cover with increasing moisture availability.

Changes in species composition and abundance occur gradually across the transect. However, several species are confined to the north-facing slope, including the shrubs *Acacia myrtifolia* and *Marianthus procumbens*, the herbs *Goodenia lanata* and *Xanthosia pusilla* and the graminoids *Gahnia radula* and *Lomandra longifolia*.

Upon the south-facing slope, an open-forest dominated by *Eucalyptus obliqua* and *E. viminalis* is underlain by a dense tall shrub stratum (Plate 2.6) composed of broad leaved and sclerophyllous species which include *Hakea lissosperma, Pomaderris elliptica, Bedfordia linearis, Coprosma quadrifida* and *Pultenaea daphnoides*, all confined to this slope and *Acacia dealbata* and *Exocarpos cupressiformis*. Where the shrubs are less dense on the upper parts of the south-facing slope, herbs, grasses and small shrubs form what is sometimes a dense ground stratum. Taxa prominent in this stratum include *Haloragis teucrioides, H. tetragyna, Stylidium graminifolium, Tetratheca glandulosa, Pultenaea gunnii, P. daphnoides, Aotus ericoides, Epacris impressa*, Orchids and *Pteridium esculentum*.

The Sandstone Transect:

The vegetation was sampled along the upper, middle and lower sections of the south-facing slope and along the upper-middle and middle-lower sections of the north-facing slope (Figure 2.2). The area in the lower sections of the north-facing slope was so altered in character, as a result of disturbance, that it could not be included in the transect. This break in the sampling is responsible for the apparently sharp vegetation change where the two slopes join (Figure 2.7).

Lichen
Moss
Other Gramineae
Epacris impressa
Danthonia spp.
Eucalyptus viminalis
Cassytha pubescens
Viola hederacea
Eucalyptus pulchella
Helichrysum dendroideum
Xanthosia pusilla
Leptospermum scoparium
Acacia genistifolia
Acacia verticillata
Helichrysum scorpioides
Leptomeria drupacea
Astroloma humifusum
Daviesia ulicifolia
Lomandra longifolia
Marianthus procumbens
Gahnia radula
Goodenia lanata
Acacia myrtifolia
Senecio spp.
Wahlenbergia spp.
Laginifera stipitata
Opercularia varia
Galium spp.
Acacia botrycephala
Banksia marginata
Dillwynia sericea
Leucopogon collinus
Dianella revoluta
Eucalyptus tenuiramis
Eucalyptus amygdalina
Haloragis tetragyna
Amperea xiphoclada
Drosera auriculata
Prasophyllum spp.
Stipa spp.
Aotus ericoides
Pultenaea gunnii
Tetratheca glandulosa
Pterostylis spp.
Other Orchidaceae
Pultenaea juniperina
Haloragis teucrioides
Pteridium esculentum
Stylidium graminifolium
Pultenaea daphnoides
Billardiera longiflora
Dianella tasmanica
Cassinia aculeata
Helichrysum purpurascens
Olearia stellulata
Eucalyptus globulus
Clematis aristata
Luzula spp.
Coprosma hirtella
Coprosma quadrifida
Bedfordia linearis
Pomaderris elliptica
Hakea lissosperma
Geranium spp.
Senecio linearifolius
Acacia dealbata
Exocarpos cupressiformis
Poa spp.
Eucalyptus obliqua

SSW   NNE

0   20   40   60   80   100 120 140 160 180 200 220 240 260

METRES

FIGURE 2.6:   Species distribution and frequency across a mudstone
              hill (see profile) in the Ridgeway Park Reserve.
              --- = a gap in the sampling.

PLATE 2.5:   The north-facing slope on the mudstone hill,
             Ridgeway Park Reserve.

PLATE 2.6:   The south-facing slope on the mudstone hill, Ridgeway Park Reserve.

Eucalyptus obliqua
Moss
Other Orchidaceae
Lichen
Poa spp.
Other Gramineae
Pteridium esculentum
Pterostylis spp.
Exocarpos cupressiformis
Eucalyptus viminalis
Stipa spp.
Tetratheca glandulosa
Cyperaceae sp.
Eucalyptus pulchella
Daviesia ulicifolia
Astroloma humifusum
Dianella revoluta
Pimelea linifolia
Helichrysum scorpioides
Senecio spp.
Lissanthe strigosa
Banksia marginata
Amperea xiphoclada
Persoonia juniperina
Pultenaea juniperina
Goodenia lanata
Leucopogon ericoides
Pimelea humilis
Lepidosperma concavum
Aotus ericoides
Haloragis tetragyna
Leucopogon virgatus
Prasophyllum spp.
Eucalyptus tenuiramis
Lomandra longifolia
Gahnia radula
Drosera auriculata
Stylidium graminifolium
Epacris impressa
Wahlenbergia spp.
Danthonia spp.
Acacia dealbata
Coprosma hirtella
Dianella tasmanica
Cyathodes glauca
Galium spp.
Billardiera longiflora
Bedfordia linearis
Geranium spp.
Coprosma quadrifida
Olearia stellulata
Polystichum proliferum
Eucalyptus globulus
Goodenia ovata
Clematis aristata
Olearia argophylla
Viola hederacea
Oxalis corniculata
Lomatia tinctoria
Helichrysum dendroideum
Pittosporum bicolor
Bursaria spinosa
Asterotrichion discolor
Cassinia aculeata
Haloragis teucrioides
Luzula spp.
Acacia verticillata
Senecio linearifolius
Oxylobium ellipticum
Diplarrena moraea
Drymophila cyanocarpa
Helichrysum purpurascens
Genista spp.
Juncus spp.
Centaurium erythraea
Leptospermum scoparium
Blechnum wattsii
Epilobium spp.

NNW   SSE

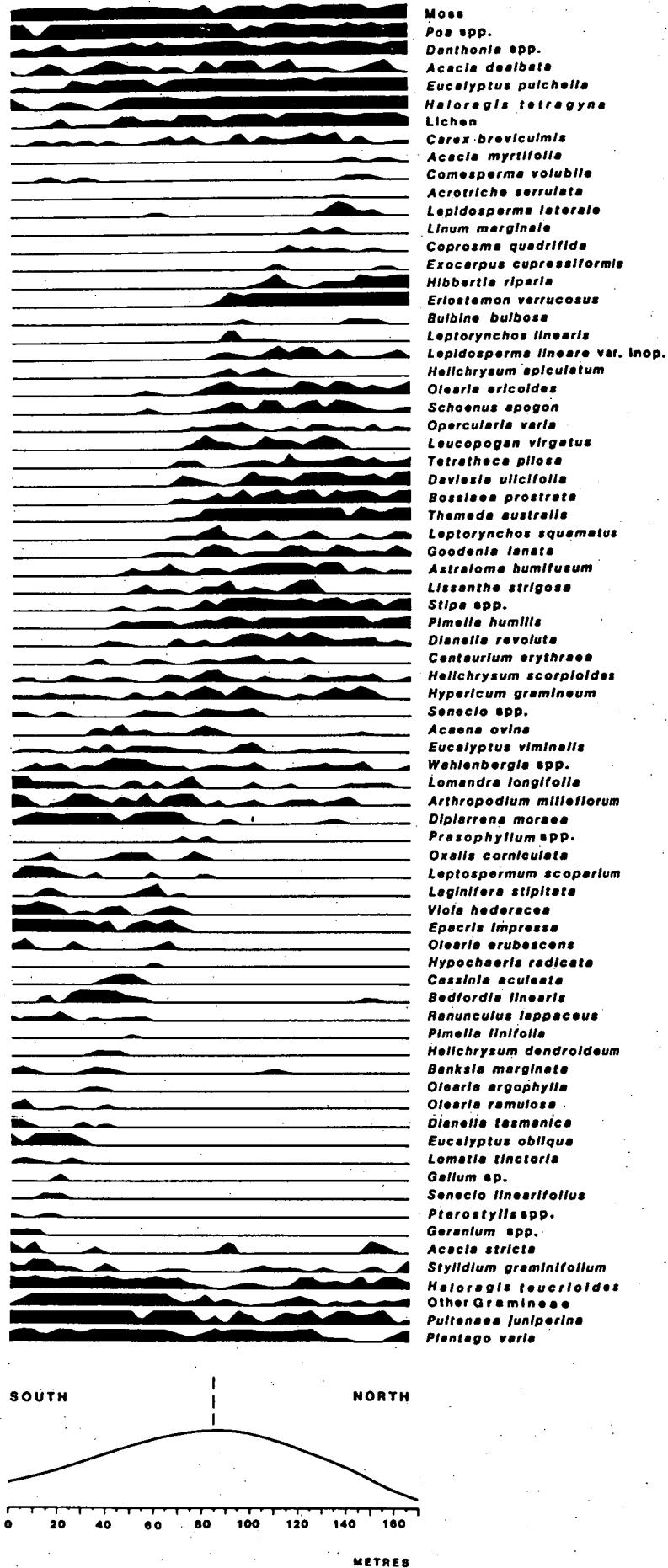0   20   40   60   80   100   120   140   160   180   200   220   240

METRES

FIGURE 2.7:   Species distribution and frequency across a sandstone
hill (see profile) in the Ridgeway Park Reserve.
--- = a gap in the sampling.

Eucalyptus obliqua and *E. tenuiramis* dominate the open-forest on the north-facing slope (Plate 2.7). The sparse open-heath under-storey includes *Leucopogon spp.*, *Tetratheca glandulosa*, *Amperea xiphoclada*, *Aotus ericoides*, *Lepidosperma concavum*, *Lomandra longifolia*, *Gahnia radula* and *Haloragis tetragyna*, which are confined to the north-facing slope and *Epacris impressa*, *Stylidium graminifolium*, *Wahlenbergia spp.*, grasses, Orchids and *Pteridium esculentum*. There is a sparse tall intermediate stratum comprising *Exocarpos cupressiformis* and *Banksia marginata.*

The tall forest on the south-facing slope is dominated by *Eucalyptus obliqua* (Plate 2.8). This species is underlain by a tall dense canopy of trees and tall shrubs including *Bedfordia linearis*, *Olearia argophylla*, *Asterotrichion discolor*, *Pittosporum bicolor*, *Oxylobium ellipticum* and *Coprosma quadrifida*, which are confined to the south-facing slope, and *Acacia dealbata*. Some herb, grass and graminoid species plus a few small shrub species are found on the forest floor, but they are of low cover. These include species whose distribution is restricted to the south-facing slope such as *Geranium sp.*, *Haloragis teucrioides*, *Galium sp.*, *Dianella tasmanica*, *Diplarena moraea*, *Luzula sp.*, and *Goodenia ovata.*

The prevalence of orchid species on the sandstone and mudstone transects is due to the large amount of bare ground (Figure 2.5). Orchids will only become established and grow where there is no competition from other plants for available resources. This also explains their paucity on the dolerite site.

Structural differences between the vegetation types, with aspect and lithology, include changes in community height and the number and density of strata.

Species Richness:

The non-parametric Mann Whitney test was used to compare species richness of 5 m^2 quadrats between slopes of different aspect and rock

PLATE 2.7: The north-facing slope on the sandstone hill, Ridgeway Park Reserve

PLATE 2.8: The south-facing slope on the sandstone hill, Ridgeway Park Reserve.

type (Table 2.3). The null hypothesis was that no differences in species richness occurred between the slopes and the rejection level was set at $P < 0.05$.

The difference in species richness between the north and south-facing slopes, is highest on the dolerite hill, and least on the mud-stone hill. Dolerite has the highest species richness on both north and south-facing slopes. To ensure these differences were not an artefact of the size of the sampling unit, species area curves were drawn for all three transects (Figure 2.8), and the 5 m^2 sampling units were found to be larger than the minimal area.

The total number of species found on the north-facing slope of the sandstone transect represents 55.4% of the total number of species found over the whole transect. This figure is much lower than those for the north-facing slopes on the dolerite (72.0%) and mudstone (71.4%) transects, while a comparison of the south-facing slopes shows the number of species (expressed as a percentage of the total number of species found over the whole transect) on the sandstone (67.8%) and mudstone (67.5%) transects to be lower than that of the south-facing slope on the dolerite transect (85.3%).

Life Form Analysis:

Table 2.4 shows the changes in lifeform between slopes of different aspect and rock type. The dolerite transect was found to contain a much higher percentage of grass, graminoid and herb species, and a much lower percentage of trees and tall shrub species when com-pared with the mudstone and sandstone transects. The percentage of grasses on the north-facing slope of the dolerite transect is an under-estimation of reality since this slope contained many more species than could be identified.

The ecological factors that influence the abundance of each life-form on slopes of different aspect and rock type are the subject of future analysis (see section on vegetation – radiation relationships).

	SPECIES RICHNESS	
	SOUTHERN ASPECT	NORTHERN ASPECT
ALL SPECIES	D 28.94 ——————— 32.71 M 16.79 15.31 S 16.7 ——————— 19.88	
TREES & TALL SHRUBS	D 4.12 ——————— 2.53 M 3.79 3.19 S 3.56 3.08	
SMALL SHRUBS	D 5.65 ——————— 9.65 M 5.21 4.96 S 3.78 ——————— 6.08	
HERBS	D 10.18 8.82 M 3.00 2.62 S 3.30 ——————— 4.56	
GRASSES	D 3.41 ——————— 4.88 M 1.71 1.65 S 2.20 1.84	
GRAMINOIDS	D 3.82 ——————— 4.82 M 0.54 0.88 S 1.41 1.68	
FERNS	D – – M 0.46 – S 0.89 0.64	

TABLE 2.3: Comparison of the species richness for each lifeform between sites differing in aspect or lithology (no cross comparisons were made between the species richness on sites differing in aspect and lithology). Significant relationships (P>0.05) denoted by a line. D = dolerite, M = mudstone, S = sandstone. (The Graminoid category excludes the Grasses).
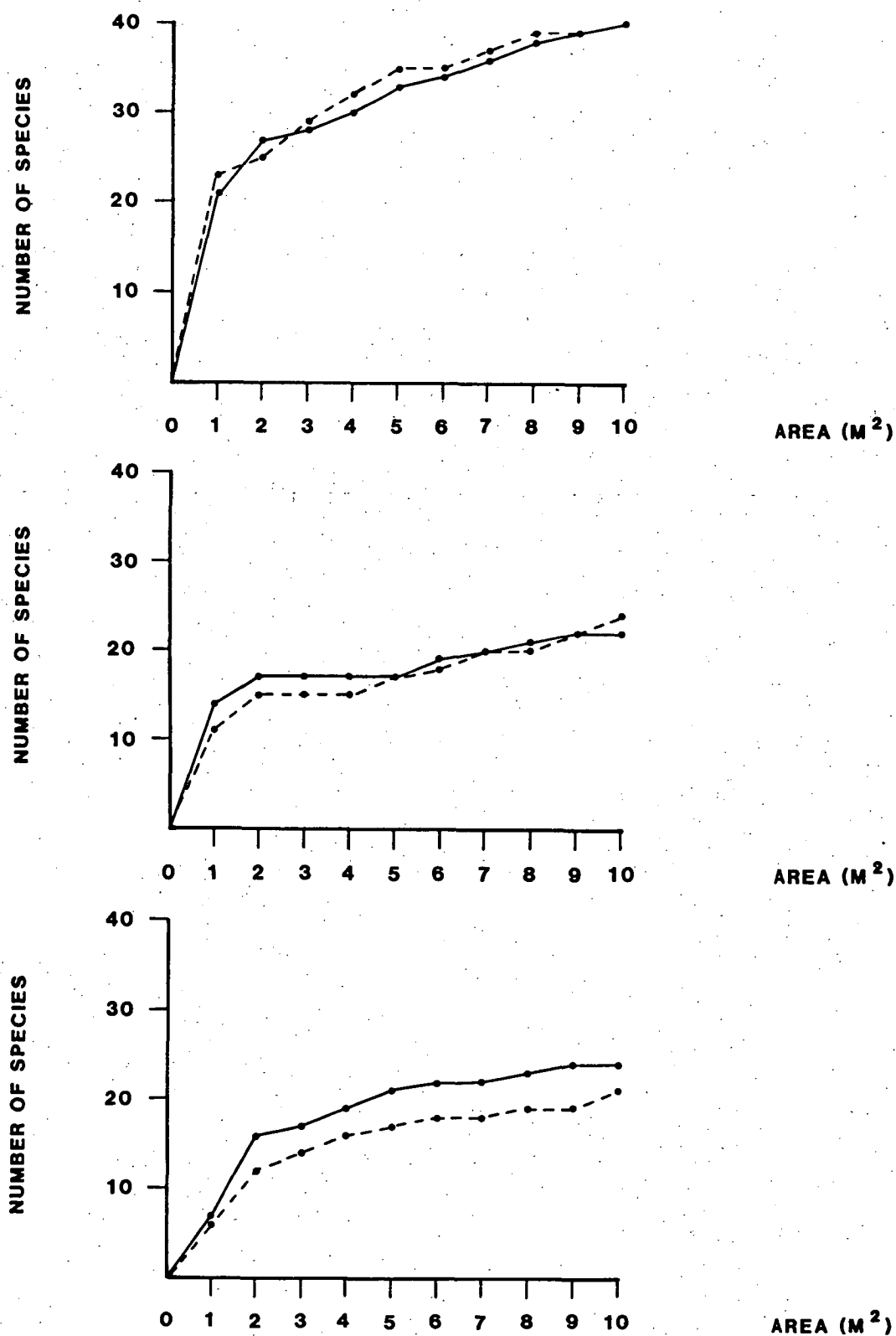
FIGURE 2.8: The species area curves for the north and south-facing slopes on the dolerite (top), mudstone (middle) and sandstone (below). —— = south-facing slope; --- = north-facing slope.

		Mean no. of species, expressed as a percentage of the total no. of species, on each slope.	
		SOUTHERN ASPECT	NORTHERN ASPECT
TREES & TALL SHRUBS	D	14.24	7.73
	M	22.57	20.84
	S	21.32	15.49
SMALL SHRUBS	D	19.52	29.50
	M	31.03	32.40
	S	22.63	30.58
HERBS	D	35.18	26.94
	M	17.87	17.11
	S	19.76	22.94
GRASSES	D	11.78	14.92
	M	10.18	10.78
	S	11.98	9.26
GRAMINOIDS	D	13.20	14.74
	M	3.22	5.75
	S	8.44	8.45
FERNS	D	0.00	0.00
	M	2.74	0.00
	S	5.33	3.22

TABLE 2.4: Analysis of lifeform between slopes of different aspect and lithology. D = dolerite transect; M = mudstone transect and S = sandstone transect.

Floristic Variation:

The similarity between the north and south-facing slopes of each transect was quantified using Sørensen's community coefficient (Sørensen 1948);

$$IS_{Mo} = \frac{2Mw}{MA + MB} \times 100$$

Two groups of five adjacent quadrats were compared, one from the north-facing slope and one from the south-facing slope. The comparison made using presence-absence data were between: (1) the groups sampled at the bottom of each north and south-facing slope, and (2) the group receiving the lowest radiation receipt on the south-facing slope, and that receiving the highest radiation receipt on the north-facing slope.

The results (Table 2.5) show that approximately one third of the total number of species found along each transect occurred on both the north and south-facing slopes. Thus the distribution of the remaining (two thirds) species was determined by topography; i.e. differences in the receipt of solar radiation. The value of 28.6% obtained from comparing the groups of quadrats at the bottom of the north and south-facing of the sandstone transect may be artifically deflated because of the break in sampling at the bottom of the north-facing slope.

Quantitative Analysis of Species Distribution Between Sites:

The number of species found only on the dolerite and mudstone transects, the dolerite and sandstone transects, and the mudstone and sandstone transects were 4, 10 and 24 respectively.

The distribution of each species on a particular aspect was placed into one of four categories depending upon whether it occurred in; (1) the dolerite and mudstone transects, (2) the dolerite and sandstone transects, (3) the mudstone and sandstone transects or (4) in all three. A further division was made (see Table 2.6), of those species restricted to the one aspect on both rock types (column 2) and those species (column 1) which may occur; (1) on both aspects in one of the

Bedrock	Comparison of groups (of quadrats) at the bottom of each north and south-facing slope.	Comparison of groups (of quadrats) receiving the highest radiation receipt (i.e. on the north-facing slope) and the group receiving the lowest radiation receipt (i.e. on the south-facing slope).
DOLERITE	34.5%	35.5%
MUDSTONE	32.4%	38.5%
SANDSTONE	28.6%	34.5%

TABLE 2.5: The percentage similarity of the north and south-facing slopes on the dolerite, mudstone and sandstone hills, Ridgeway Park Reserve.

	D - M		D - S		M - S		D - M - S	
	No. of species found on this aspect on both rock types	No. of species restricted to the one aspect on both rock types.	No. of species found on this aspect on both rock typs	No. of species restricted to the one aspect on both rock types.	No. of species found on this aspect on both rock types.	No. of species restricted to the one aspect on both rock types.	No. of species found on this aspect on both rock types	No. of species restricted to the one aspect on both rock types.
North facing slope	3	1	5	1	14	4	21	0
South facing slope	5	0	9	3	17	10	20	3

TABLE 2.6: The number or species found on a particular aspect and combination of rock types. D = dolerite, M = mudstone and S = sandstone.

two rock types or (2) on all three rock types, but only in two was it on the aspect under consideration. The results (Table 2.6) were then expressed as a percentage of the total number of species occurring on that rock type (Table 2.7).

The south-facing slopes, in all the combinations of rock type, are more alike than the north-facing ones: i.e. there is a tendency for the vegetation to converge on these slopes (cf. Hogg and Kirkpatrick 1974). The sites that share the least number of species are dolerite and mudstone, while those with the highest number of species in common are mudstone and sandstone, a trend that was found on both the north and south-facing slopes. In all situations approximately a third of all species on a particular rock type were found on the other two. Therefore, two-thirds of the species were restricted to particular lithologies which implies that their distribution was dependent upon one or a combination of several ecological factors including soil moisture availability, soil nutrient status, and grazing.

2.5.2 Ecological Factors Influencing the Forest Communities

Radiation Receipt:

Figures 2.9, 2.10 and 2.11 illustrate the radiation receipt for; (1) the solstice months of June and December, and (2) for the whole year, along the dolerite, mudstone and sandstone transects respectively. The highest values of radiation occur in December, on the north-facing slope, and the differences in radiation receipt between the three slopes are least in this month and greatest in June.

The dramatic difference between the radiation receipt of the north and south-facing slopes on the mudstone and sandstone transects is an artefact of the location of the transects. Over a hillslope, the change will be one of gradual decline from the north to the south-facing slope, as is shown for the dolerite transect (Figure 2.9).

The radiation receipt in December for some of the sites along the north-facing slope of the dolerite transect is low because of the

	Total No. of species upon transect	D-M		D-S		M-S		D-M-S	
		Column 1	Column 2	Column 1	Column 2	Column 1	Column 2	Column 1	Column 2
		No. of species restricted to the one aspect on both rock types.	No. of species found on this aspect on both rock types.	No. of species restricted to the one aspect on both rock types.	No. of species found on this aspect on both rock types.	No. of species restricted to the one aspect on both rock types.	No. of species found on this aspect on both rock types.	No. of species restricted to the one aspect on both rock types.	No. of species found on this aspect on both rock types.
North facing slope — 54 D	54	5.6	1.9	9.3	1.9	-	-	38.9	-
55 M	55	5.4	1.8	-	-	25.4	7.3	38.2	-
49 S	49	-	-	10.2	2.0	28.6	8.2	42.9	-
South facing slope — 64 D	64	7.8	-	14.1	4.69	-	-	31.3	4.7
52 M	52	9.6	-	-	-	32.7	19.2	38.5	5.8
61 S	61	-	-	14.8	4.92	27.9	16.4	32.8	4.9

TABLE 2.7: The number of species, found on a particular aspect and combination of rock types, expressed as a percentage of the total number of species on each slope. D = dolerite, M = mudstone and S = sandstone.
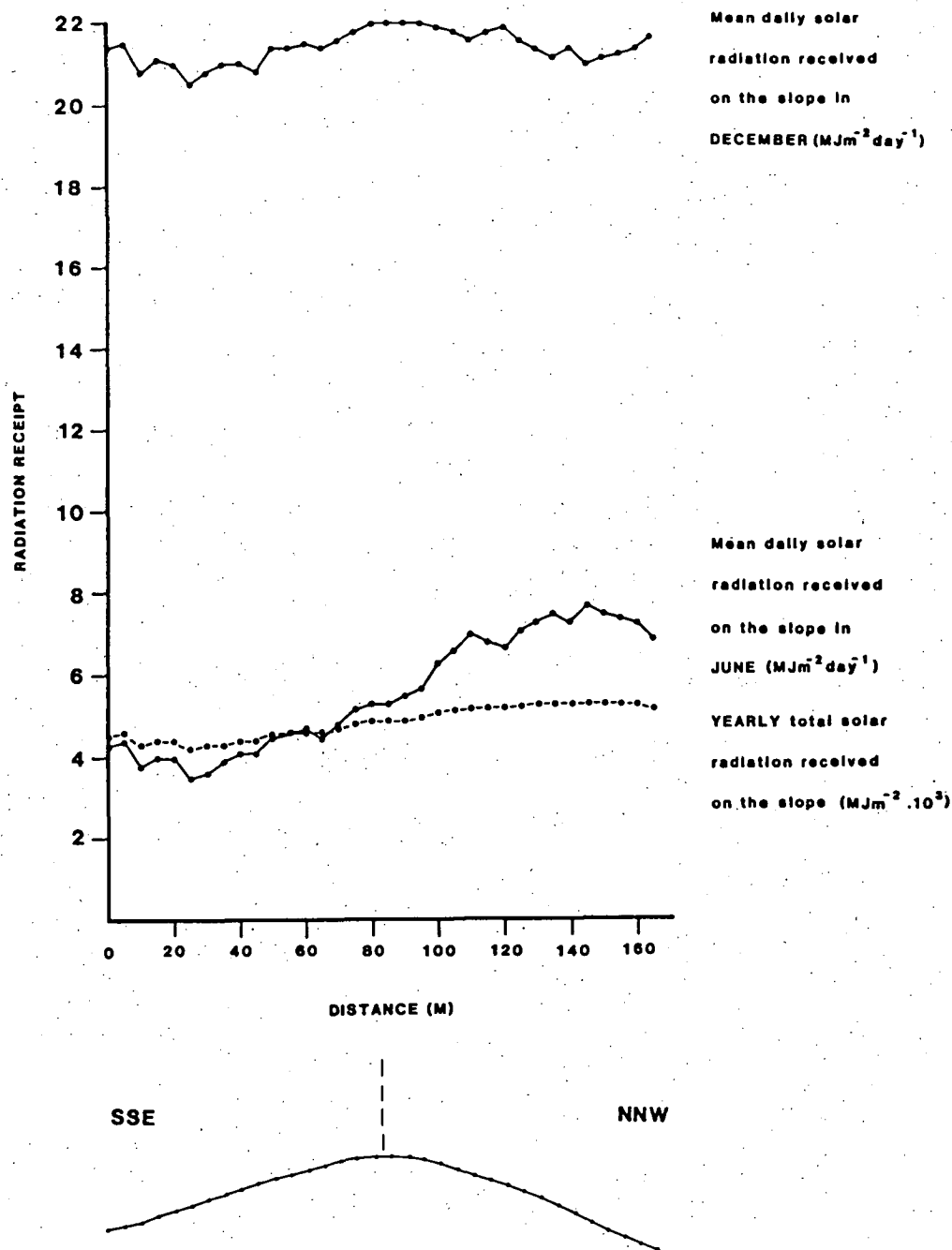
FIGURE 2.9: The solar radiation received across the dolerite
hill in December, June and for the whole year.
--- = a gap in the sampling.
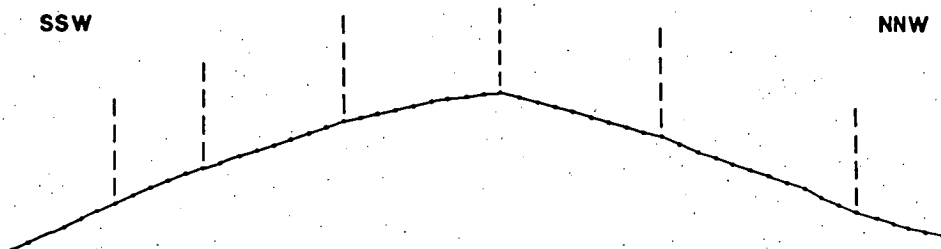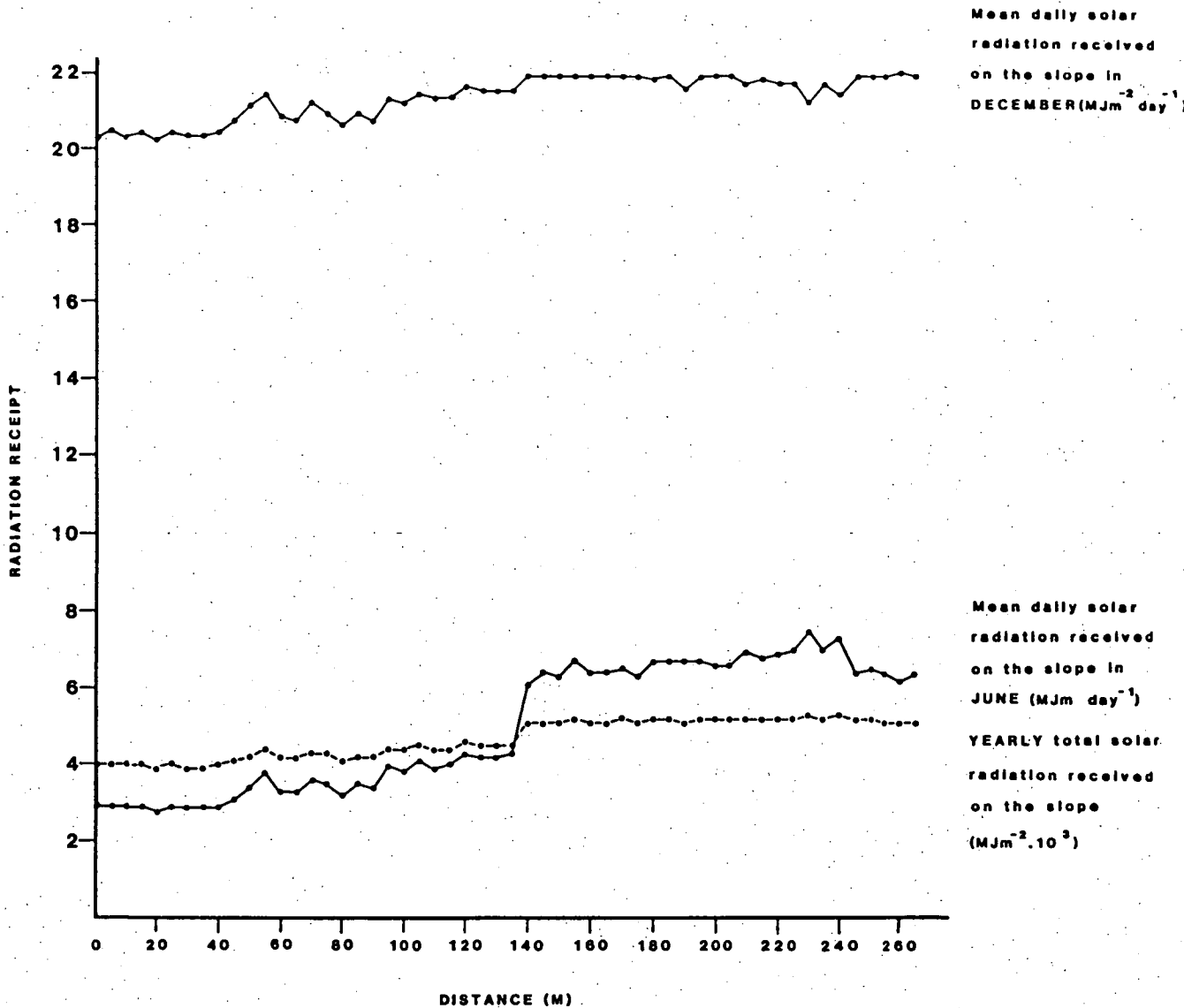
FIGURE 2.10: The solar radiation received across the mudstone hill in December, June and for the whole year.
--- = a gap in the sampling.
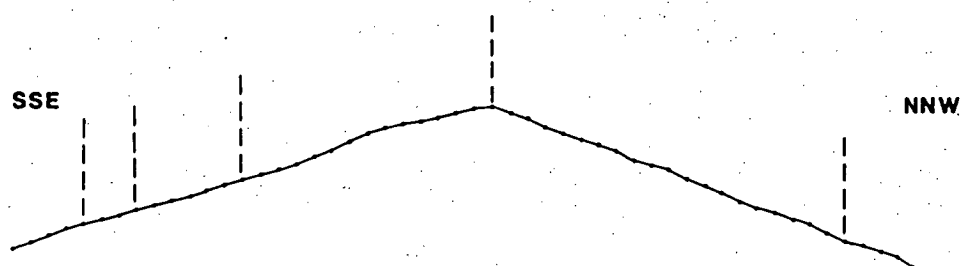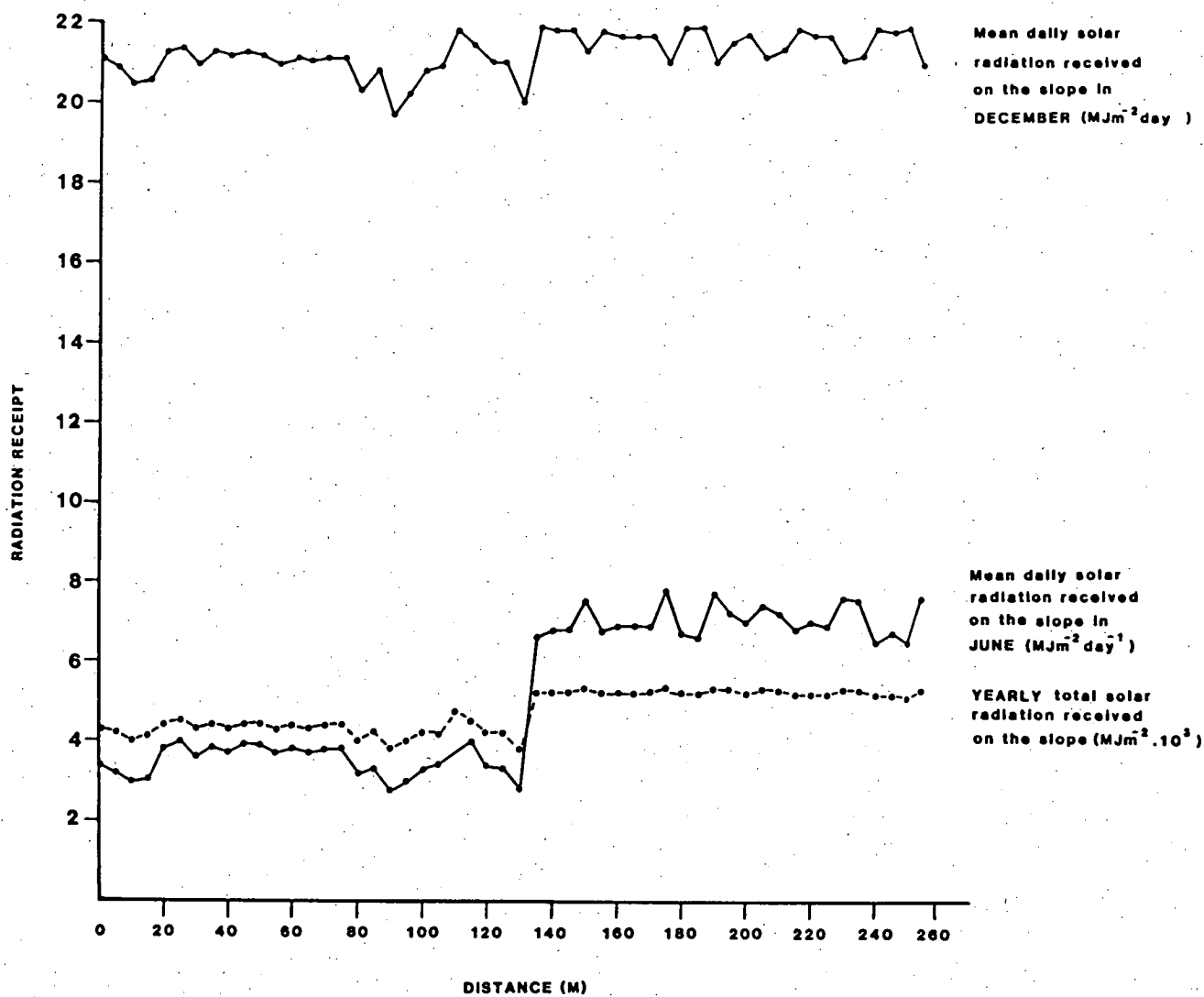
FIGURE 2.11: The solar radiation received across the sandstone
hill in December, June and for the whole year.
--- = a gap in the sampling.

steep angle of the hillslope at these locations (i.e. where rock outcrops).

Air Temperature:

Figure 2.12 shows the mean maximum and minimum temperatures recorded along the three transects during the winter of 1984. Temperature varies only slightly between sites and aspects.

Soil Depth:

Figure 2.13 shows the depth of the soils along the three transects. The soils on the south-facing slopes of all three sites were deeper than those on the north-facing slopes. The podzols on the sandstone bed-rock were the deepest of the three soils, while the brown earth was the shallowest.

Soil depth (and the proportion of fines in the soil) usually increases downslope because of the downward movement of the soil particles (McColl 1969). However, the podzolic soils on the mudstone bedrock appear to become shallower towards the bottom of the north-facing slope. This is probably due to disturbance of the environment, as many paths and tracks criss-cross the base of the slope which adjoins an area of private housing (this was taken into account when deriving mean soil depth, on the north-facing slope of the mudstone transect, for use in deriving the soil water capacity of this soil).

Rock Content in Soils:

Rocks reduce the amount of water that can be held by a given volume of soil. Thus, as the rock content increases in a soil, the depth of penetration by a given volume of water also increases (see discussion).

The percentage rock contents of the brown earth, podzolic soil
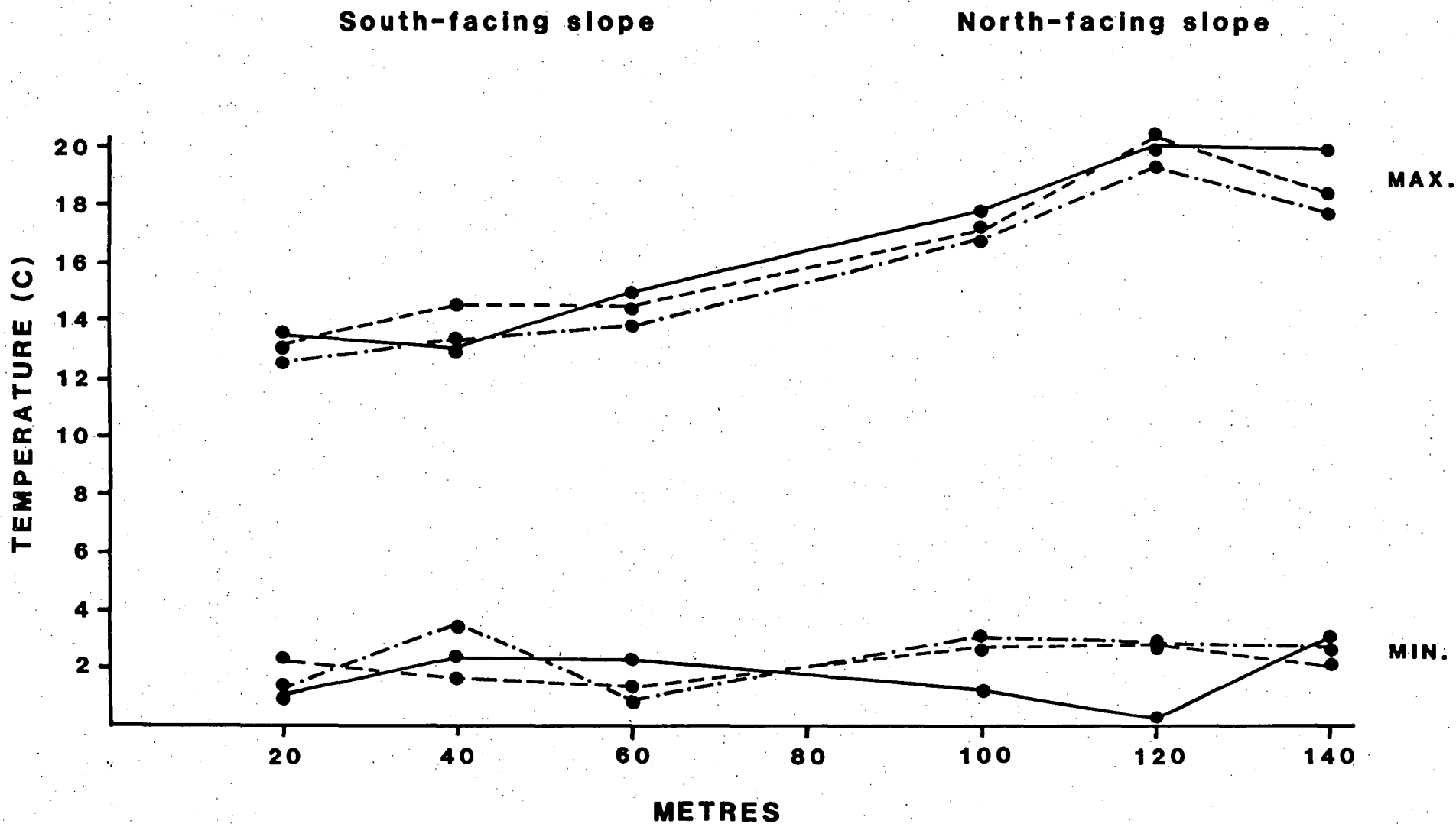
FIGURE 2.12: The mean maximum and minimum temperatures received across each of the three hills during the Winter of 1984. —— = dolerite hill; --- = mudstone hill; -.-.-. = sandstone hill.

FIGURE 2.13: Soil depth data along transects across dolerite, sandstone and mudstone hills in the Ridgeway Park Reserve.

and podzol were 20%, 36% and 12% respectively.

Soil Nutrients:

Soil pH may be used as an approximate guide to the fertility
of a soil because of its effects upon; (1) the amount of nutrient
release by weathering, (2) the solubility of nutrients and (3) the
number of nutrient ions stored in the soil (Buckman and Brady 1960;
Thompson and Troeth 1973). Slightly acid soils are generally the
most fertile (Briggs 1977), and most plant nutrients are available to
plants within a range of 6.5 - 7.5 (Thompson and Troeh 1973). Hence,
the browth earth, with a pH of 6.0 - 7.0, is likely to be the most
fertile of the three soils (Figure 2.14).

The soils on south-facing slopes are usually more acid than those
on north-facing slopes due to, amongst other things, the higher rate
of leaching, and the increased amounts of organic matter upon them.
The podzols and brown earths may deviate from this expected
pattern because of the greater abundance of broad leaves species
on the south-facing slope, which may add bases to the soil, and/or the
method of sampling. The pH of the podzolic soils was measured from
samples taken from relatively deep in the profile because hazard reduction
burns had altered the nature of the soil near the surface. The podzols
and brown earths, however, were sampled from just beneath the humus layer,
a part of the profile in a continual state of flux. Here, the rate of
decay of organic matter, the release of organic acids and nutrients into
the soil and the rate of leaching is continually changing, probably
causing pH to vary in space and time.

The Soil Model:

The modelled daily values of soil moisture (SM) for each of the
three soils were compared at twenty day intervals (Figure 2.15). The
peaks in SM correspond to the period during which most rain falls,
Winter and Spring.
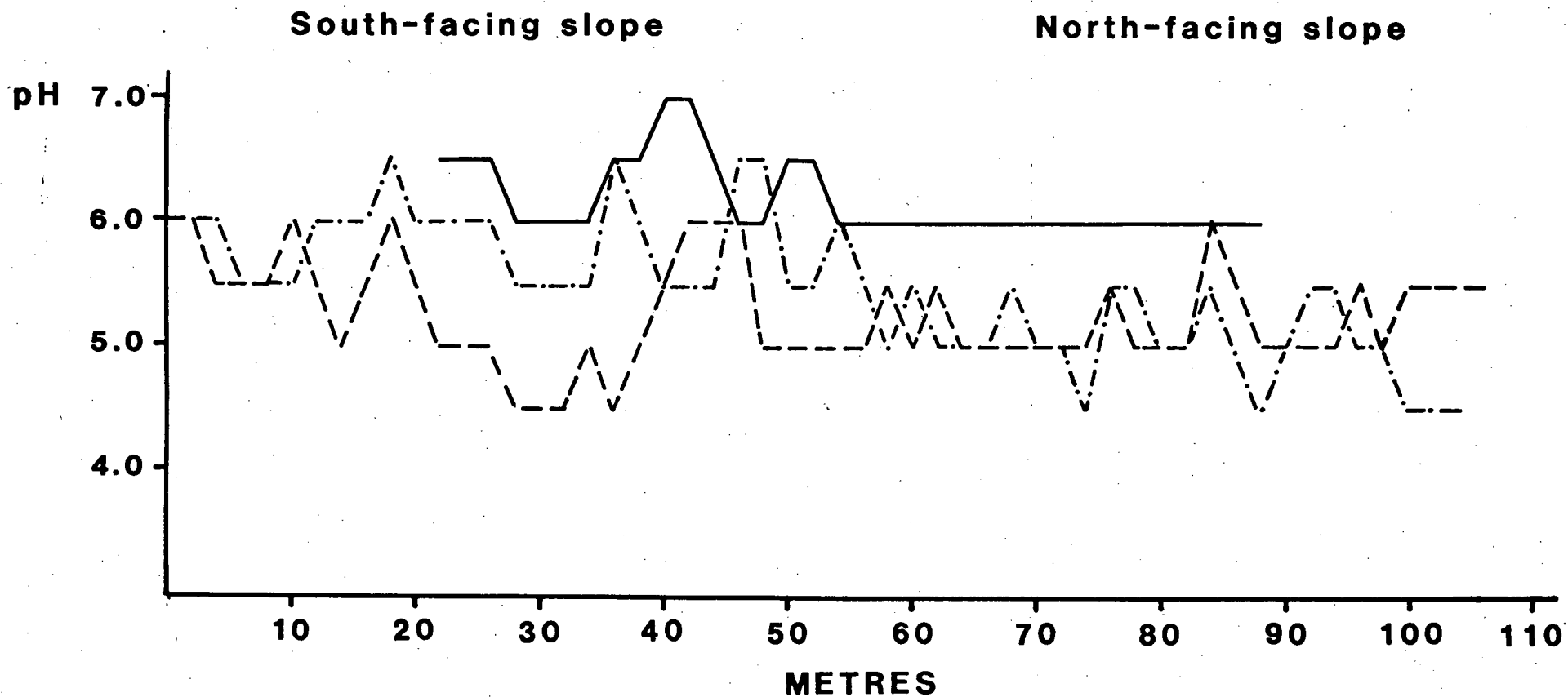
FIGURE 2.14: pH data for the brown earth, podzolic soil and podzol along the dolerite, mudstone and sandstone hills respectively. ——— = brown earth; — — — = podzolic soil; —·—·—·= podzol
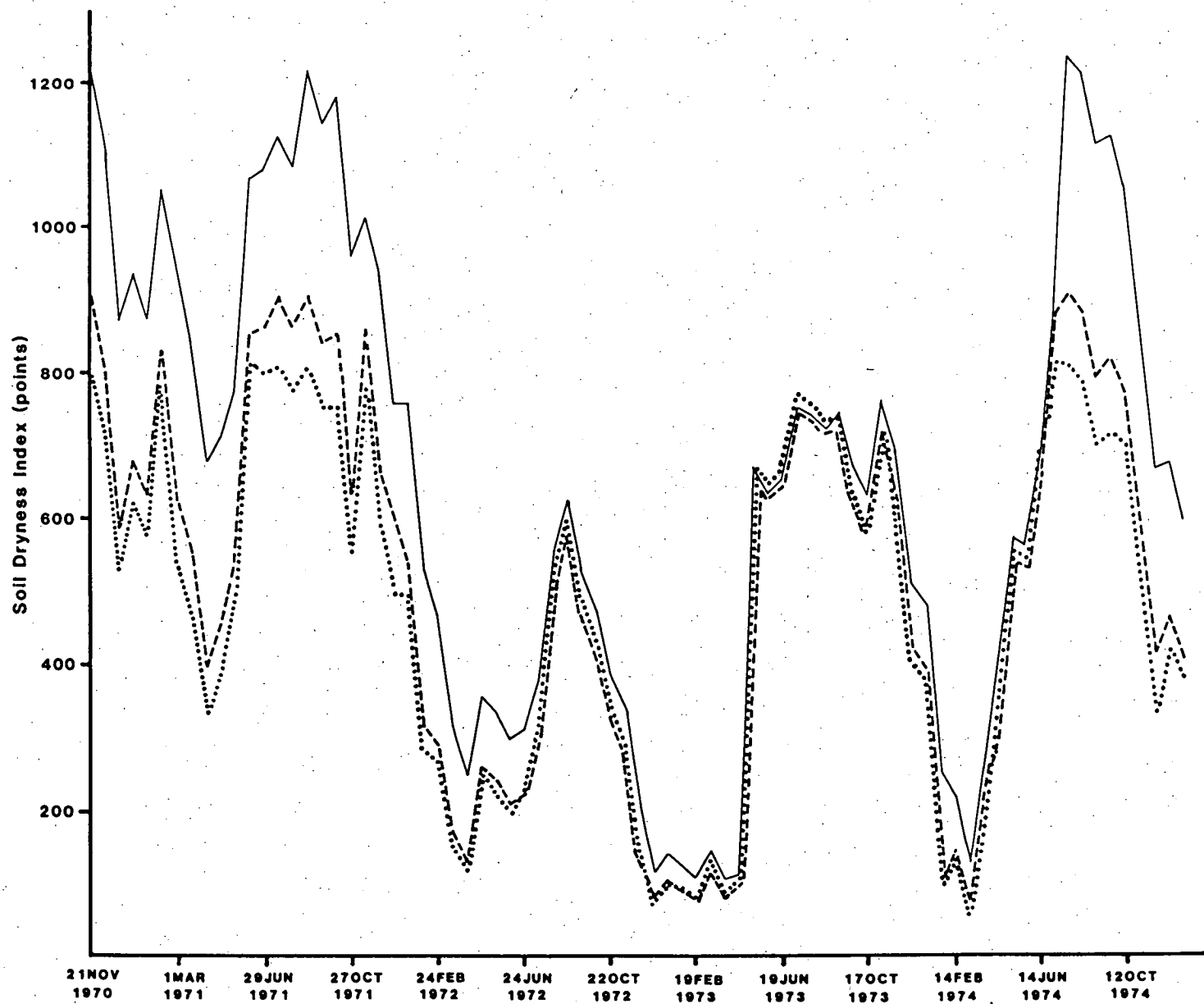
FIGURE 2.15: The change in soil moisture, in the brown earths (...), podzolic soils (---) and the podzols (——), over time.

During years of "high" rainfall the difference between the soils was at a maximum. 1972 and 1973 were years of low rainfall and it was during these years that; (1) the amount of water in all three soils was low and (2) the difference in the amount of water between the soils was negligible, so much so that the pattern established in years of high rainfall (namely the podzol and the brown earth being the wettest and driest soils respectively) was occasionally altered.

Histograms were plotted, showing the number of days that the SM fell within each class interval, for all three soil types (Figure 2.16). This illustrates that the soil subject to the greatest amount of dryness, that is the one with the highest number of days in which the SM falls between 0-50 points, was the brown earth on the dolerite bedrock. The histograms also show a close similarity between the values of SM for the brown earth and podzolic soils (see Discussion). However, the range of values for soil dryness were much larger in the podzolic soil. Thus, the podzolic soil was generally wetter than the brown earth.

In the sample taken, seventy-seven comparisons were made between the daily SM of the three soils. The SM of the podzol in all cases was higher than that of the podzolic soil, and in 90.9% of the cases higher than that of the brown earth. In 64.9% of the cases the SM of the podzolic soil was higher than that of the brown earth. These results were compared statistically using the χ^2 test. The null hypothesis stated that there was no difference in the SM between the soils, and the rejection level was set at $P < 0.05$. The null hypothesis was rejected with daily values of SM for the podzol being significantly higher than those of the podzolic soil and the brown earth. In turn, the daily values of SM for the podzolic soil were found to be significantly higher than those for the brown earth.

2.5.3 Relationships Between Vegetation and Radiation by Substratum

To determine the nature of the differential effect of the three soils upon species distribution, the values of radiation received by the transects in three periods (June, December and Annually) were divided
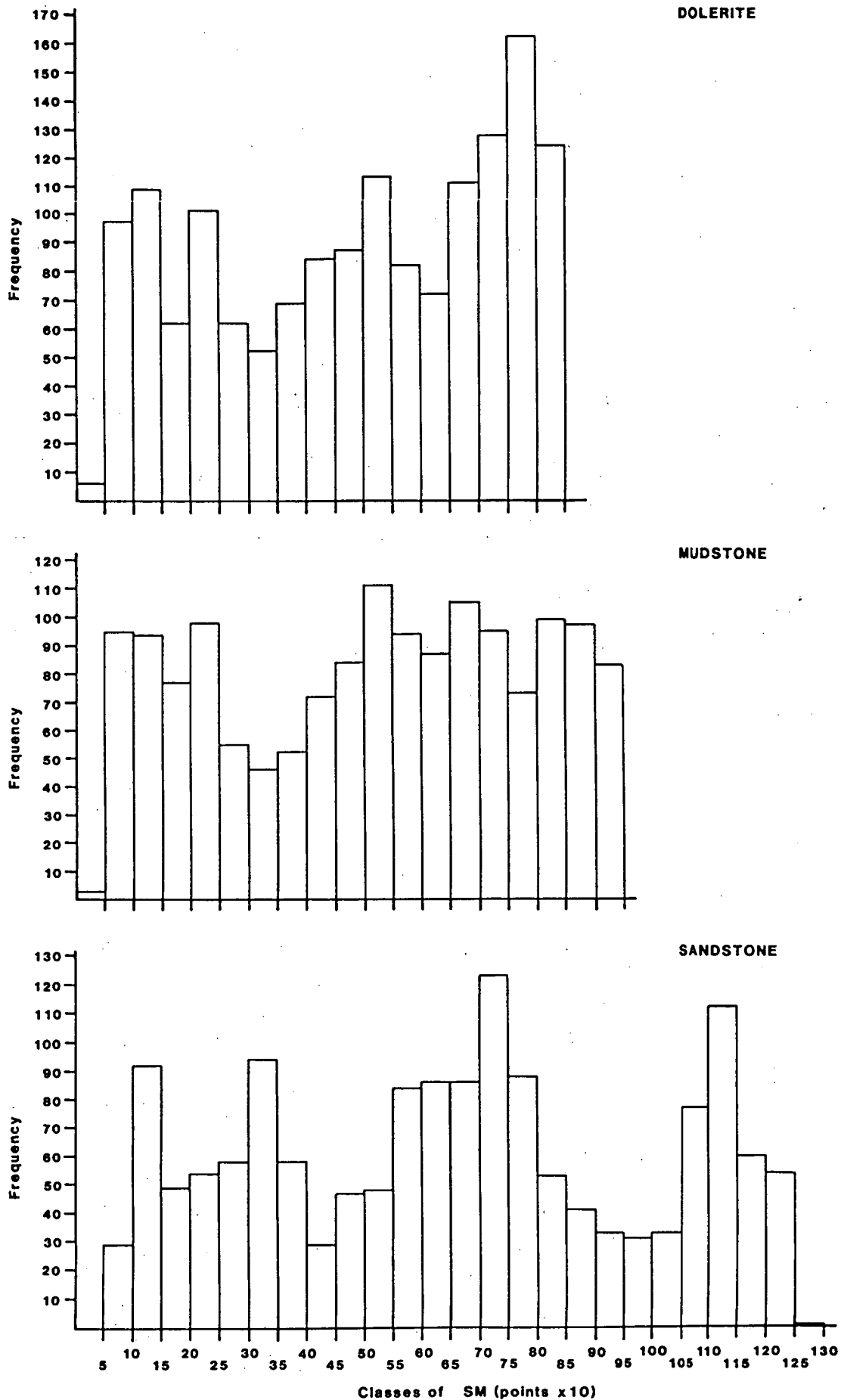
FIGURE 2.16: Histograms showing the range and frequency of soil
moisture in the soils on the dolerite, mudstone and
sandstone hills.

into classes and the mean frequency of every species on each soil type was derived for that class. The class intervals were determined so as to ensure at least a number of cases in each class on each rock type.

Any species with a frequency of less than 10.0 in all three radiation classes was not included in the main analysis. Thus, 17 of the 37 species that occurred on all three transects were treated separately (henceforth these species will be referred to as G_2 species and those species with a frequency of more than 10.0 in all three radiation periods as G_1 species).

Figure 2.17 (a-f) shows the mean frequency of selected species with increasing radiation. The response of each species was then "classified" according to the order in which the species frequency peaked between the rock types (see Tables 2.8 and 2.9). For example, comparing the response curve of *Epacris impressa* between the three transects (see Figure 2.17b) shows that the curve upon the dolerite transect (D) reaches its peak at a lower level of radiation in the June and Annual radiation periods compared with the curve upon the sandstone (S) and the mudstone (M) transects, and that the curve upon the sandstone transect peaks at a lower level of radiation than that on the mudstone transect. Thus, *Epacris impressa* falls into the classification D-S-M for these two radiation periods (see Table 2.8).

For most species the total response curve was incomplete and in many instances there was not enough information to determine the order of peaking between the rock types. For instance, *Bedfordia linearis* reached its peak frequency on the dolerite and mudstone transects in the same radiation class interval. In the final analysis, when the response of a species between rock types was placed into one of six classifications (M-D-S, M-S-D, D-S-M, D-M-S, S-M-D, S-D-M), a species whose response was tied as in M+D-S, was classified with half peaking in the order M-D-S and half in the order D-M-S.

Table 2.10 shows the number of (G_1) species whose response to increasing radiation between the three soils, follows each of the six combinations. The likelihood of a species peaking in one or other of the combinations was compared statistically using the χ^2 test. The data

(a) *Bedfordia linearis*

June Radiation
(MJm^{-2}Day^{-1})

December Radiation
(MJm^{-2}Day^{-1})

Annual Radiation
(MJm^{-2}Yearx10^3)
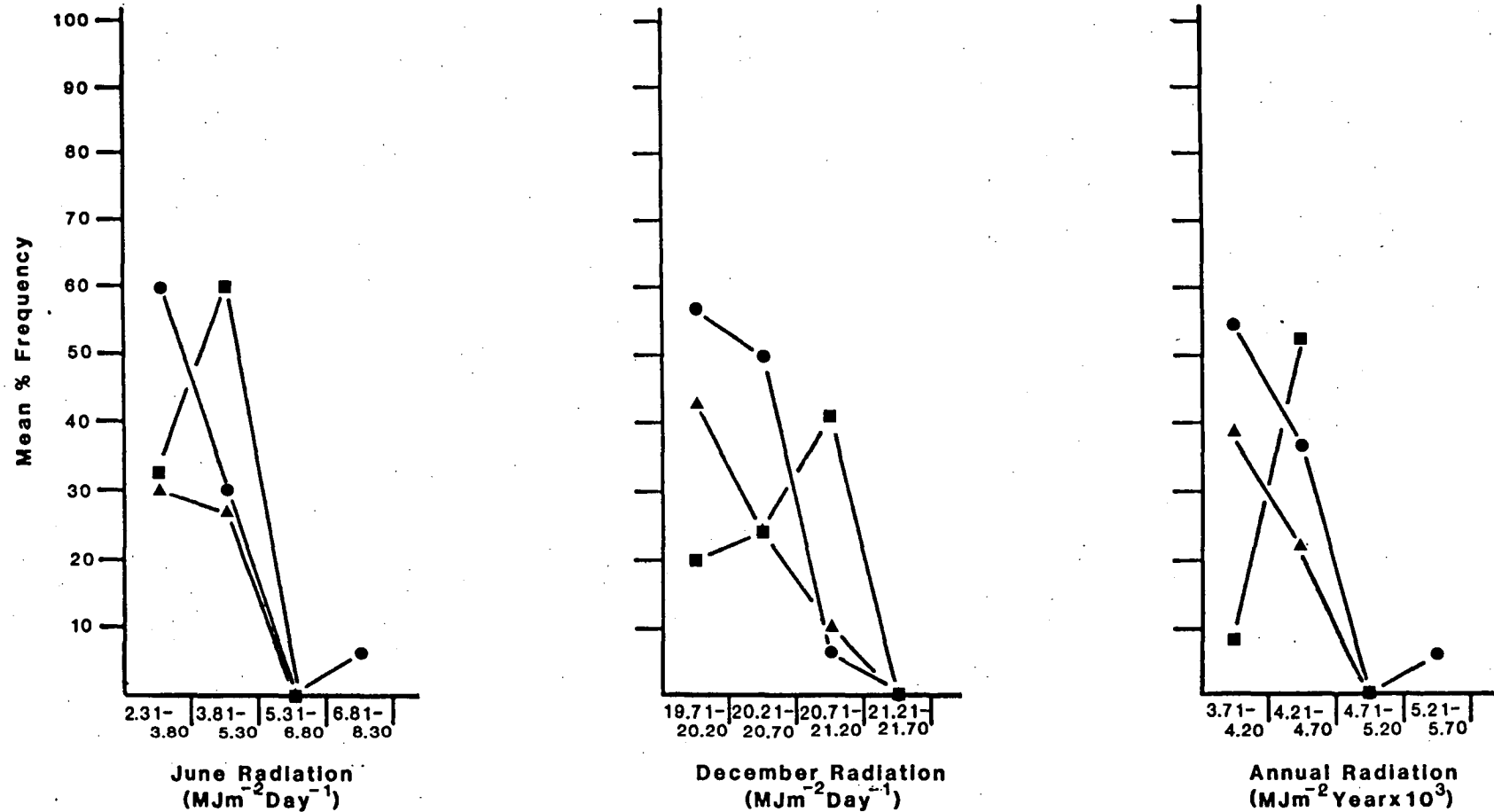
FIGURE 2.17 (a-f): The frequency of six species, (a) *Bedfordia linearis*, (b) *Epacris impressa*,
(c) *Goodenia lanata*, (d) *Leptospermum scoparium*, (e) Other *Gramineae*,
(f) *Pultenaea juniperina*, with increasing June, December and Annual Radiation.
(●) = dolerite hill, (▲) = mudstone hill and (■) = sandstone hill.
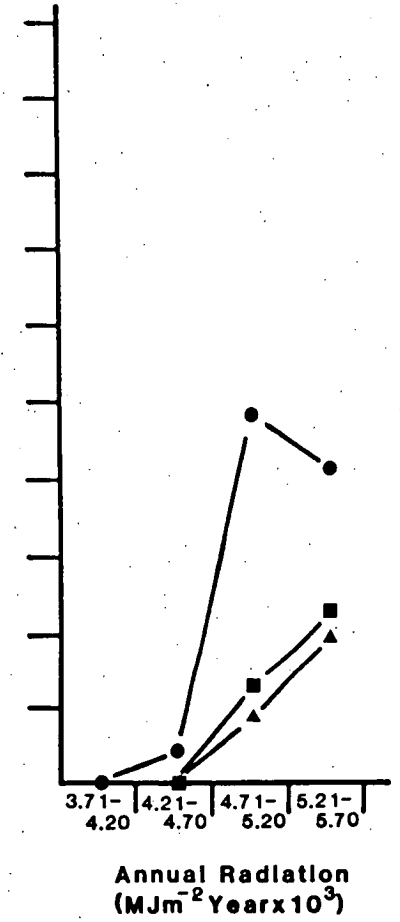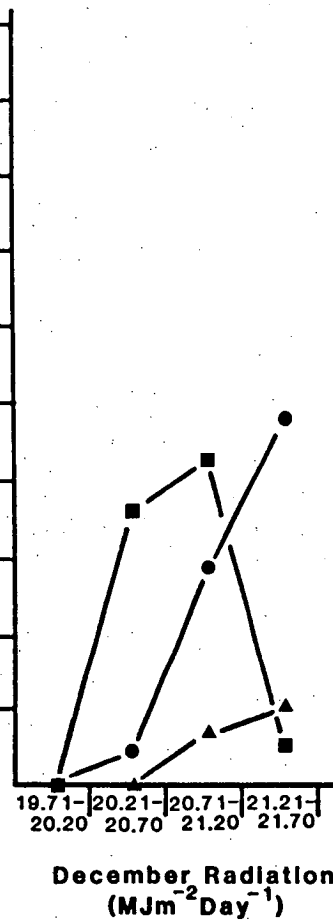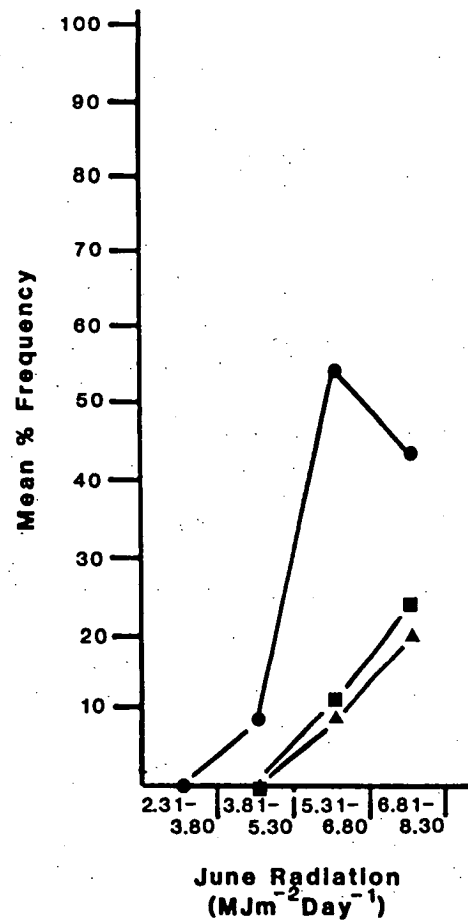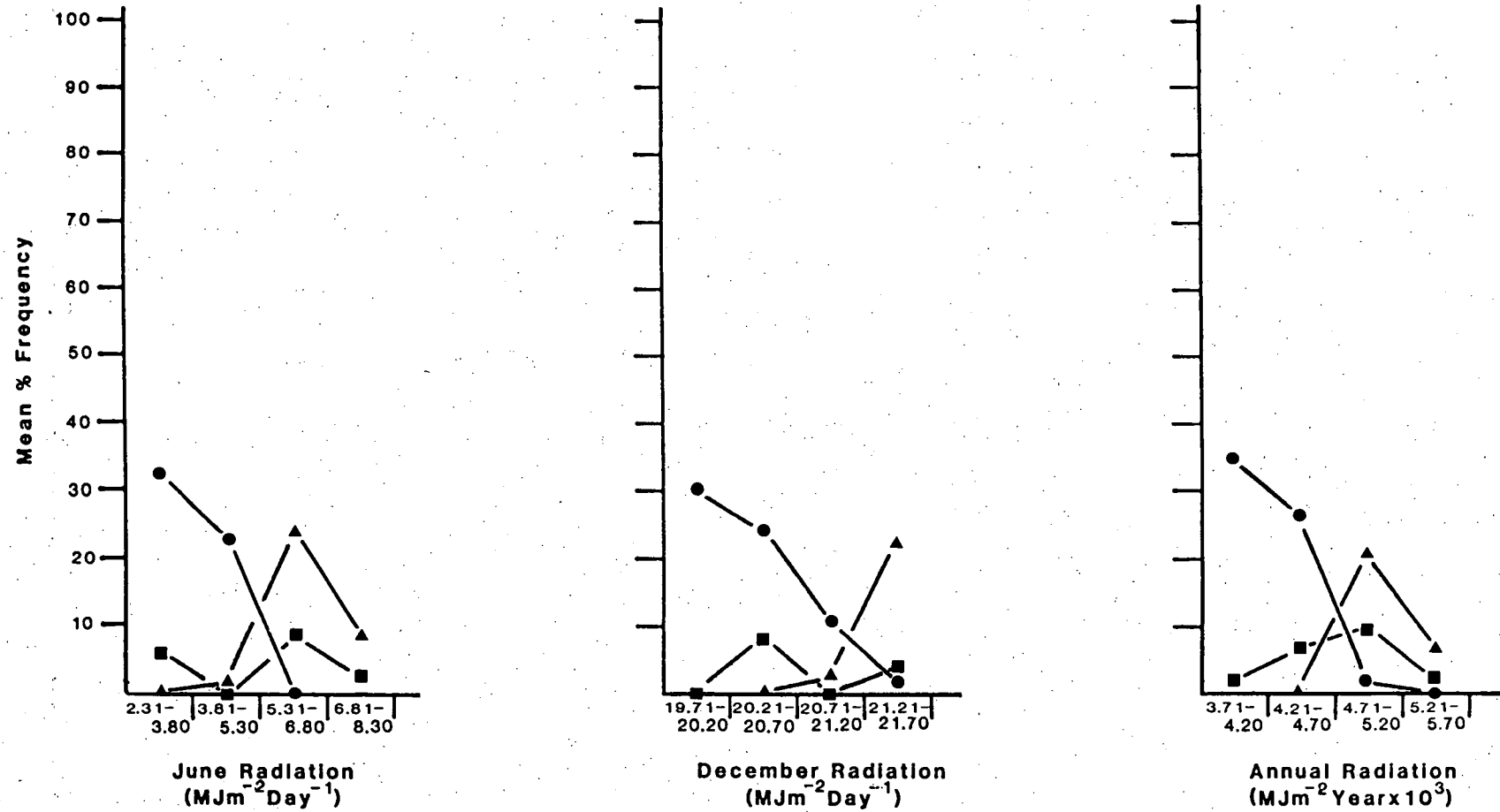
(b) *Epacris impressa*

June Radiation
(MJm^{-2}Day^{-1})

December Radiation
(MJm^{-2}Day^{-1})

Annual Radiation
(MJm^{-2}Yearx10^3)

Mean % Frequency

51

(c) *Goodenia lanata*

June Radiation
(MJm^{-2}Day^{-1})

December Radiation
(MJm^{-2}Day^{-1})

Annual Radiation
(MJm^{-2}Yearx10^3)

Mean % Frequency

52

(d) *Leptospermum scoparium*

(e) *Other Gramineae*

June Radiation
(MJm^{-2}Day^{-1})

December Radiation
(MJm^{-2}Day^{-1})

Annual Radiation
(MJm^{-2}Yearx10^3)

(f) *Pultenaea juniperina*

Mean % Frequency

| June Radiation (MJm^{-2}Day^{-1}) | December Radiation (MJm^{-2}Day^{-1}) | Annual Radiation (MJm^{-2}Yearx10^3) |

2.31–3.80 3.81–5.30 5.31–6.80 6.81–8.30

19.71–20.20 20.21–20.70 20.71–21.20 21.21–21.70

3.71–4.20 4.21–4.70 4.71–5.20 5.21–5.70

		JUNE RADIATION	DECEMBER RADIATION	ANNUAL RADIATION
MUDSTONE	M-D-S	*Poa spp.* -	- *Eucalyptus viminalis*	- -
	M-S-D	-	-	*Acacia dealbata*
	M-D+S	*Cassinia aculeata* -	*Cassinia aculeata* -	- *Haloragis tetragyna*
	M+D-S	*Bedfordia linearis* - *Gramineae* *Haloragis tetragyna* - *Stylidium graminifolium*	*Bedfordia linearis* - - - *Moss* *Stylidium graminifolium*	*Bedfordia linearis* *Geranium spp.* - - - *Stylidium graminifolium*
DOLERITE	D-M-S	- - -	*Epacris impressa* *Gramineae* -	- *Lomandra longifolia*
	D-S-M	*Epacris impressa* - -	- *Leptospermum scoparium* *Lomandra longifolia*	*Epacris impressa* - -
	D-S+M	*Eucalyptus obliqua* *Eucalyptus viminalis* - *Goodenia lanata* *Leptospermum scoparium* *Lomandra longifolia*	- - - -	- *Eucalyptus viminalis* *Gramineae* *Goodenia lanata* *Leptospermum scoparium* -
SANDSTONE	D+S-M	*Geranium spp.* *Haloragis teucrioides*	- *Haloragis teucrioides*	- *Haloragis teucrioides*
	S-D-M	-	-	-
	S-M-D	-	-	-
	S-D+M	*Danthonia spp.* - - -	*Danthonia spp.* - *Goodenia lanata* -	*Danthonia spp.* *Daviesia ulicifolia* - *Lichen*
	S+M-D	*Acacia dealbata* - -	*Acacia dealbata* - *Poa spp.*	- *Cassinia aculeata* *Poa spp.*
	S+M+D	*Daviesia ulicifolia* *Dianella tasmanica* - - - *Lichen* *Moss*	*Daviesia ulicifolia* *Dianella tasmanica* *Eucalyptus obliqua* *Geranium spp.* *Haloragis tetragyna* *Lichen* -	*Dianella tasmanica* *Eucalyptus obliqua* - - - *Moss*

TABLE 2.8: The order in which, with increasing radiation, each (G_1) species reaches its peak frequency on the rock types. D = dolerite transect, M = mudstone transect, S = sandstone transect.

		JUNE RADIATION	DECEMBER RADIATION	ANNUAL RADIATION
MUDSTONE	M-D-S	-	-	Prasophyllum spp.
	M-S-D	Coprosma quadrifida -	Coprosma quadrifida Exocarpos cupressiformis	Coprosma quadrifida -
	M-D+S	Helichrysum dendroideum - -	Helichrysum dendroideum Prasophyllum spp. Stipa spp.	Helichrysum dendroideum -
	M+D-S	Dianella revoluta Pterostylis spp. Prasophyllum spp. Pultenaea juniperina -	- - - -	Dianella revoluta Pterostylis spp. - Senecio spp.
DOLERITE	D-M-S	Banksia marginata - Senecio spp. -	- Pterostylis spp. Pultenaea juniperina -	Banksia marginata - Pultenaea juniperina - Wahlenbergia spp.
	D-S-M	-	-	-
	D-S+M	Astroloma humifusum - Helichrysum scorpioides Stipa spp. Viola hederacea -	- Banksia marginata - - Viola hederacea Wahlenbergia spp.	Astroloma humifusum - Helichrysum scorpioides - -
	D+S-M	Galium spp. Wahlenbergia spp.	- -	Galium spp.
SANDSTONE	S-D-M	-	Galium spp.	-
	S-M-D	-	-	-
	S-D+M	- -	Dianella revoluta -	- Exocarpos cupressiformis
	S+M-D	- - Eucalyptus pulchella - -	Astroloma humifusum Helichrysum scorpioides - Senecio linearifolius Senecio spp.	- - Eucalyptus pulchella Senecio linearifolius -
	S+M+D	- Exocarpos cupressiformis Senecio linearifolius - -	Eucalyptus pulchella - - - -	- - Stipa spp. Viola hederacea

TABLE 2.9: The order in which, with increasing radiation, each (G_2) species reaches its peak frequency on the rock types. D = dolerite transect, M = mudstone transect, S = sandstone transect.

were grouped into those species which with increasing radiation first reached their peak frequency upon; (1) the mudstone transect, (2) the dolerite transect and (3) the sandstone transect. This was necessary in order that the expected value be greater than 5 in 100% of the cases and therefore the results of the test valid (Mueller-Dombois and Ellenberg 1974). The null hypothesis was that there was no difference in the response of a species, to the radiation receipt, on the three soils (the brown earths, the podzolic soils and the podzols). All three radiation periods were subjected to the analysis and the rejection level was set at $P>0.05$. None of the results were significant, yet the trend in all three radiation periods was for more species (45.6%) to reach their peak frequency at lower levels of radiation on the dolerite transect compared with the mudstone and sandstone transects.

When the G_2 species were included in the above analysis, none of the results were significant at $P>0.05$ although the x^2 value of 9.70 for the June radiation period was significant at $P<0.10$. More species responded to increasing radiation in the order D-M-S, than to any other combination (see Table 2.11) and again the trend was for more species to peak upon the dolerite transect first (45.0%).

Due to the method of dealing with species (G_1 plus G_2) whose response was tied between rock types (i.e. D+M-S, M+S-D and S+D-M) there may have been unnecessary distortions in the trends. So the x^2 analysis was performed again, with these species excluded (Table 2.12). Those species which peaked first on one rock type and whose response was identical for the other two rock types (i.e. D-M+S, M-D+S and S-D+M) were included in the analysis because again, the data set had to be grouped into three to ensure the validity of the test (see conditions of first x^2 analysis).

The x^2 value of 11.41 for June was significant and the null hypothesis (see description of first x^2 analysis) was rejected. The x^2 value of 5.25 for the annual radiation period, just failed to be significant $(0.05<P \geqslant 0.10)$

	JUNE RADIATION			DECEMBER RADIATION			ANNUAL RADIATION		
	Column 1	Column 2	Column 3	Column 1	Column 2	Column 3	Column 1	Column 2	Column 3
M-D-S ⎫ M M-S-D ⎭	4.17 1.67	5.84	(29.20%)	4.00 2.50	6.50	(32.50%)	2.50 3.00	5.50	(27.50%)
D-S-M ⎫ D D-M-S ⎭	5.17 5.17	10.34	(51.70%)*	3.50 4.50	8.00	(40.00%)*	4.00 5.00	9.00	(45.00%)*
S-M-D ⎫ S S-D-M ⎭	1.67 2.17	3.84	(19.20%)	3.00 2.50	5.50	(27.50%)	3.00 2.50	5.50	(27.50%)

TABLE 2.10: Number of G_1 species that with increasing radiation peak in each of the combinations of rock types (Column 1). Data grouped to show number of species that peaked first on each transect (mudstone, dolerite or sandstone; Column 2). This figure is represented as a percentage (Column 3). Asterisk denotes when the majority of species peak on the dolerite transect first. M = mudstone transect, D = dolerite transect, S = sandstone transect.

	JUNE RADIATION			DECEMBER RADIATION			ANNUAL RADIATION		
	Column 1	Column 2	Column 3	Column 1	Column 2	Column 3	Column 1	Column 2	Column 3
M-D-S ⎱ M M-S-D ⎰	7.00 4.00	11.00	(29.73%)	5.67 8.17	13.84	(37.41%)	5.83 5.83	11.66	(31.51%)
D-S-M ⎱ D D-M-S ⎰	8.50 11.50	20.00	(54.05%)*	5.17 8.17	13.34	(36.05%)	5.83 10.83	16.66	(45.03%)*
S-M-D ⎱ S S-D-M ⎰	2.50 3.50	6.00	(16.22%)	5.67 4.17	9.84	(26.59%)	4.83 3.83	8.66	(23.41%)

TABLE 2.11: Number of G_1 plus G_2 species that with increasing radiation peak in each of the combinations of rock types (Column 1). Data grouped to show number of species that peaked first on each transect (mudstone, dolerite or sandstone; Column 2). This figure is represented as a percentage (Column 3). Asterisk denotes when the majority of species peak on the dolerite transect first. M = mudstone transect, D = dolerite transect, S = sandstone transect.

	JUNE RADIATION			DECEMBER RADIATION			ANNUAL RADIATION		
	Column 1	Column 2	Column 3	Column 1	Column 2	Column 3	Column 1	Column 2	Column 3
M-D-S } M M-S-D }	2.00 } 2.00 }	4.00	(23.53%)	3.00 } 4.00 }	7.00	(35.00%)	2.00 } 3.00 }	5.00	(25.00%)
D-S-M } D D-M-S }	5.50 } 6.50 }	12.00	(70.59%)*	3.50 } 5.50 }	9.00	(45.00%)*	4.00 } 7.00 }	11.00	(55.00%)*
S-M-D } S S-D-M }	0.50 } 0.50 }	1.00	(5.88%)	1.50 } 2.50 }	4.00	(20.00%)	2.00 } 2.00 }	4.00	(20.00%)

TABLE 2.12: Number of selected species (i.e. those whose response was not tied between rock types), that with increasing radiation peak in each of the combinations of rock types (Column 1). Data grouped to show number of species that peaked first on each transect (mudstone, dolerite or sandstone; Column 2). This figure is represented as a percentage (Column 3). Asterisk denotes when the majority of species peak on the dolerite transect first.
M = mudstone transect, D = dolerite transect, S = sandstone transect.

Table 2.13 shows the response of each lifeform to increasing radiation on the three soils. The Table shows the response of G_1, and G_1 plus G_2 species for all three radiation periods. From a consideration of the G_1 species, the number of lifeforms that follow the 'trend' of peaking at a lower level of radiation on the dolerite compared to the mudstone and sandstone transects, was 4, 2 and 3 in June, December and in the Annual Radiation period respectively. The figures for the G_1 plus G_2 species were 3, 0 and 4 respectively.

For the G_1 species, the shrubs and graminoids follow this 'trend' in all three radiation periods, the herbs in two radiation periods, and the trees and tall shrubs in one. For the G_1 plus G_2 species, the trend is less apparent, while the grasses do not follow it at all (see Discussion).

In all the analyses, the trend was most weakly expressed in the December radiation period. Yet during this month the vegetation is subjected to very high temperatures and water deficits. The fact that no significant trends were found may simply be because the differences in the December radiation receipt between north and south-facing slopes are very small compared with those for June or the year (see Figures 2.9, 2.10 and 2.11), and the summer water deficit may be largely a product of the effects of winter and spring radiation patterns on evapotranspiration.

2.6 DISCUSSION

2.6.1 Determination of the Ecological Factor(s) Controlling
        Forest Community Patterns

The results show that the distribution of species in this study area is related to the pattern of solar radiation receipt on all three sites, or rather to an environmental variable, controlled by incident radiation, whose expression in the environment is therefore merely a reflection of the pattern of solar radiation receipt. Many species reach

their maximum frequency at a lower value of incident radiation on the
dolerite compared to the mudstone and sandstone sites. In turn, species
on the mudstone site reach their maximum frequency at a lower value of
solar radiation receipt than those on the sandstone site. Furthermore,
the environmental variable(s) determining the vegetation patterns also
influence the composition and structure of the communities (section 2.5.1).
From the comparison of variables such as species richness and the percen-
tage of each lifeform on the different aspects and lithologies, the mud-
stone and sandstone transects were the most alike, and the dolerite the
most different.

The ecological factors examined to determine which was probably
responsible for controlling the shifts in species distribution patterns
in relation to radiation receipt included; soil nutrient status, the
temperature received on the slopes, soil moisture availability and
grazing by insects (see Chapter Three).

Incident radiation does not directly affect soil nutrient status
and furthermore the shift in species distribution between the three sites
was caused by a factor (henceforth called the primary environmental
variable) that was most limiting on the dolerite site and least limiting
on the sandstone site. The pattern of soil fertility; i.e. the most and
least fertile soils being the brown earths and podzols respectively,
could not, therefore, possibly account for the observed shifts in species
distribution. However, soil nutrient status does influence species
distribution patterns, as some species are restricted to particular soil
types within the study area even where these soil types overlap in their
likely soil water availability.

Despite the slight variation in temperature between the transects,
no species reaches its altitudinal limit within the study area, making
temperaure an unlikely cause of observed species distribution patterns.

Modelling of the soil moisture content of the three soils on a
daily basis showed that the soil subject to the greatest amount of dryness
was the brown earth, and that the soil with consistently the most water
available for plant growth was the podzol. It is therefore probable that
soil moisture availability is the primary environmental variable

controlling species distribution between the three sites. Species including *Eucalyptus obliqua* and *Epacris impressa*, which are only absent, among the three transects, from the north-facing slope of the dolerite transect, are found on the north-facing slopes of dolerite sites subject to higher yearly rainfall totals (K.J.M. Dickinson pers. comm.).

2.6.2. The 'Inverse Texture Effect'

From the soil model it was shown that the daily values obtained for the soil moisture content of the brown earth and podzolic soils were very similar over the long-term. However, the pattern of water avail-ability between the three soils as predicted by the model (see Results) is likely to be exaggerated in reality, with the brown earth being much drier than either the podzol or, more importantly, the podzolic soil. The model under-estimated the effects of soil texture and structure and did not take into account variations in the stoniness of the soil surface or the amount of organic matter in the soil (Lyon and Buckman 1943; Noy-Meir *et al.* 1973; Thompson and Troeh 1973).

The effect of soil texture upon the distribtuion and structure of plant communities in Australia has been discussed by Beadle (1948), Jackson (1958), Carrodus and Specht (1965), and Noy-Meir (1974).

Soil texture and structure influences; (1) capacity, (2) water potential distribution and (3) permeability (Noy-Meir 1973, 1974). The particles comprising sandy soils (i.e. the podzol) are spherical-cubed in shape and relatively large hence, the pore spaces in the soil are large. Most water there moves 'quickly' and 'easily' through the soil under the influence of gravitational forces. The particles comprising clay soils (i.e. the brown earth) are platy in shape and relatively small hence, the pore spaces in the soil are small. The structure of these particles is such that they have a much larger surface area to volume ratio and therefore a larger surface available to bind water (and minerals) per unit of soil than those of sandy soils. Most of the water entering the clay soil therefore, will be held by matric forces to the surface of the particles and very little will drain away. As a result of the effects of soil texture and structure, any water entering the sandy soil will pene-trate to a much greater depth than the same amount of water entering a

clay soil (Jackson 1958; Carrodus and Specht 1965). Hence, the clay
soil has a far greater proportion of water in the top soil, and therefore
water loss from this soil, through evaporation, is much higher (Rowan
and Downes 1963; Specht 1972; Noy-Meir 1973, 1974). The reduction in
the water content of the soils through evaporation is especially high in
the study area, because of a number of factors including: (1) the
relatively high amounts of summer rainfall (Table 2.2); (2) the large
number of rainfall events and (3) the high values of incident radiation,
particularly those received on the north-facing slopes (Noy-Meir 1973).

The brown earths hold water at much greater tensions than the
podzols and podzolic soils at all pressures (Robinson 1979). Therefore,
the ratio of marginal water to normally available water is higher in the
clay based soil; that is, a greater proportion of water is held at
pressures too high to be available to most plants (Buckman and Brady 1960;
Noy-Meir 1974). The amount of ecologically effective water available for
plants in the brown earth is hence reduced, except for those species
adapted to utilize it.

The amount of water entering the three soils may also be reduced
by the effects of soil texture and structure. The permeability of sandy
soils is higher than clay ones. Therefore, for a given amount of water
more will be infiltrated and less lost by runoff in sandy soils (Noy-Meir
1974). However, two processes negate this; (1) the rate of infiltration
is dependent on the water content of the soil, so that the drier soil
(the brown earth) will have a relatively greater infiltration rate than
the more moist one (the podzol; Jackson 1958) and (2) after a prolonged
period without rain, the clay minerals comprising the brown earth will
shrink, causing great cracks to appear in the surface. In such situations
the permeability of the soil is increased. However, at the same time
water loss through evaporation will increase, as a result of the larger
surface area of the soil exposed to the atmosphere.

On a stony surface, such as the north-facing slope of the mudstone
transect, runoff is decreased and more water is detained so that the
amount of water entering the podzolic soil is higher than predicted by
the water balance model (Hillel and Tadmor 1962; Noy-Meir *et al.* 1973).
However, the podzolic soils tend to develop a hygroscopic layer at the

soil surface which initially hinders the infiltration of water and
therefore water loss via evaporation and runoff is for a time increased.

Stones derived from the sedimentary bedrock are scattered through
the podzols and podzolic soils. These stones are porous (K. Nicholls
pers. comm.) and increase the available moisture supply in the two soils.
(The effect of the percentage stone content on the amount of water avail-
able for plant growth is considered in Specht's model; see Methodology.)

No measurement was made of the organic content in the three soils,
although this factor does affect the moisture-carrying capacity of the
soil (Thompson and Troeh 1973).

2.6.3. Species Whose Distribution is Governed by an Ecological Factor Other Than Soil Moisture Availability

Table 2.14 shows the ten species that do not relate to the moisture
gradient in two or more of the radiation periods. The response of
fifteen other species was undetermined; i.e. their response varied
between the radiation periods.

Of the ten species occurring in Table 2.14 only four (marked by
an asterisk) are G_1 species. Due to the low frequency of the remaining
six (G_2) species, the effect of the moisture gradient cannot be
rejected as a possible control of species distribution patterns.

A high percentage (42.9%) of the trees and tall shrubs did not
relate to the moisture gradient. *Acacia dealbata* occupied much drier
environments on the dolerite compared to the sedimentary strata. This
may reflect the higher frequency of low intensity hazard reduction burns
on the north-facing slopes of the sandstone and mudstone sites.
Eucalyptus pulchella was found predominantly on the dolerite site, with
some individuals on the north-facing slope of the mudstone transect.
Those individuals identified as *E. pulchella* on the sandstone were
probably hybrids with *E. amygdalina*. The distribution of *E. pulchella*
may be a reflection of the soil fertility gradient, with the species
being abundant on the most fertile site and absent from the least fertile
site. *Exocarpos cupressiformis* is a semi-parasitic plant (Curtis 1967).

Lifeform	Total No. of species in this lifeform	Species not relating to moisture gradient	Percentage of species not relating to the moisture gradient
Trees and Tall Shrubs	7	*Eucalyptus pulchella* *Acacia dealbata* * *Exocarpos cupressiformis*	42.9 %
Shrubs	8	*Cassinia aculeata* * *Coprosma quadrifida* *Helichrysum dendroideum*	37.5%
Herbs	13	*Senecio linearfolius* *Prasophyllum spp.*	15.4 %
Gramineae	4	*Danthonia spp.* * *Poa spp.* *	50.0%

TABLE 2.14: The species in each lifeform which do not relate to the moisture gradient. The G_1 species are denoted by an asterisk.

The additional source of nutrients that may be derived from this habit, in all likelihood render *E. cupressiformis* partially independent of the soil moisture gradient.

The distribution pattern of the shrubs *Cassinia aculeata* and *Helichrysum dendroideum* and the herb *Senecio linearifolius* was also found to be unrelated to soil moisture availability. All three are probably a reflection of a disturbance gradient. *C. aculeata* and *H. dendroideum* occupied much drier sites on the dolerite and sandstone than on the mudstone transect and *S. linearfolius* occupied much drier sites on the dolerite transect compared to the other two. *C. aculeata* is indicative of disturbed areas, being able to quickly colonize cleared land (Curtis 1963). *H. dendroideum* is often found on the margin of woodlands and *S. linearfolius* is abundant in disturbed places and after fire (Curtis 1963). Both the sandstone and mudstone transects have been subject to disturbance; i.e. frequent (every four to five years) hazard reduction burns and clearance in and around the margins of the reserve, especially in the area bordering the mudstone transect.

Coprosma quadrifida is subject to intensive grazing and its distribution pattern may be a reflection of differential grazing between the transects.

Of the two genera of orchids found, the moisture gradient played no role in determining the distribution of *Prasophyllum spp.* and its effect on *Pterostylis spp.* was undetermined. This is probably because the distribution of orchids depends on the prevalence of bare ground in the environment. The percentage of herbs whose distribution were independent of soil moisture content was very low. However, it should be borne in mind that this figure may be unrepresentative because of the time of year the study was undertaken i.e. many geophytes missed recording, and of those that were growing, some individuals were identified, but only to generic level, the majority being grouped into one category (Orchidaceae).

Of the grasses 50.0% did not appear to relate to the moisture gradient, although this figure may be artifically inflated because of the placing of many unidentified species into one group (Gramineae). It seems

probable that a combination of two factors are responsible for the pre-
dominance of grasses on the north-facing slope of the drier dolerite
transect viz: the higher fertility of the brown earth, and the shallow-
ness of this soil.

Future work, both field studies and experimental, is required to
determine the ecological parameters influencing these and all the species
whose response to the soil moisture gradient was ill-defined.

2.6.4 Changes in Species Morphology, Anatomy and Physiology with Decreasing Water Availability

The large-scale effects of soil moisture availability discussed
thus far, i.e. the partial control of forest community composition,
structure and distribution, are visually readily apparent. However, at
a microcosmic scale there is the more subtle effect of water availability
upon the morphology, anatomy and physiology of species at two levels:
within a species and within a genus.

Some species including *Haloragis tetragyna*, *H. teucrioides*
and *Stylidium graminifolium*, show an increase in leaf area with increas-
ing water availability. An overall reduction in leaf size decreases the
temperature and transpiration rate of the leaves, so conserving water
(Cowan 1981). The replacement of a species by another in the same genus,
along a moisture gradient, also shows a tendency for increasing leaf size
with increasing moisture availability (see below). To a certain extent
this pattern is displayed in the eucalypts. The eucalypts inhabiting the
more mesic environments (*E. obliqua* and *E. globulus*), have larger leaves
than those inhabiting the more xeric environments (*E. viminalis* and
E. amygdalina). However, this pattern is not consistent, as *E. pulchella*,
which is less drought resistant than *E. viminalis* (Kirkpatrick and Marks
in press), has smaller leaves than the latter. This emphasizes that the
adaptation of a species to decreasing water availability, is an inte-
grated system of biochemical, anatomical, physiological as well as
morphological characteristics (Sinclair 1980; Ashton, Bond and Morris
1975).

Increasing Water Availability

————————————————⟶
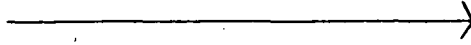
| Olearia ericoides | — | O. erubescens | — | O. stellulata |
| | | O. argophylla | — | O. ramulosa |

Tetratheca pilosa   ————————   T. glandulosa

Pimelea humilis   ————————   P. linifolia

Haloragis tetragyna   ————————   H. teucrioides

Dianella revoluta   ————————   D. tasmanica

————————————————⟶
Increasing Leaf Size

Plant size is reduced as the availability of water decreases.
Acacia dealbata forms tiny shrubs, less than one metre in height on the
north-facing slope and trees on the south-facing slope of the dolerite
transect. Other species showing similar increases in height, with
increasing water availability include *Pultenaea juniperina, Bedfordia
linearis, Banksia marginata,* and *Leptospermum scopaerium.* Within the
genus *Eucalyptus,* species occupying the cooler, moister environments
(*E. obliqua* and *E. globulus*) are taller than those occupying the warmer
drier ones (*E. viminalis* and *E. pulchella*). The change from *Dianella
tasmanica* to *D. revoluta* is also accompanied by a reduction in plant size.

There is also some evidence that the replacement of a species by
another in the same genus, as moisture availability changes, also involves
a change in lifeform. For example, the replacement of *Goodenia lanata*
(a herb) by *G. ovata* (a herb/shrub) and *Senecio spp.* (a herb) by
S. linearifolius (a herb/shrub).

Other reported responses of plants to water stress include a
reduction in cell size and intercellular volume of leaves, an increase
in vein density, stomatal frequency and thickness of the palisade layers
and changes in the patterns of tree roots (Kramer 1969; Ashton 1975;
Cowan 1981).

On a wider scale, as soil moisture availability increases there
is a reduction in sclerophylly and an increase in broad leaved species.

CHAPTER 3   INSECT PREDATION ON SAPLING EUCALYPTS

3.1   INTRODUCTION

Loss of foliage to insect grazing in eucalypts has been reported
to be very high. Some species sustain leaf area losses of anything
between 15-50% (Burdon and Chilvers 1974a,b; Kile 1974; Fox and
Morrow 1983), compared with 1-10% in Northern Hemisphere forests
(Ohmart et al. 1983a,b). This phenomenon of high grazing levels in
Eucalyptus has promoted two areas of study; firstly to determine why
foliage losses are so high in eucalypts and secondly to determine the
effect of this on tree growth and, ultimately, stand composition.

Research into the level of grazing has centred upon isolating
those factors that cause some species to be very heavily predated while
others remain relatively unscathed. Such factors include: (1) differences
in the quality of the foliage and (2) in the density of species, (3) the
composition of forest stands and (4) plant vigour.

The quality of the foliage varies according to the content and
concentration of allelochemics and nutrients, and plant physical defence
mechanisms. All three may act, often in combination, to influence
insect feeding preferences (Carne 1965; Soo Hoo and Fraenkel 1966;
Feeny 1975; Rhoades and Cates 1975; Bech and Reese 1976; Fox and
McCauley 1977; Morrow and Fox 1980; Edwards 1982).

It is possible that the amount of insect grazing is dependent
upon the density of eucalypt species, or the density of subgeneric groups
such that an increase in host density results in a disproportionate
increase in insect fauna (Chilvers and Brittain 1972; Burdon and
Chilvers 1974).

The level of insect grazing may also be influenced by the partic-
ular mix of species in a community, i.e. some species may function

together to regulate insect feeding (plant defence guilds; Atsatt
and O'Dowd 1976). For instance, a host plant surrounded by plants
giving off repellent odours may be protected from insect predation.

Finally, a weakened or stressed plant has a lower resistance
to insects. Reduction in plant vigour may arise as a result of
environment stress (i.e. drought) or biotic factors (i.e. competition,
disturbance). For example, the quality of food, nutrient uptake,
carbohydrate and nitrogen metabolism are all affected by moisture
stress (White 1969, 1974, 1975; Mattson and Addy 1975; Lansberg and
Wylie 1983). A stressed plant, in devoting most of its available
nitrogen and energy towards photosynthesis and growth may not have the
reserves to produce nitrogen based allelochemics needed in defence
(Edwards and Wratten 1980). Hence, the composition of allelochemics
and the 'chemical halo' will vary. The outcome of this is that although
the incidence of allelochemic compounds, nutrients and physical defence
mechanisms are genetically determined, their ultimate expression is the
result of modification by the environment (Mattson and Addy 1975;
Levin 1976). Many studies have undertaken research to determine the
effects of plant quality upon the levels of grazing among species; but
few have determined whether variations in nutrient content, tree density
etc. along environmental gradients may influence insect grazing patterns
along that gradient.

Through a series of experimental studies insects have been
shown to reduce height growth (Greaves 1966; Carre et al. 1974),
reduce radial growth (Readshaw and Mazanec 1969; Morrow and LaMarche
1978), reduce the size of the seed store (see Morrow 1977a for resumé),
and ultimately cause tree death (Mazanec 1966; Elliott et al. 1980).
Conversely, insect activities have been shown to stimulate leaf product-
ion (Mattson and Addy 1975; Lowman 1982) although not in eucalypts.

Few studies have extensively measured anything but the effects
of leaf area losses on eucalypt growth. The way in which missing
leaves, the number of leaves per shoot and mean shoot length are
affected by insect activities and the implications these may have upon
tree growth and hence forest community composition has received little
attention in the literature.

Most studies, furthermore, use one sampling unit, the single leaf to record foliage losses to the tree (Kile 1974; Journet 1981; Fox and Morrow 1983), although there have been studies assessing damage to the entire crown (Elliott *et al.* 1980). Leaf area loss is determined either visually or by passing the leaf through a leaf area meter. More recently, Ohmart (1983a,b) has determined the annual consumption of foliage by measuring the frass fall from insects. From these studies he has found that only 2-3% of the annual leaf production of mature trees is lost through insect defoliation (these figures are similar to those derived for defoliation in Northern Hemisphere forests). Ohmart *et al.* (1983a) suggests that among the reasons why his estimates of foliage consumption are so much lower than those found by other workers, and why the estimates of leaf area loss vary between studies are: (1) by randomly picking leaves off a tree, more than one year's damage is being recorded; (2) by measuring damage in for instance January and February when the leaves are not fully expanded, leaf area losses may be overestimated, since any feeding by an insect on young leaves represents a much greater area lost compared to the same amount of feeding on an expanded leaf; and (3) the study of insect grazing had tended to focus upon areas where outbreaks have occurred (Greaves 1966; Kile 1974; Elliott *et al.* 1980), or upon small trees on which the insect population and therefore level of grazing may be very different (Burdon and Chilvers 1974a,b; Carne *et al.* 1974; Fox and Morrow 1983), or in disturbed areas where the levels of grazing differ from those in undisturbed areas (Carne 1965; Fox and Morrow 1983).

In any forest community, however, the composition, abundance and distribution of species is to a large extent determined by the conditions at the outset of community development. Thus the factors influencing small trees (of which the level of insect damage is only one) may be more important than those influencing mature trees, in moulding the shape of the future forest.

There were four aims in this research, the first of which was
to measure the level of grazing in young trees in the dry sclerophyll
forests of south-eastern Tasmania. Hitherto, research in these forests
had been limited to studies of defoliation in areas where outbreaks
of insects occurred (Greaves 1966; Kile 1974) or studies that had not
involved extensive sampling (Duff *et al.* 1983). The second aim was to
use the shoots of trees as the main sampling unit by which to measure
insect damage over time, with the leaf as the secondary sampling unit.
By measuring damage as soon as the leaf unfolds and continuing until it
reaches its maximum size, the damage recorded is that attributable to
the current season and the effects of leaf growth on the percentage
damage may be analysed. The third was to measure other variables that
may effect forest community composition including missing leaves, the
number of damaged leaves, the number of leaves per shoot and mean shoot
length. The effects of all these variables on tree growth will be
assessed by series of experimental studies. The fourth aim was to
determine the importance of environment variables on the effects of
defoliation. Some information was also collected on the taxa of insect
predators found within the study area.

3.2 METHODS

3.2.1 Site and Species Selection

The field sites selected for study had to fulfil the following
criteria: (1) contain small trees, two-three metres in height; (2)
cover a wide range of topographical environments; and (3) be within
easy access of Hobart.

Where the Hydro-Electric Commission run transmission lines
through an area they clear the ground beneath the pylons by burning.
After a period of time these swathes, which are approximately 40 metres
wide, are covered by even-aged regrowth vegetation (Plate 3.1).
Transmission lines run approximately north-south through the forest in
Ridgeway Park Reserve, near Hobart (Figure 2.1). Two strips of land
beneath these transmission lines were chosen as the sites for the study

PLATE 3.1: The transect across the sandstone hillslope.

of insect-eucalypt relationships: one running across an area of
dolerite, and the other across an area of sandstone (Figure 2.2).
Both sites encompass a north and south-facing slope. Henceforth, the
slopes on the dolerite bedrock shall be referred to as Chimney Pot
North (CPN) and Chimney Pot South (CPS), and the slopes on the sandstone
as Ridgeway North (RWN) and Ridgeway South (RWS).

Sites differing in geology and pedology were chosen so that the
gradient in soil moisture availability would be greater than that imposed
by aspect alone, and therefore any effects of soil moisture availability
on the level of defoliation would be maximised. The ordering of sites
with increasing water availability is CPN, RWN, CPS, RWS (Chapter Two).
CPN and CPS are more exposed than RWN and RWS, being approximately 200
metres higher above sea level (Figure 2.2), and the soil is more fertile
on the former sites compared with the latter (Chapter Two).

A survey was undertaken to establish the abundance of eucalypt
species. This revealed that *Eucalyptus obliqua, E. pulchella* and
E. viminalis (adult foliage) were suitable for sampling on CPN and CPS,
E. obliqua, E. tenuiramis and *E. viminalis* (adult and juvenile foliage)
on RWN, and *E. obliqua* and *E. viminalis* (adult and juvenile foliage) on
RWS.

3.2.2 Selection of Trees for Sampling

It was important that the trees sampled within each species be,
as far as possible, similar in terms of the quantity and quality (i.e.
the nutritional, biochemical and physical properties of the leaf, and
the microclimate surrounding it) of the foliage available
to grazing insects. This ensures that any differences in the type and
levels of grazing found between species and aspects is due to the partic-
ular characteristics of the foliage and/or to environmental differences
between the sites, rather than being an artefact of the age of the tree,
tree vigour or the number of shoots available for feeding, oviposition
or other factors (Carne 1966; Ohmart 1983). Accordingly, a tree survey
was undertaken in which the following variables were measured as direct
and indirect surrogates for leaf quantity and quality respectively:

(1) tree height; (2) the diameter of the trunk above the lignituber
(this variable is a crude measure for the amount of foliage in the tree);
(3) the height to the intersection of the adult-juvenile foliage;
(4) the distance of the trunk from the furthermost point of the foliage
in a northerly, southerly, easterly and westerly direction; and (5) the
number of potential new shoots in the upper crown. Also taken into
account were: (6) the species of tree surrounding the individual being
examined, and whether there was any contact between the former and the
latter; (7) the shape of the tree; and (8) accessibility in the field.

Results from the measurements of variables (1) to (5) for trees
in each species, were subjected to a principal components analysis (p.c.a.)
to determine the trees on different sites which were most alike.

Up to 15 trees per species per site were selected from the results
of the p.c.a. Taking into account variables (6) to (8), approximately
10 of the 15 trees were finally chosen, 5 for the purpose of recording
insect damage over time (untreated trees) and 5 for the investigation of
tree growth in the absence of insect grazing (treated trees). In some
instances the sample size ended up being smaller than 10 (Table 3.1).
This was due to a number of factors including: (1) the inability to find
up to 10 similar trees per species in a site; (2) the mortality of
several trees during the growing season due to severe climatic conditions
i.e. high winds and drought; and (3) the almost total defoliation of
some *E. viminalis* trees on RWN by *Trichosurus vulpecula* and *Pseudocheirus
peregrinus* (Possums), which meant they could no longer be sampled for
insect damage.

3.2.3 Selection of Leaves and Shoots for Sampling

Two different sized sampling units were used in the analysis of
insect damage, the single leaf and the shoot (Southwood 1978).

Leaves approximately one year in age (henceforth known as old
leaves) on three species, *E. obliqua*, *E. tenuiramis* and *E. viminalis*
(adult foliage) were sampled on one site, RWN. On each tree a branch
facing in a north, south, east and westerly direction was selected and

six leaves per branch were earmarked for sampling.

In the analysis of insect grazing between sites and species over time, the shoot was chosen as the sampling unit for the following reasons: (1) the damage sustained by a shoot, rather than a leaf, was considered a fairer representation of the damage sustained by the tree as a whole; (2) similarly, the shoot gives a good indication of the proportion of damaged to undamaged leaves, missing to existing leaves and changes in leaf growth as experienced by the tree as a whole; and (3) it was necessary to be able to identify the unit measured through-out the duration of the study by means of some form of tagging that would not attract insects or hinder their access to the foliage. At the beginning of the growing season, shoots were more obviously suited to tagging than the tiny individual leaves.

Shoots have been used before in the study of insect populations (Carne 1966). Because the number of leaves per shoot varies throughout the growing season (with leaf abscission and new growth), and because shoots that are dominant at the beginning of the growing season do not always remain so, shoots are not always a suitable sampling unit for use in studies making detailed analyses of insect populations (De Little 1979). However, in the context of this study, the shoots could be sampled since a detailed analysis of insect populations was not undertaken, and shoots were considered a better reflection of the changes occurring to the tree.

Between 10-20 shoots were tagged per tree at the beginning of the growing season in October/November 1982. Generally the growth of new shoots was delayed compared to other years, because of the very dry winter. This was especially apparent on trees occupying the south-facing slopes, and even on the south-facing aspect of individual trees. Conse-quently, some shoots were not tagged until mid-December 1982. Table 3.1 shows the maximum number of shoots tagged per site.

The method of tagging followed that used by the Forestry Commission, in which Dymo tape is placed around a shoot and secured with a staple. The following criteria were used to determine the selection of shoots: (1) the presence of four fully formed expanded, undamaged leaves, more

| | CPN | | | | CPS | | | | RWN | | | | RWS | | | | Total no. of shoots in UT trees | Total no. of shoots in T trees |
| | UT | | T | | UT | | T | | UT | | T | | UT | | T | | | |
	No. of trees	No. of shoots	No. of trees	No. of shoots	No. of trees	No. of shoots	No. of trees	No. of shoots	No. of trees	No. of shoots	No. of trees	No. of shoots	No. of trees	No. of shoots	No. of trees	No. of shoots		
E. obliqua	5	71	4	76	4	48	4	74	5	65	5	68	5	57	5	82	241	300
E. pulchella	5	69	5	86	5	56	5	71									125	157
E. viminalis (adult foliage)	5	86	5	93	5	67	4	61	4	51	5	79	4	52	3	66	256	299
E. viminalis (juvenile foliage)									5	54	5	84	3	44	2	27	98	111
E. tenuiramis									5	79	5	58					79	58
	226				171				249				153				Σ =799	
			255				206				289				175			Σ =925

TABLE 3.1: The number of trees and shoots sampled per species, per site. UT = untreated trees. T = treated trees.

than 1 cm long, taken from (2) all aspects of the tree and (3) from all sections of the crown.

Insects have been found to concentrate on different portions of the crown, and at different aspects (see Southwood 1978 for a review). Hence any possible variation in percentage damage with aspect and height in the crown should be measured, in order that subtle differences between the species in the quality of foliage in different parts of the tree are not masked by taking the mean for the trees as a whole.

The effect of aspect within the tree was analysed. The effect of the position of the shoots in the crown could not be examined because: (1) in some trees the number of utilizable shoots (see criteria above) at the different levels in the crown were too few in number; and (2) juvenile foliage in *E. viminalis* was usually restricted to lower portions of the crown. However, Carne (1966) noted that the location of egg batches was not influenced by the height of the foliage in young trees.

3.2.4. Experimental Studies

The shoots tagged on the five trees per species per site earmarked for a study of the effects of insects on tree growth were sprayed with the insecticide Malathion 50.

Malathion is an organo-phosphorus insecticide which acts by interfering with the general nervous system of insects. It works in the following manner. Acetylcholine transmits nerve impulses between the nerve and striated muscle, thereby stimulating muscle contraction. Any remaining acetylcholine not used in this reaction must be hydrolysed by the enzyme acetylcholine esterase back to choline and alcohol in order for the muscle to relax.   Malathion

inhibits the enzyme acetylcholine esterase thus leading to a build-up
of acetylcholine in the muscle which causes permanent contraction of
the muscles and therefore death (Stryer 1981).

Spraying was initially carried out every two-three weeks. However,
during the summer it was noticed that some leaves, primarily the adult
leaves of *E. viminalis*, had developed unusual red markings that seemed
in some way attributable to the insecticide. Spraying frequency was
therefore reduced to periods when the insect population became particul-
arly abundant and the leaves appeared to lose their immunity to attack.

Spraying commenced at the beginning of the growing season, when
the shoots were tagged, and ceased in May/June.

3.2.5 Insect Damage Studies

3.2.5.1 Data Collection

3.2.5.1.1 Defoliation Levels

During October 1982, the old leaves were examined to establish
the amount of damage caused by insects.

Insect damage on trees was visually measured using the following
damage classification system:-

1	=	no damage
2	=	1-< 5% damage
3	=	5-<10% damage
4	=	10-<25% damage
5	=	25-<50% damage
6	=	50-<75% damage
7	=	75%+ damage
8	=	dead

This method of measuring insect damage was adopted because it is easy,
quick and readily quantifiable, and had been successfully used in the
assessment of defoliation of whole trees (Carne *et al.* 1974; Elliott

et al. 1980). However, levels of damage were so low that most leaves were classified into categories 2 or 3. Consequently, in the analysis of the level of damage sustained by shoots, a more sensitive measure had to be used and therefore it was decided to determine percentage damage per shoot visually. The damage classification system was used to describe the levels of damage attributable to each of the damage category types (see Section 3.2.5.1.2).

Percentage damage (also referred to as actual damage) per shoot in untreated trees was recorded monthly during the period December 1982 to May/June 1983 six times in all. This period is the time of peak insect occurrence in the environment (Morrow 1977b; Fox and Morrow 1983; Ohmart *et al.* 1983b). Data collection took two-three weeks and because of this a different site was visited daily and the trees and shoots in that site visited in random order each time. By adopting this procedure it was hoped to minimize the discrepancies caused by the long data collection period and eliminate any bias when collecting insects caused by their prevalence at certain times of the day and in certain weather conditions.

The percentage of actual damage per shoot in treated trees was recorded once, in May/June 1983, after one season of spraying with insecticide.

At the same time as the level of percentage damage sustained by each shoot was evaluated, other variables were measured: (1) the length of the shoot; (2) the number of leaves on the shoot; (3) the number of leaves that were damaged; (4) the number of missing leaves and (5) the amount of damage attributable to each of the four damage categories (see Section 3.2.5.1.2). The number of missing shoots was also recorded.

Missing leaves and shoots may occur as a result of a number of factors, including extensive herbivore activity (i.e. insects, possums), adverse climatic conditions (drought, high winds, storms), plant viruses and other pathogens or leaf abscission (which in itself may be effected by some of these factors). The level of damage caused by insects alone may therefore be higher than the actual damage figures suggest. Consequently, a figure representing the percentage total damage [D_T] to a

shoot was derived by summing: (1) the actual damage $[D_A]$ of the shoot, determined by expressing the percentage actual damage in terms of the total number of leaves (i.e. existing and missing), and (2) the hidden damage $[D_H]$ of the shoot, determined by expressing the number of leaves lost in terms of the total number of leaves.

$$D_T = \frac{D_H + D_A}{N} . 100 \qquad (12)$$

Thus, if a whole six-leaf shoot was missing, the total damage would be 100%:

$$D_T = \frac{6 + 0}{6} \times 100 = 100$$

If two leaves were missing, and the remaining 4 had over half their area lost through insect damage, the total % damage would be:

$$D_R = \frac{2 + \frac{4}{2}}{6} \times 100 = 66.7\%$$

3.2.5.1.2 Assessment of Damage Types

A pilot study was undertaken in the winter of 1982 to determine how the different types of insect damage could be categorized, and the extent to which these could be attributed to a particular insect species or genus. After Landsberg and Wylie (1983), I identified in the field four categories of damage: (1) leaf chewers; (2) leaf miners and skeleton-izers; (3) 'leaf distortion' (Landsberg and Wylie (1983); and (4) mis-cellaneous leaf damage. The majority of insects are leaf chewers mainly belonging to the orders Lepidoptera, Hymenoptera, and Coleoptera (Franklin 1970; Matthews 1976). They remove whole portions of the leaf (Plate 3.2). Other insects (leaf miners and skeletonizers) remove only parts of the leaf. Leaf miners are insect larvae that tunnel inside the leaf and eat the tissue between the upper and lower epidermis. The damage caused by these insects is recognised by the presence of large areas of upraised opaque tissue (Plate 3.3). Some species are skeletonizers or miners for part of the life-cyle, and leaf chewers for the rest. Generally the overall effect of leaf chewers, skeletonizers and miners is to reduce the total photosynthetic capacity of the tree. However, where damage

Table 3.2   Leaf chewing damage on E. viminalis (juvenile foliage)

Table 3.3   The injury caused by leaf miners on E. obliqua

is high, tree health and height may be reduced, leading ultimately to tree death (Anderson 1960; Bamber and Humphreys 1965; Greaves 1966; Mazanec 1966b; Osborne 1973; Elliott *et al.* 1980).

Leaf distortion includes that damage caused by sapsuckers (aphids; Hemiptera), psyllids (Homoptera), and gall formers. Sapsuckers have piercing mouthparts that enable them to tap the plant sap from the leaves, stems or roots. They may have a depressant effect on plant metabolism and cause the stunting of shoots and leaves (Osborne 1973; Morrow 1977b). Where damage is excessive, tree death may result (Osborne 1973). The injury they inflict appears as the curling or crinkling of a leaf or a change in the colour of the foliage from green to yellow-white.

Leaf galls are large growths (Plate 3.4) which may be formed by the action of insect saliva (Matthews 1976). They may contain a large number of associated gall organisms, not all of which are insects. Leaf galls cause metabolic and developmental changes to localized areas of the plant and may reduce the overall fitness of the tree (Osborne 1973).

Miscellaneous damage was all that damage sustained by the leaf which could not be readily attributed to the activities of insects, but may have been caused by them. This included holes in the leaf blade and necrotic patches. Fungi could sometimes be determined as causing the latter, when the black heads of the sporophytes were visible.

The damage caused by some insect species/genera could be identified, for example: (1) the leaf chewing damage of the *Paropsis* beetle and its larvae (see Kile 1974, Figure 1); (2) the damage of the leaf miners and skeletonizers *Acrocercops sp.*, *Protolechia sp.*, and *Uraba lugens;* and (3) the damage caused by certain kinds of galls: *Ctenarytaina sp.*, *Fergusonina sp.*, and *Glycaspis sp.* However, the amount of damage inflicted by these overall was so small that they were not considered separately.

The amount of damage caused by each of the four damage types on every sampled shoot was quantified using the damage classification system.

Table 3.4 Plant galls on E. viminalis (adult foliage)

3.2.5.2   Data Analysis

Scores obtained from using the damage classification system were converted to percentages by taking the mid-point of each class to represent the amount of damage; i.e. if the damage to a shoot was measured as 3 (5-<10%), it was assumed to have sustained 7.5% leaf area loss.

For each of the variables measured per leaf (percentage damage) and per shoot (percentage actual damage, percentage total damage, percentage missing leaves, percentage of damaged leaves, shoot length, the number of leaves per shoot and the percentage of each type of damage; leaf chewers, skeletonizers and miners, leaf distortion and miscellaneous damage) a mean value per tree was derived.

The mean percentage damage of leaves and shoots on the trees of three species of eucalypt on RWN were compared using the Mann-Whitney U-test (see below). However, the values of mean percentage damage to the leaves were not directly comparable to the percentage damage figure derived for the shoots. To overcome this problem, the shoots were classified into classes according to the level of percentage damage they sustained (method of classification described in Section 3.2.5.1.1). The percentage damage to a shoot was then taken as the mid-point of the class to which it had been assigned. Mean percentage damage per tree and therefore per species was then derived, and compared with those values of percentage damage to old leaves.

The ten variables measured per shoot in the untreated trees were then subject to two analyses: (1) the general analysis and (2) the species site analysis. In the general analysis, the mean values of each of the 10 variables derived for the trees of one species were compared with those of another species over the same sites (the between-species analysis). For instance, the trees of *E. pulchella* occur only on CPS and CPN, so they were compared with the trees of *E. obliqua* and *E. viminalis* (adult foliage) occurring on CPS and CPN, whereas the comparison between *E. obliqua* and *E. viminalis* (adult foliage) was between trees occurring on all four sites. Secondly, the species occurring on one site

were compared with the same species occurring on another site (the between-site analysis).

In the species-site analysis, two comparisons were made: (1) between each of the species occurring on a site; and (2) within one species occurring on different sites. In the species-site analysis the percentage of each of the four types of damage was normalized. The overall results from the species-site analysis are given only when they differ from those of the general analysis.

To determine, in the comparison of the variables between the sites and species, whether the values of each of the 10 variables sustained by one species or upon one site were significantly larger than those sustained by another species or upon another site, the Mann-Whitney U-test was used. The null hypothesis was that there was no difference in the level of each of the ten variables between the sites or between the species. The rejection level was decided at P = 0.05. However, because of the large number of calculations involved, of which one in 20 would have been significant by chance, the level of probability of each significant result was placed into one of 3 categories, so that the strength of the comparison could be gauged:(see below).

$$0.01 < P \geqslant 0.05$$
$$0.001 < P \geqslant 0.01$$
$$P \geqslant 0.001$$

Finally, the values of percentage actual damage, percentage total damage, percentage missing leaves, percentage damaged leaves, mean shoot length and mean number of leaves per shoot for untreated trees was compared with those values for treated trees using the Mann-Whitney U-test.

3.2.6 Insect Collection

At the same time as an assessment of damage was being made for a shoot, any insect on, or in the near vicinity of that shoot was collected and placed in a specimen jar for identification. Insects

were usually handpicked, although in cases where the individual was very small, a pooter was used.

3.3 RESULTS

3.3.1 Patterns of Insect Damage Upon Eucalypts

3.3.1.1 The Effect of Aspect Within the Tree

All the shoots of a particular species on each site were compared to establish whether mean percentage damage per shoot varied with aspect. The amalgamation of the data from all five trees per species per site ensured an adequate representation of shoots from all aspects. Care has to be taken with interpretation, as it is possible this procedure could bias the results if a tree sustaining particularly high insect damage contained a high number of shoots facing in any one direction.

No consistent pattern was evident within or between the species on the different sites (Figure 3.1[a-d]).

To determine whether a relationship between percentage damage and aspect develops with prolonged insect grazing, the leaf area losses of "old" leaves (i.e. approximately 12 months in age) growing in north, south, east and westerly directions were compared. All leaf area loss data was collected only on the RWN site, and then only for the species *E. obliqua*, *E. tenuiranis* and *E. viminalis* (adult foliage).

There were no significant differences in the damage incurred between the four aspects in any of the three species examined (Table 3.2). As a result of these findings, mean percentage shoot damage per tree was used in all subsequent analyses.

A relationship between percentage damage and aspect has been shown to occur, although the aspect of the foliage subject to the most intense insect damage seems to vary (Carne 1965; White 1970a,b; Southwood 1978; Lowman 1983). In the studies upon eucalypts, a relationship between aspect and damage may occur only in mature trees (Carne 1966),

(a) CPN

E.obliqua

E.pulchella
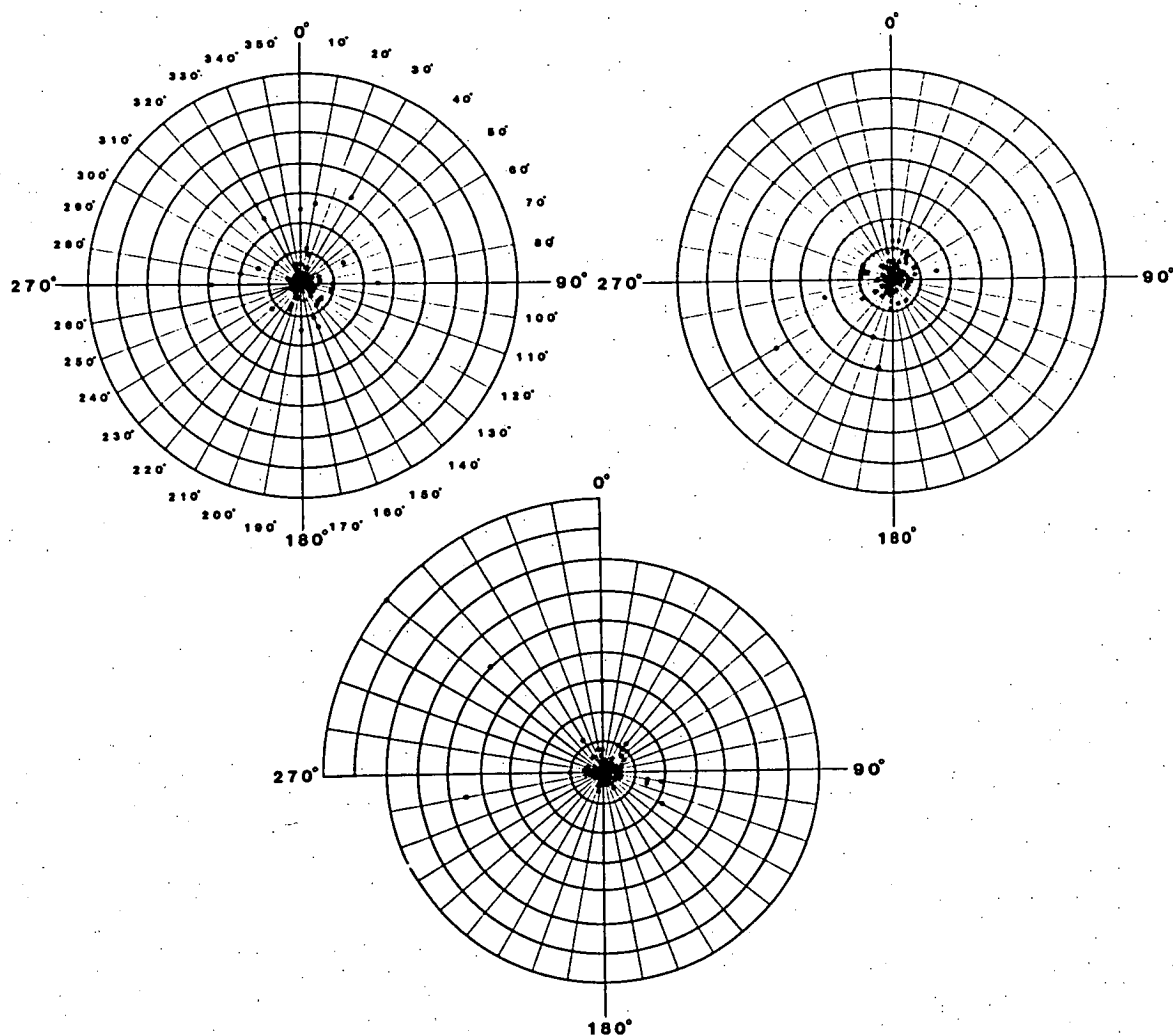
E.viminalis (adult foliage)

FIGURE 3.1: The percentage damage sustained per species on
different aspects within the tree at each of the
different sites. Each diameter ring represents
an increase of 10% insect damage.

0° = North. + = where two or more values concur
(a) on CPN

(b) CPS

E.obliqua   *E.pulchella*
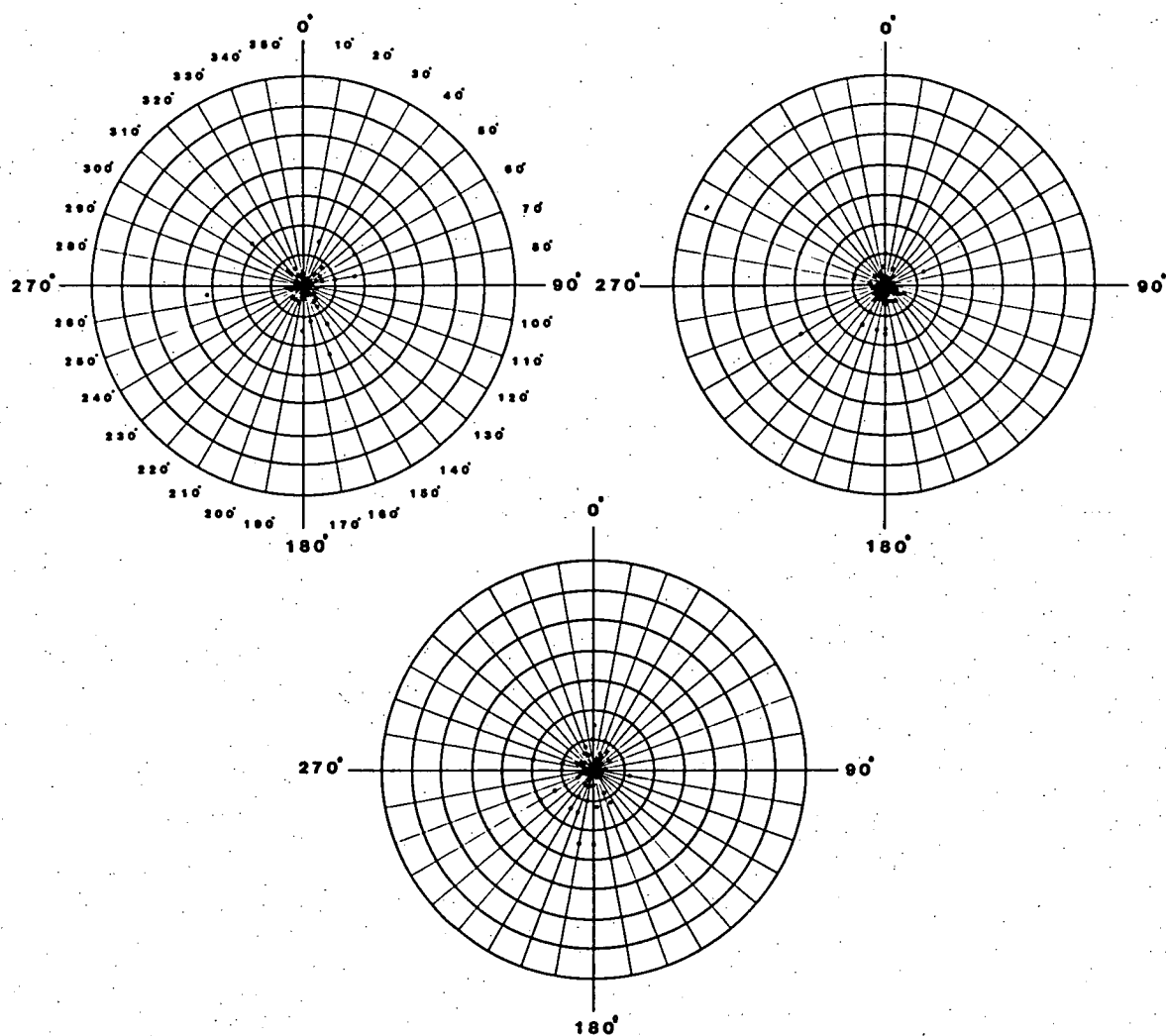
E.viminalis (adult foliage)

<u>FIGURE 3.1</u> (continued):   (b) on CPS

(c) RWN

E.obliqua   *E.tenuiramis*
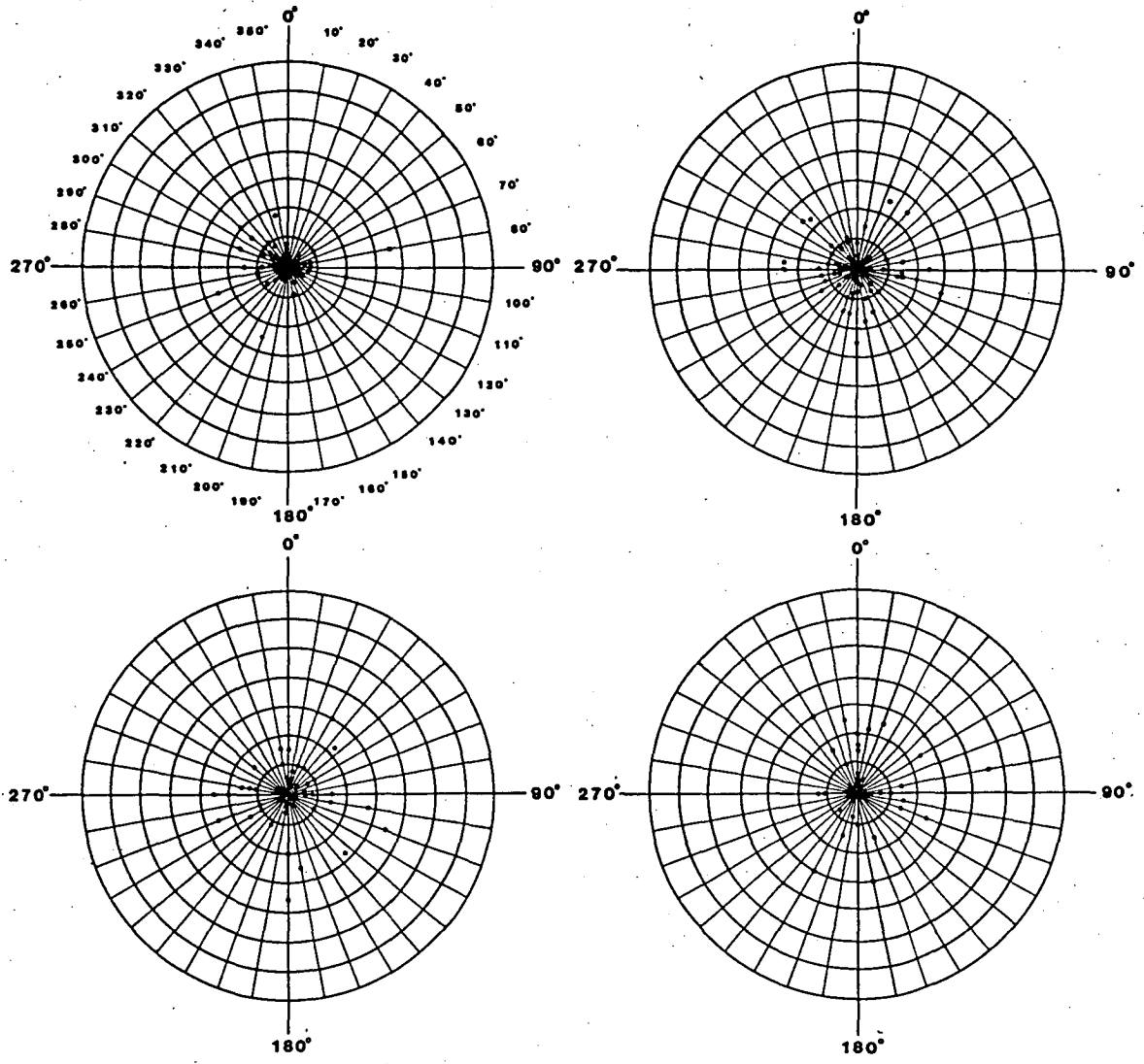
E.viminalis (adult foliage)   *E.viminalis* (juvenile foliage)

FIGURE 3.1 (continued):   (c) on RWN

(d) RWS
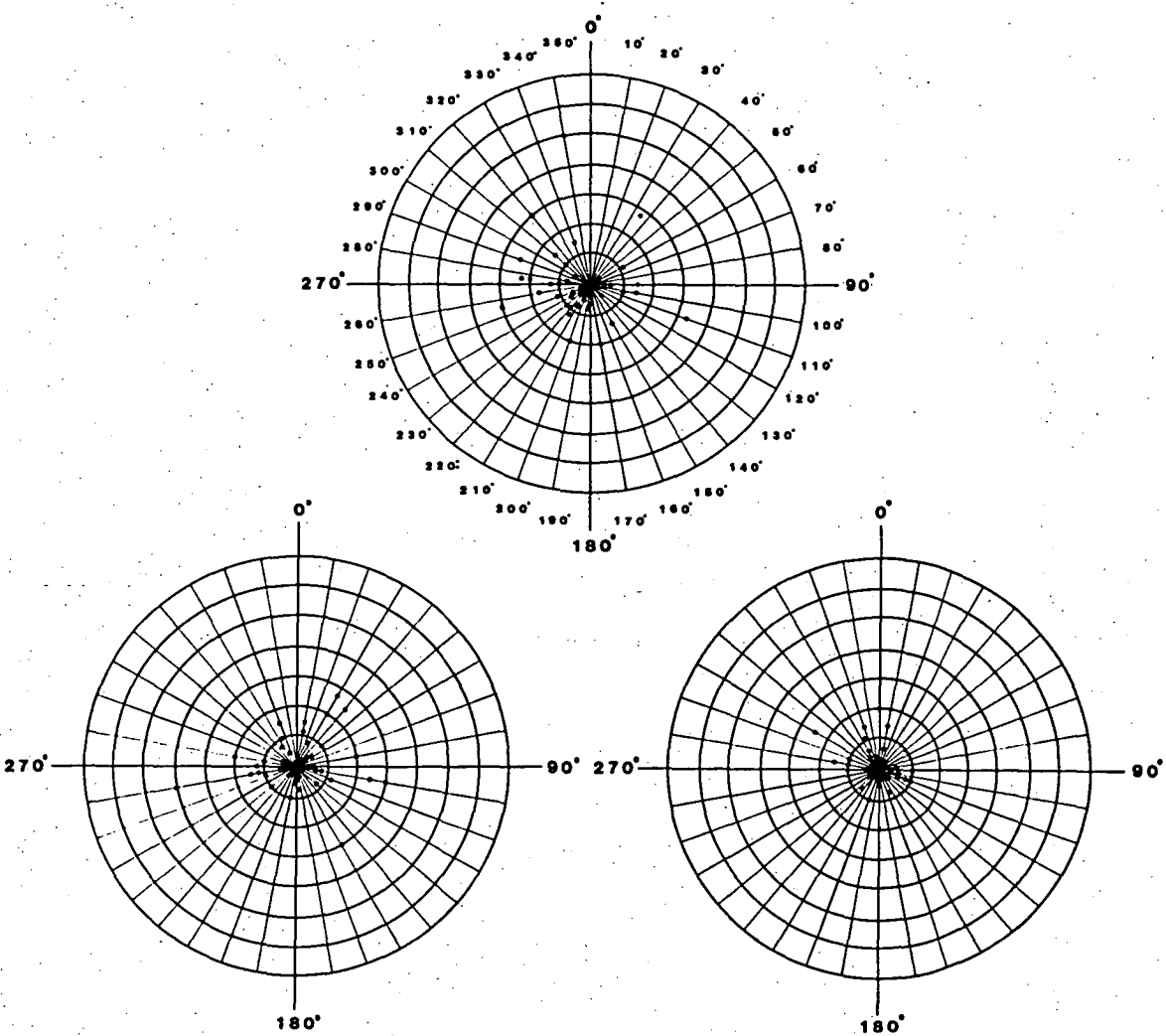
E.obliqua

E.viminalis (adult foliage)

E.viminalis (juvenile foliage)

FIGURE 3.1 (continued):   (d) on RWS

	E. viminalis (adult foliage)	E. obliqua	E. tenuiramis
North	12.14	22.14	5.83
East	13.96	18.10	8.42
South	11.25	20.36	13.06
West	21.15	24.29	7.31

TABLE 3.2: The mean percentage leaf area loss of leaves occurring in a north, south, east and westerly direction; on *E. viminalis, E. obliqua* and *E. tenuiramis*

	Leaves (one year old)	Shoots (6 months old)
E. obliqua	21.2	9.0
E. tenuiramis	8.7	10.9
E. viminalis (adult foliage)	14.6	13.9

TABLE 3.3: The mean percentage damage on different aged foliage of three species of eucalypts. Significant relationships denoted by a line.

or on mature leaves (Lowman 1982), or where infestation by insects is relatively high (White 1970a).

3.3.1.2 *The Vulnerability of Different Aged Foliage to the Activities of Insects*

Table 3.3 shows the mean percentage damage sustained by shoots from October/November 1982 – May/June 1983 and the mean percentage damage sustained by "old" leaves during the previous year (October 1981 – October 1982), on the RWN site.

The mean percentage damage sustained by the old foliage of *E.obliqua* (table 3.3) was significantly higher than that sustained by the young foliage ($0.001 < P \geqslant 0.01$; cf. Kile 1974). In contrast, there were no significant differences between the level of damage in the old and young foliage of *E. tenuiramis* and *E. viminalis* (adult foliage). Thus it seems probable that *E. obliqua* is continually subject to insect damage throughout at least the first year of a leaf's lifespan of approximately 18 months (Jacobs 1955), whereas damage to the species *E. tenuiramis* and *E. viminalis* appears to be concentrated within the first six months of a leaf's life. The differential response to insect damage between species is interesting (cf. Ohmart *et al.* 1983) because it appears to contradict the current view that it is always the young leaves which sustain the highest amount of damage (Carne 1966; White 1971; Rogers and Westman 1979).

3.3.1.3 *Analysis of Patterns of Insect Damage*

Histograms were plotted for each species per site, showing the number of shoots whose level of insect damage fell into each of the damage classes (Figures 3.2[a-d]).

The histograms are all negatively skewed, and all but three (*E. pulchella* on CPN, *E. viminalis* (adult foliage) on RWN and *E. obliqua* on RWS) have the highest number of shoots in the first damage class (0-4%). Some shoots are very highly damaged (50%+), but these

E. obliqua   **E. pulchella**   **E. viminalis (adult foliage)**

Percentage Damage
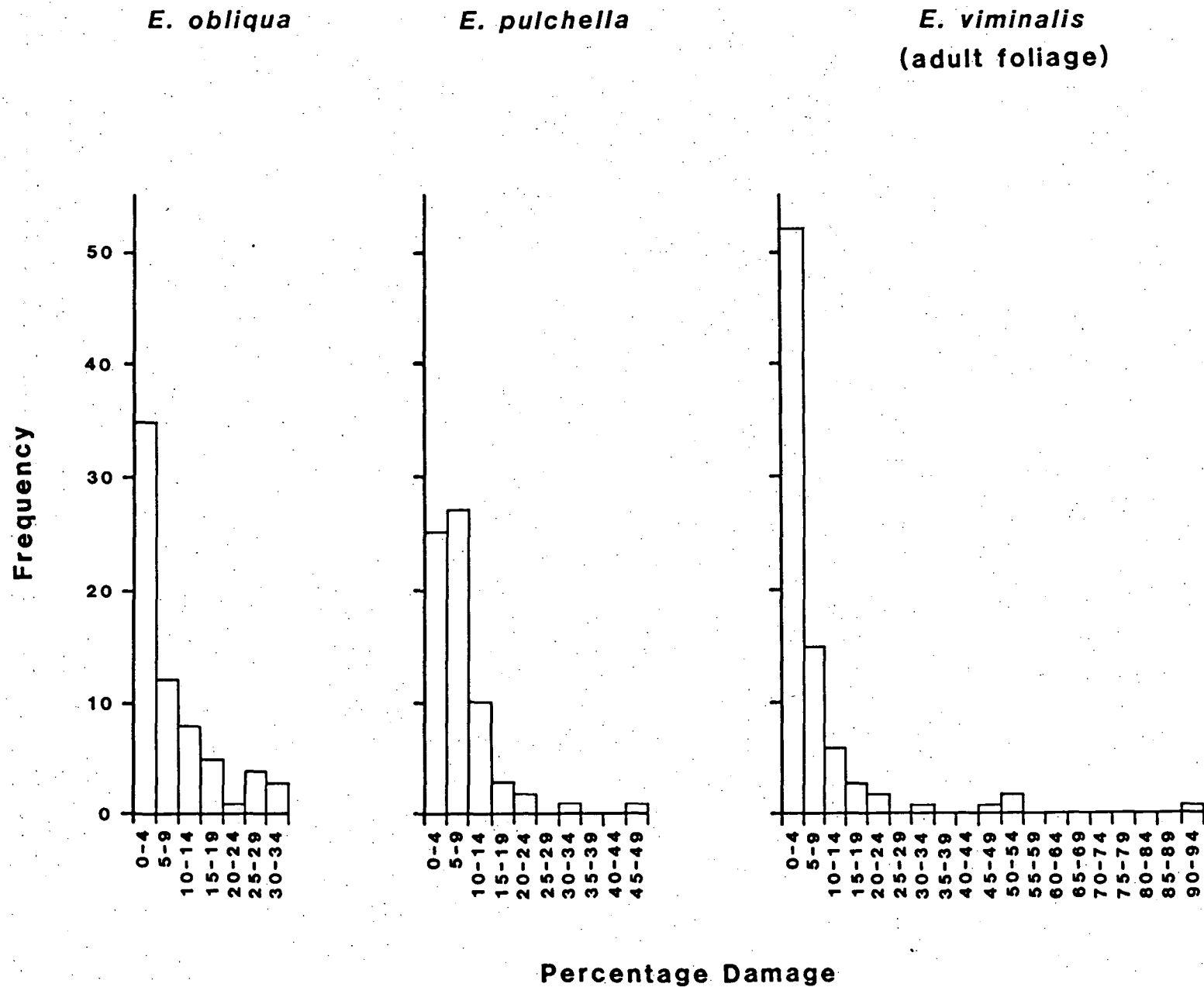
<u>FIGURE 3.2</u>:   The distribution of damage on the shoots in each species, at the different sites: (a) on CPN

E. obliqua **E. pulchella** **E.viminalis (adult foliage)**

Percentage Damage
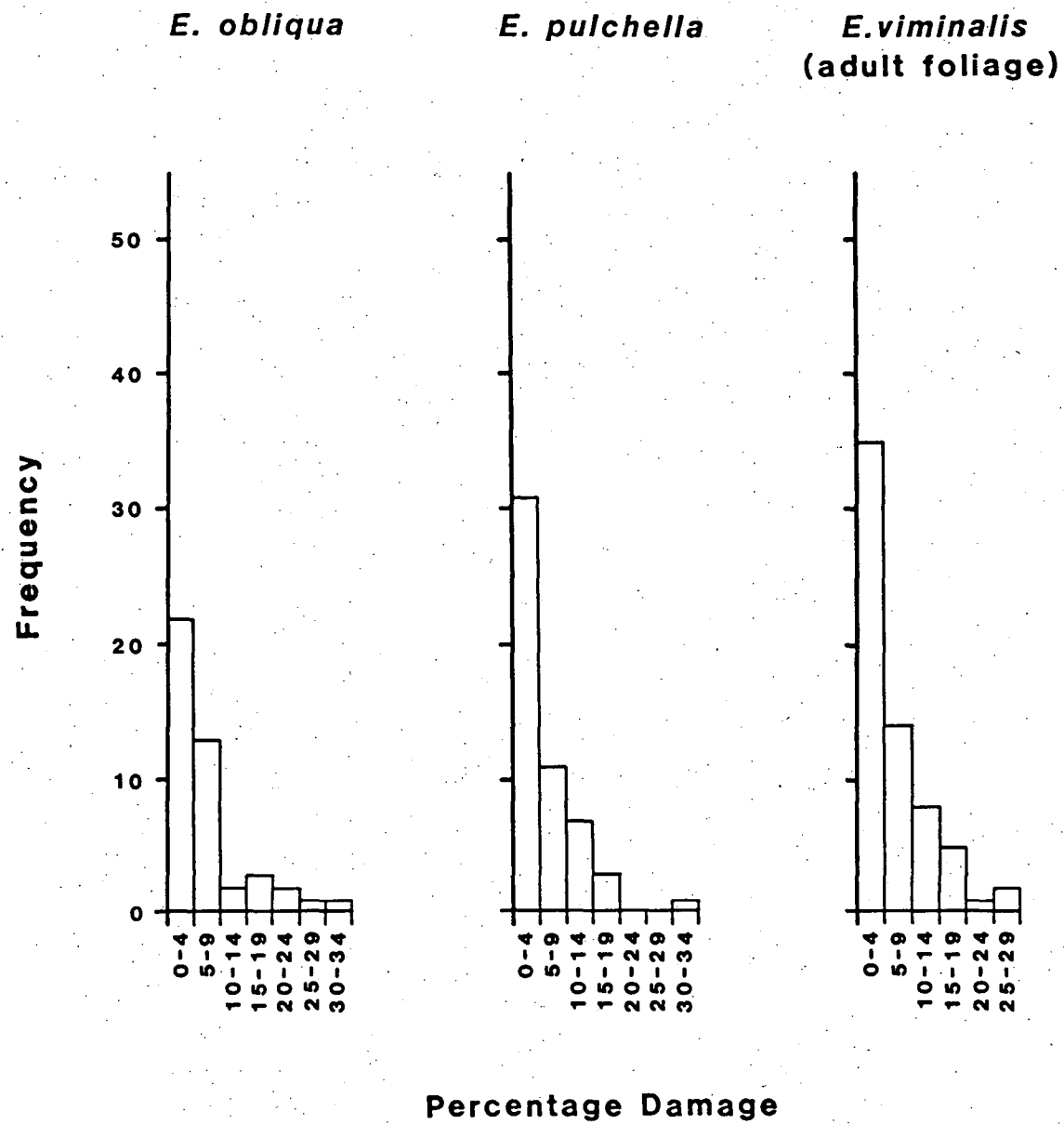
FIGURE 3.2 (continued): (b) on CPS

E. obliqua

E. viminalis
(adult foliage)

E. viminalis
(juvenile foliage)

E. tenuiramis

Frequency

Percentage Damage
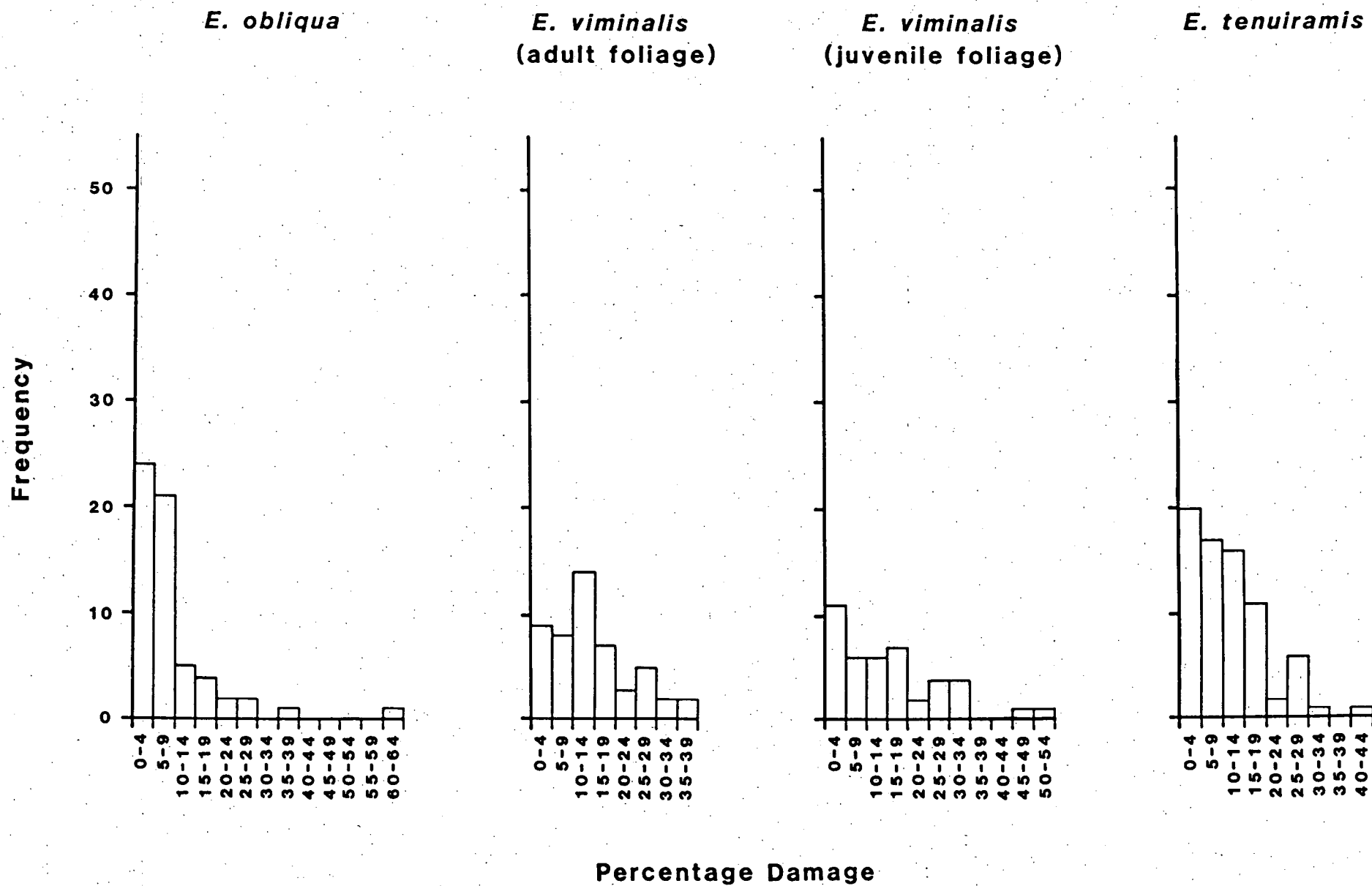
FIGURE 3.2 (continued): (c) on RWN

E. obliqua   *E. viminalis*   *E. viminalis*
                (adult foliage)   (juvenile foliage)

Frequency

Percentage Damage
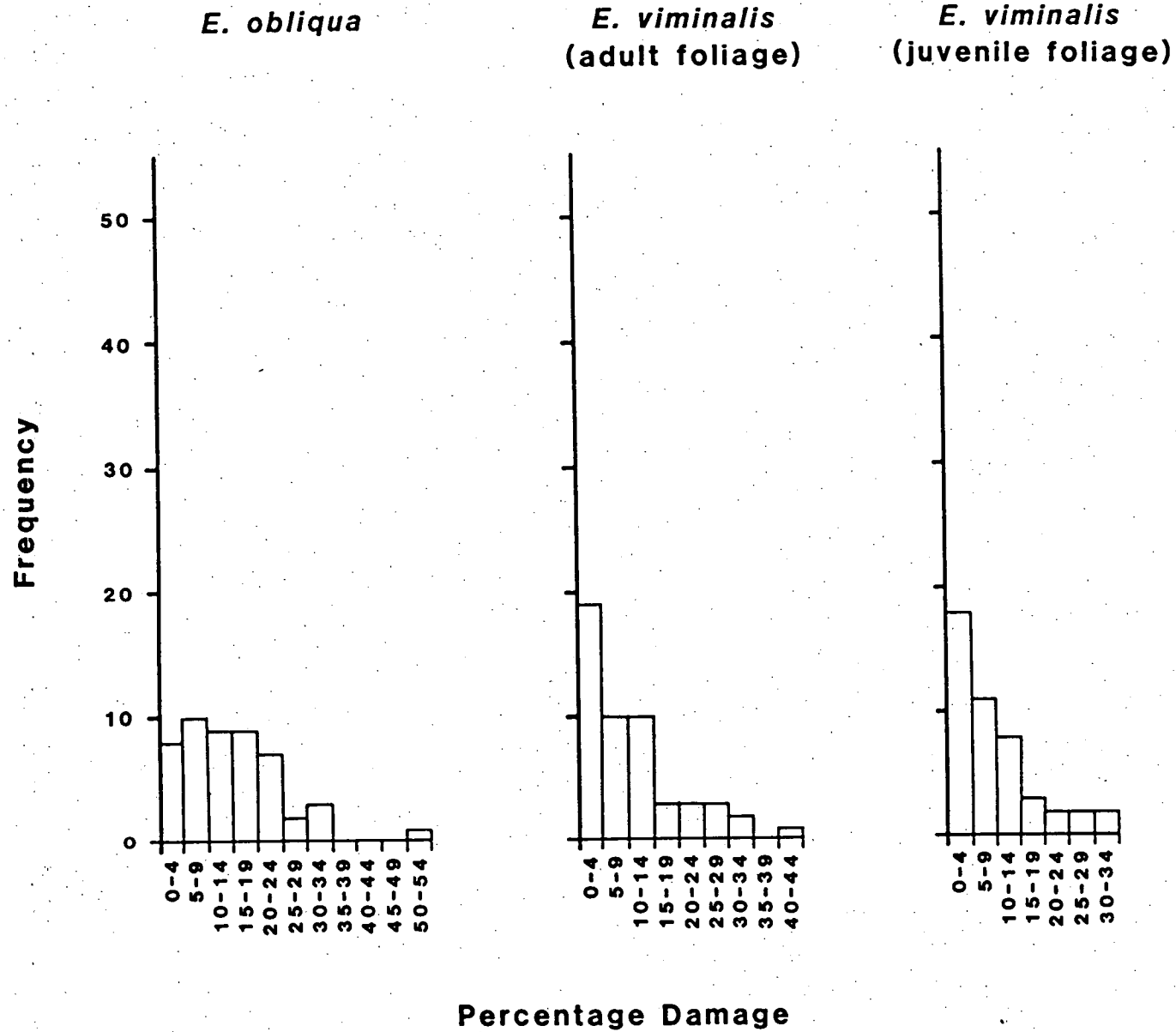
<u>FIGURE 3.2</u> (continued): (d) on RWS

are rare. The negative skew displayed by the data is most pronounced
on the Chimney Pot Hill sites; hence, the majority of shoots here are
confined to the lower classes of damage compared with shoots on the
Ridgeway sites.

Figure 3.3(a-d) shows the changes in mean percentage damage to
each tree over time. There is no consistent trend. The shoots of
some trees sustain more damage in the first month than at any other
time. Other trees show a gradual increase in percentage damage over
time, while others still display one or more peaks in percentage damage
over the growing season. For only 50.5% of the trees is the percentage
damage at a maximum in May/June: i.e., at the end of the period of
intense insect activity (see below). Another 27.2% peak in April and
15.5% in March (Tables 3.4 and 3.5).

The differences in the patterns of change in percentage damage
over time between the different trees may be explained by the timing
of a number of factors including: (1) peak insect activity; (2) seasonal
shoot growth; and (3) litterfall. Insect activity increases during
spring, is at a peak in mid-summer and declines during late February.
There may be another upsurge in autumn due to the emergence of adults
(Carne 1965, 1966; Greaves 1966; Fox and Morrow 1983; Ohmart *et al.*
1983).

Shoot growth in all but one species (*E. pulchella*; see Section 3.3.1.4)
is binodal; that is, there are two peaks in shoot growth, spring and
autumn (Specht and Brouwer 1975; Rogers and Westman 1981). The timing
of litterfall may vary between the species (Rogers and Westman 1979).
However, 70-80% usually occurs between December and March (Ohmart
et al. 1983a). Litterfall in *E. obliqua* has been correlated with mean
maximum temperature (Attiwill *et al.* 1977; Turnbull and Madden 1983).
The outcome of this is that leaf growth and leaf fall may occur
together, although the former occurs first (Rogers and Westman 1981).

Thus the upsurge of mean percentage damage in some trees during
April-May/June is probably due to the emergence of adults from mature
larvae at the same time as new shoot growth is prevalent on the trees.
Such insects feed voraciously in order to survive the winter (Carne

(a) CPN

E. obliqua *E. pulchella* *E. viminalis* (adult foliage)

Mean Percentage Damage

30
25
20
15
10
5
0

O/N D J F M A M/J
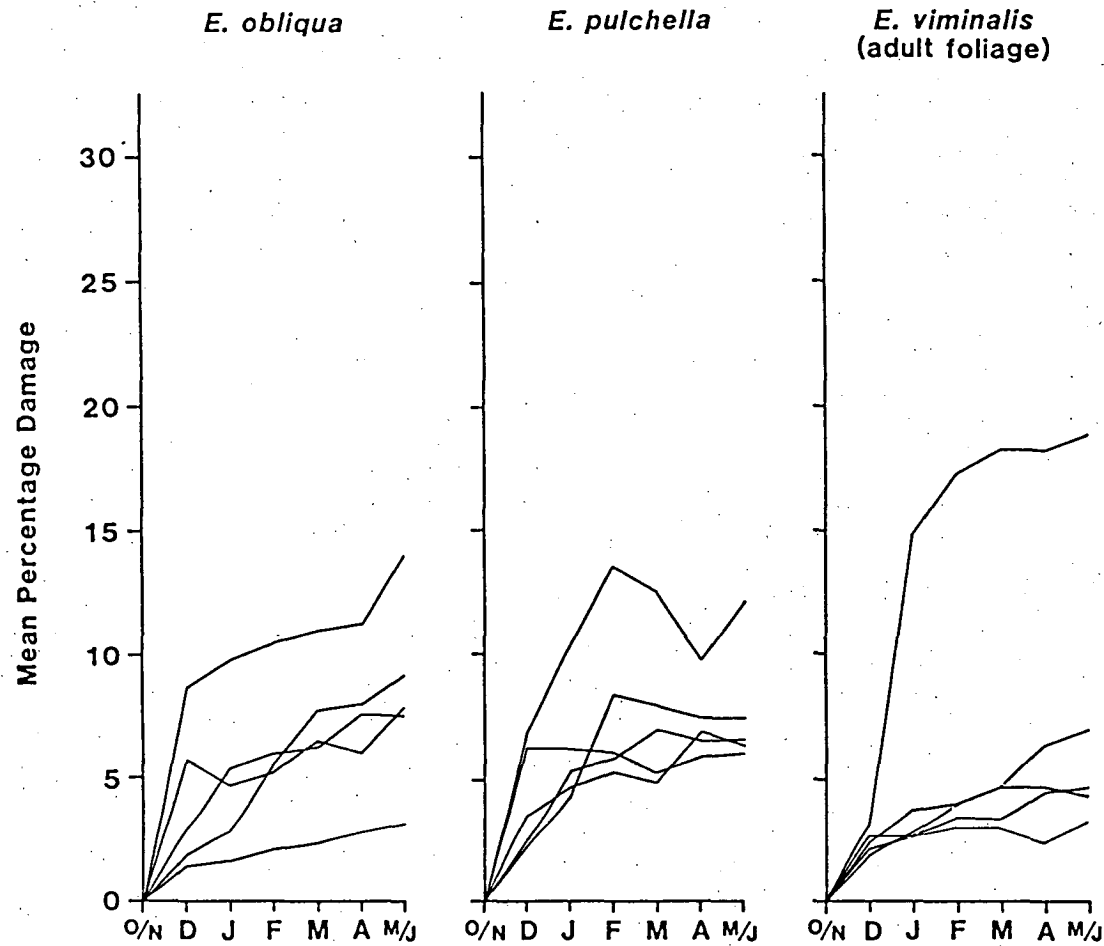
<u>FIGURE 3.3;</u> The mean percentage damage found on the trees over time, in each species at the different sites. O/N = October/November; D = December; J = January; F = February; M = March; A = April, M/J = May/June
(a) on CPN

(b) CPS
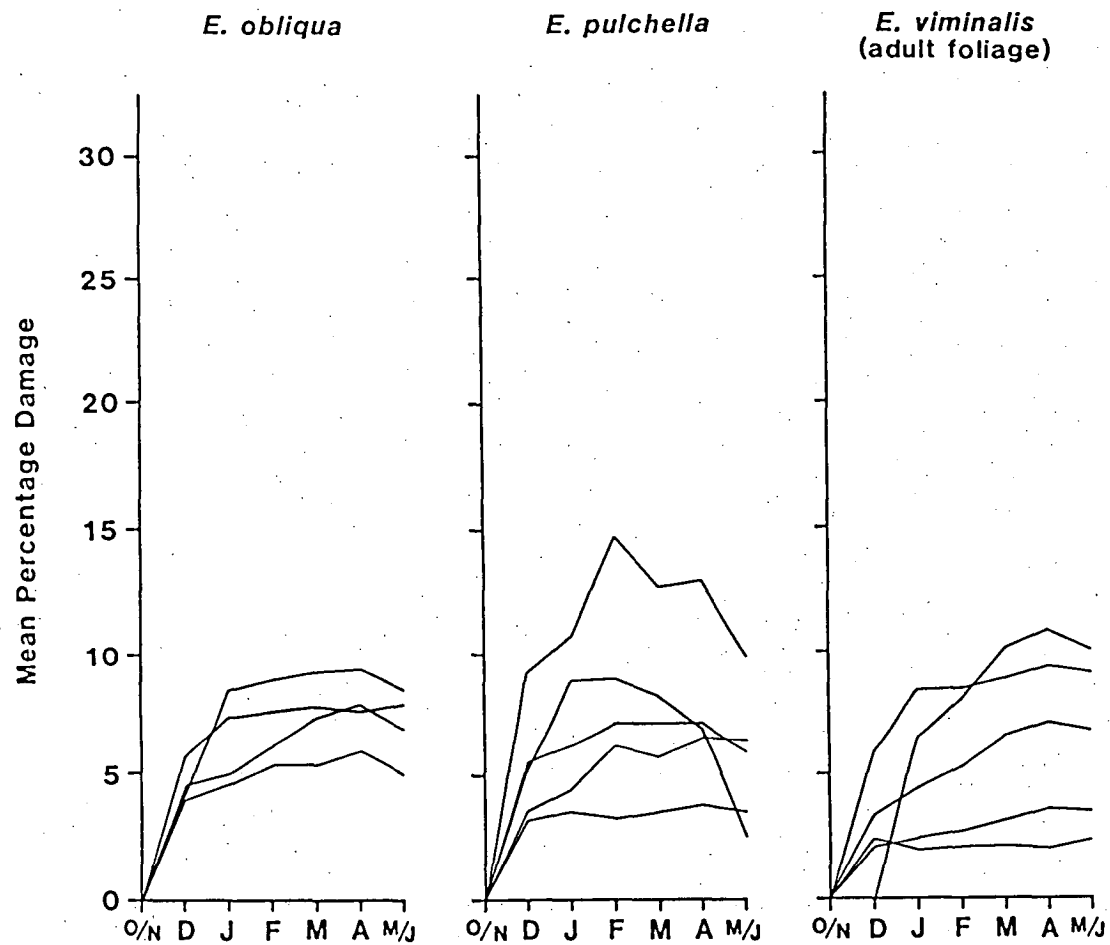
FIGURE 3.3 (continued): (b) on CPS

(c) RWN

E. obliqua

E. viminalis (adult foliage)

E. viminalis (juvenile foliage)

E. tenuiramis
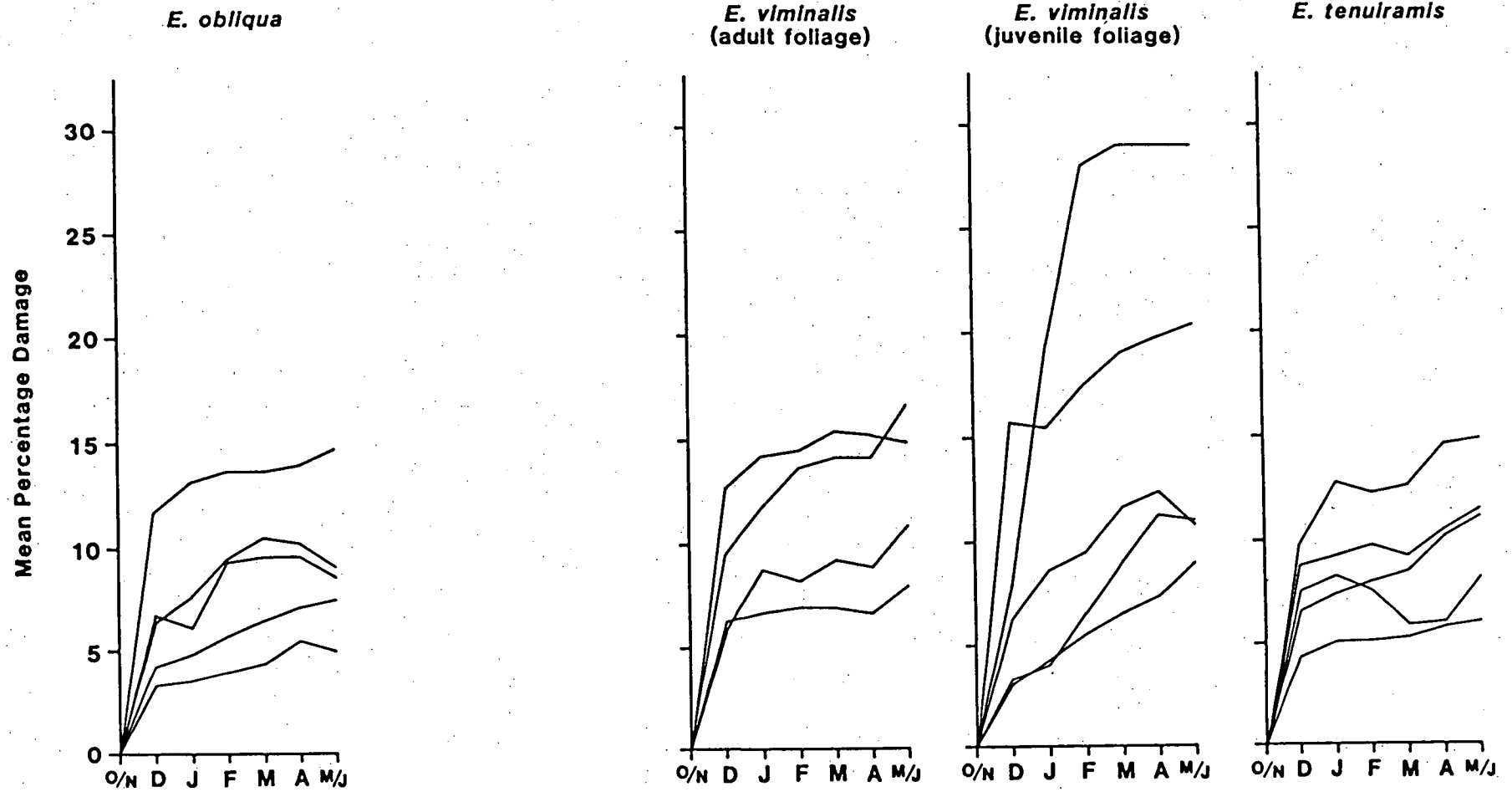
FIGURE 3.3 (continued): (c) on RWN

(d) RWS

E. obliqua

E. viminalis
(adult foliage)

E. viminalis
(juvenile foliage)
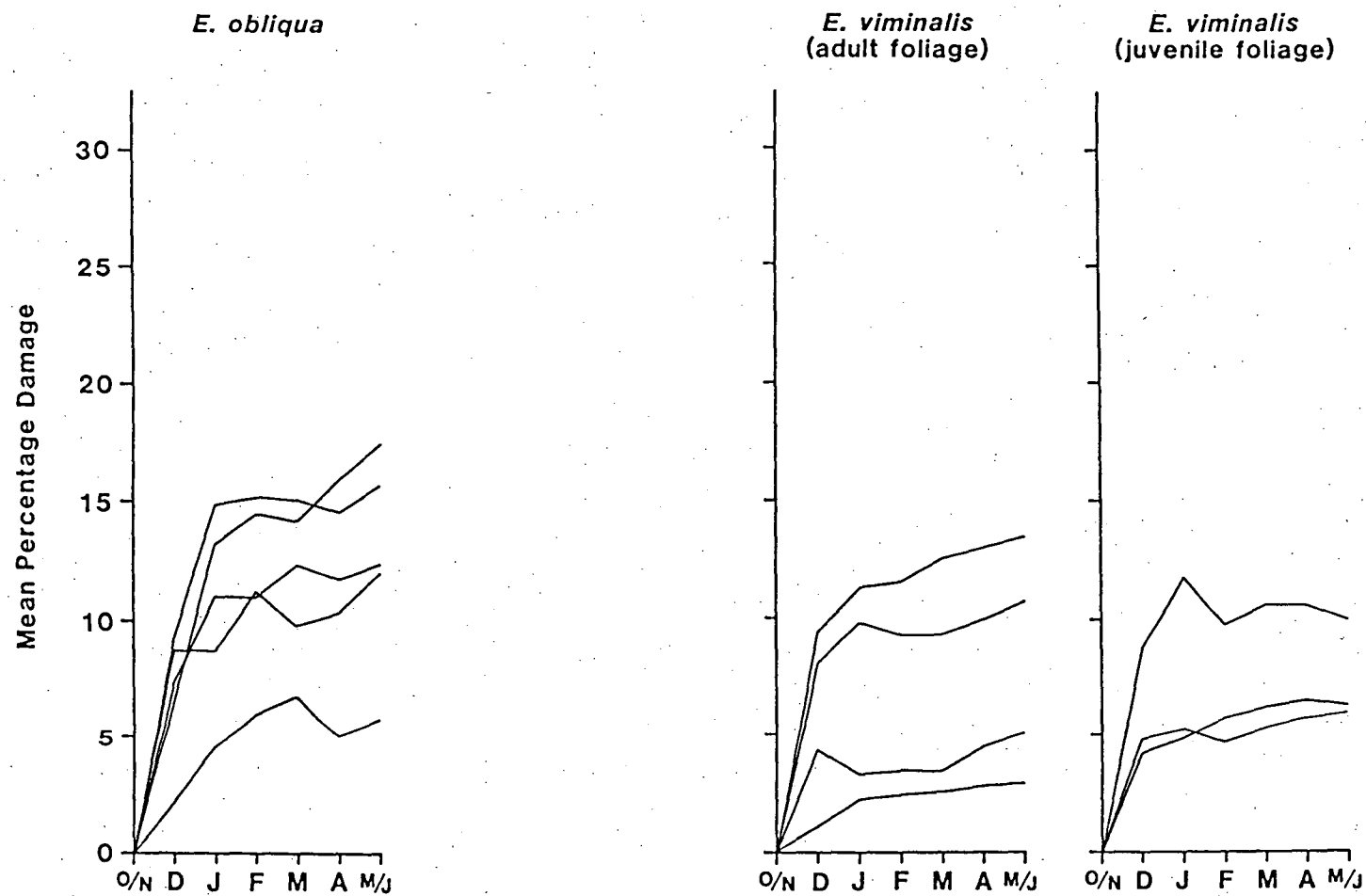
FIGURE 3.3 (continued): (d) on RWS

Species	CPN D	J	F	M	A	M/J	CPS D	J	F	M	A	M/J	RWN D	J	F	M	A	M/J	RWS D	J	F	M	A	M/J
E. obliqua					1	4				3	1			1.5	1.5		2				2		3	
E. pulchella	1	2	1	1					3	2														
E. viminalis (adult foliage)				0.5	0.5	4				4	1			1			3							4
E. viminalis (juvenile foliage)														0.3		2.3	2.3		1			1	1	
E. tenuiramis																	5							

TABLE 3.4: The month in which the trees of each species on the different sites, sustain maximum insect damage.

D = December; J = January; F = February; M = March; A = April and M/J = May/June

	Number of trees which sustain max. damage in each of the time periods	First column expressed as a percentage
December	0.0	0.0
January	2.0	3.3
February	5.0	8.3
March	6.3	10.5
April	16.3	27.2
May/June	30.3	50.5

TABLE 3.5: The number of trees that sustain maximum insect damage in each time period.

1965). The decline in insect damage after reaching a peak in February/ March, for some trees, may be due to the growth of previously damaged leaves, the presence of many new leaves, the shedding of highly damaged leaves, or a combination of these (Kile 1974; Morrow 1977; Rogers and Westman 1981; Ohmart *et al.* 1983a).

Another feature of the data is for one tree to be much more highly damaged than others of the same species on the same site; e.g. *E. viminalis* (adult foliage) on CPN and *E. viminalis* (juvenile foliage) on RWN (Burdon and Chilvers 1974b). There is no strong evidence to suggest that this phenomenon is restricted to certain sites or species. It was noticed that trees subject to very high damage during the 1981-82 growing season had also been highly damaged during previous years. Other researchers have noted this tendency for some trees to be repeatedly attacked (Carne 1966). Pryor (1952) found that where one tree showed repeated susceptibility or repeated resistance to insect attack, it was a hybrid and so its relative susceptibility or resistance was inherited from one of its parents.

3.3.1.4 Estimates of Actual Damage

Figures 3.4(a-d) show the change in mean percentage damage for each species on a site, over time. Most species show a gradual increase in percentage damage, with the greatest amount of insect damage being sustained in the first six weeks (i.e. November – mid-December). Table 3.6 shows the time period in which each species sustains its highest amount of damage. Approximately half the species are most highly damaged in May/June (see Section 3.3.1.3 for an explanation of the changes in mean percentage damage, within the species, over time). Interestingly, *E. pulchella* is the major exception to this pattern, evidencing maximum percentage damage on CPN and CPS in mid-February. This may represent the period of peak insect activity in this species. *E. pulchella* is different from other species in that it exhibits new growth all year round. Hence, the upsurge in insect activity, and therefore insect damage, experienced by many of the other eucalypt species in April-June with the occurrence of new foliage, is not apparent in *E. pulchella* (see Section 3.3.1.3).

The mean percentage damage sustained by *E. obliqua, E. pulchella,
E. viminalis* (adult and juvenile foliage) and *E. tenuiramis* in May/June
is 9.3%, 6.7%, 8.6%, 11.8% and 10.4% respectively (Table 3.7). Other
studies show the percentage leaf area loss for small regrowth trees to
be in the order of 7-15% for *E. obliqua* (Fox and Morrow 1983) and
12-13% for *E. viminalis* (Burdon and Chilvers 1974; Fox and Morrow 1983).
The percentage damage to *E. obliqua* lies at the lower end of the range
of values obtained from the collation of the results from these studies.
The level of damage sustained by *E. viminalis* (adult foliage), however,
is much lower than the values found in the literature.

(a) Between-Species Comparison

In the general analysis there were no significant differences
between the level of (actual) damage sustained by the different species,
although in the species-site analysis the percentage damage of
E. viminalis (juvenile foliage) on RWN just failed to be significantly
higher than that of *E. obliqua* ($0.05 < P \geqslant 0.10$).

In the insect damage survey undertaken by Fox and Morrow (1983)
the percentage foliage losses in *E. obliqua* and *E. viminalis* (adult
foliage) from relatively undisturbed upland forests and woodlands
(approximately 800 m a.s.l.), were also found not to differ significantly
from one another.

Duff *et al.* (1983) also found the level of damage in *E. viminalis*
(juvenile foliage) in the dry sclerophyll forests of SE Tasmania to be
higher than that in *E. pulchella*. However, no statistical test was
conducted to discover if the levels of damage between the two species
were significantly different.

Burdon and Chilvers (1974a) found the leaf area loss in Symphyomyrtus
trees to be higher than that in Monocalyptus trees, although interestingly
E. viminalis did not sustain such high levels of damage as the other
Symphyomyrtus species sampled (*E. dalrympleana*), and in fact there was
no significant difference between the level of damage sustained by
E. viminalis and that sustained by some of the Monocalyptus species

(a) CPN

(b) CPS
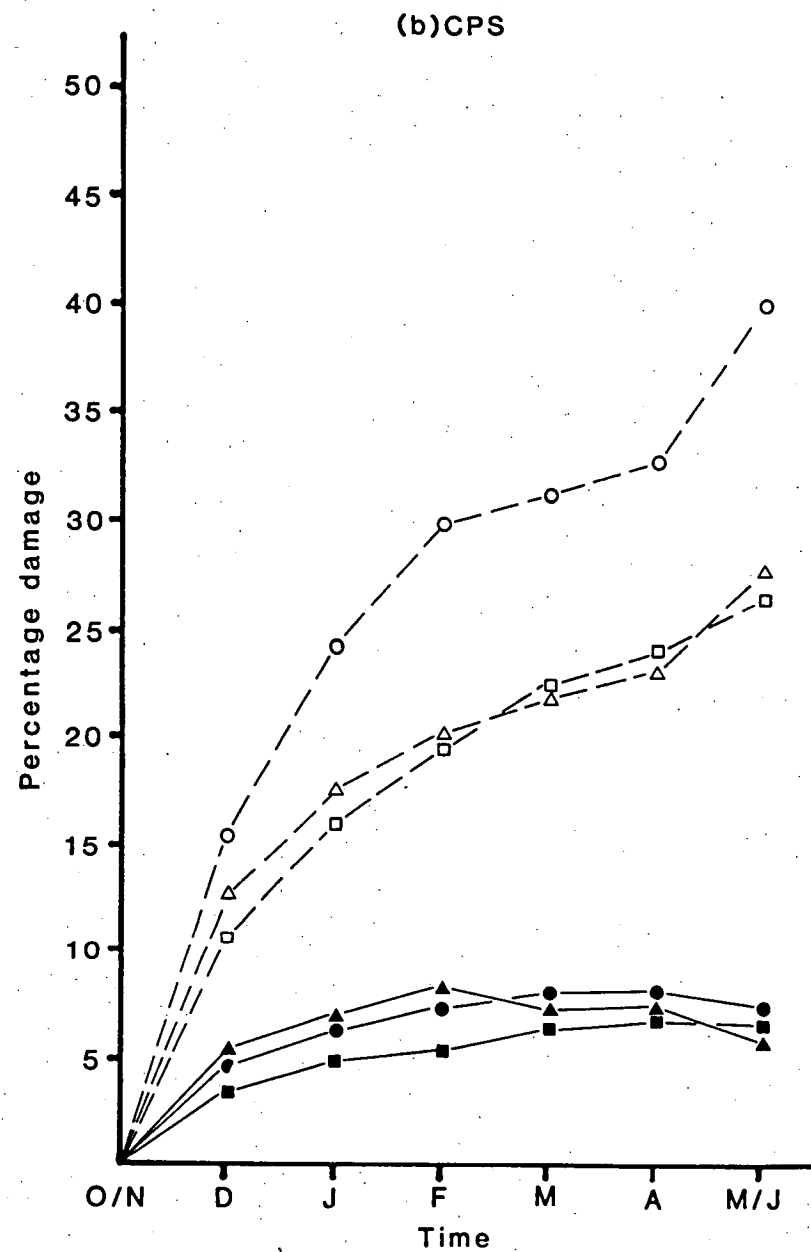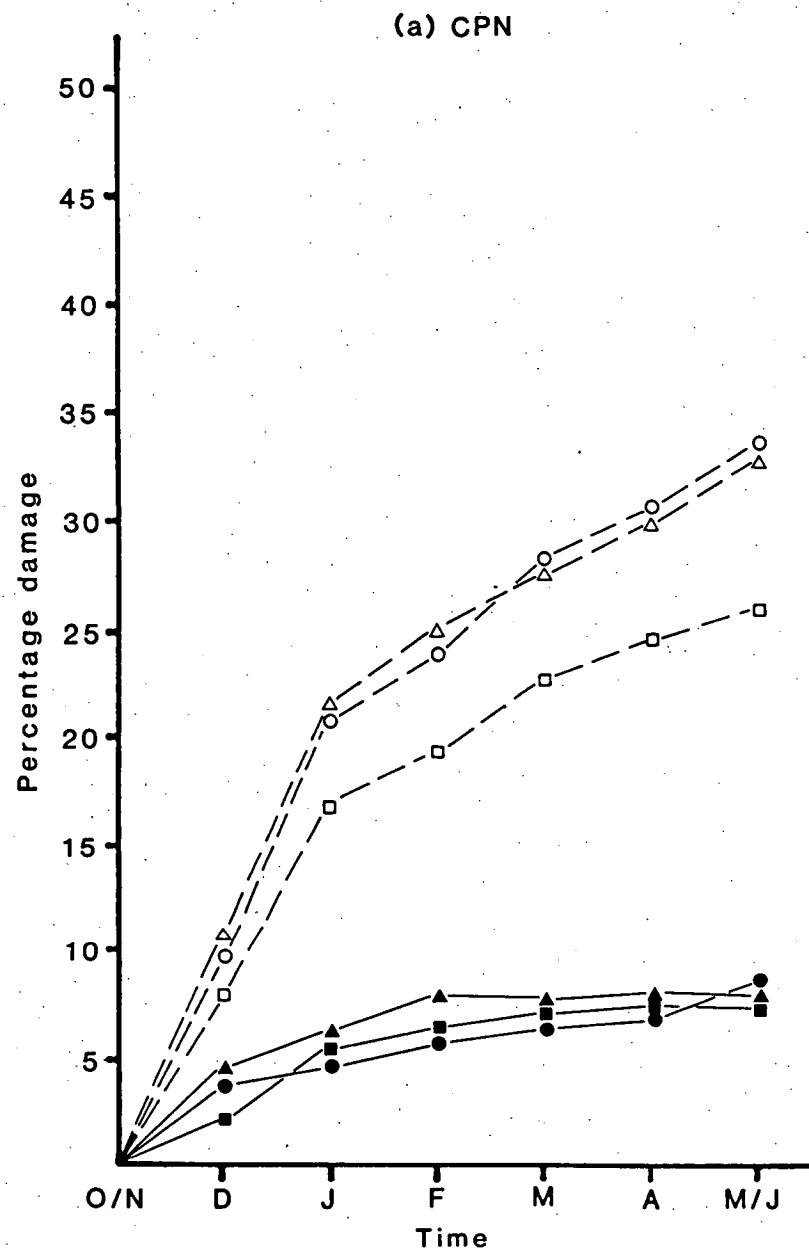
FIGURE 3.4 (continued): (c) on RWN; (d) on RWS.
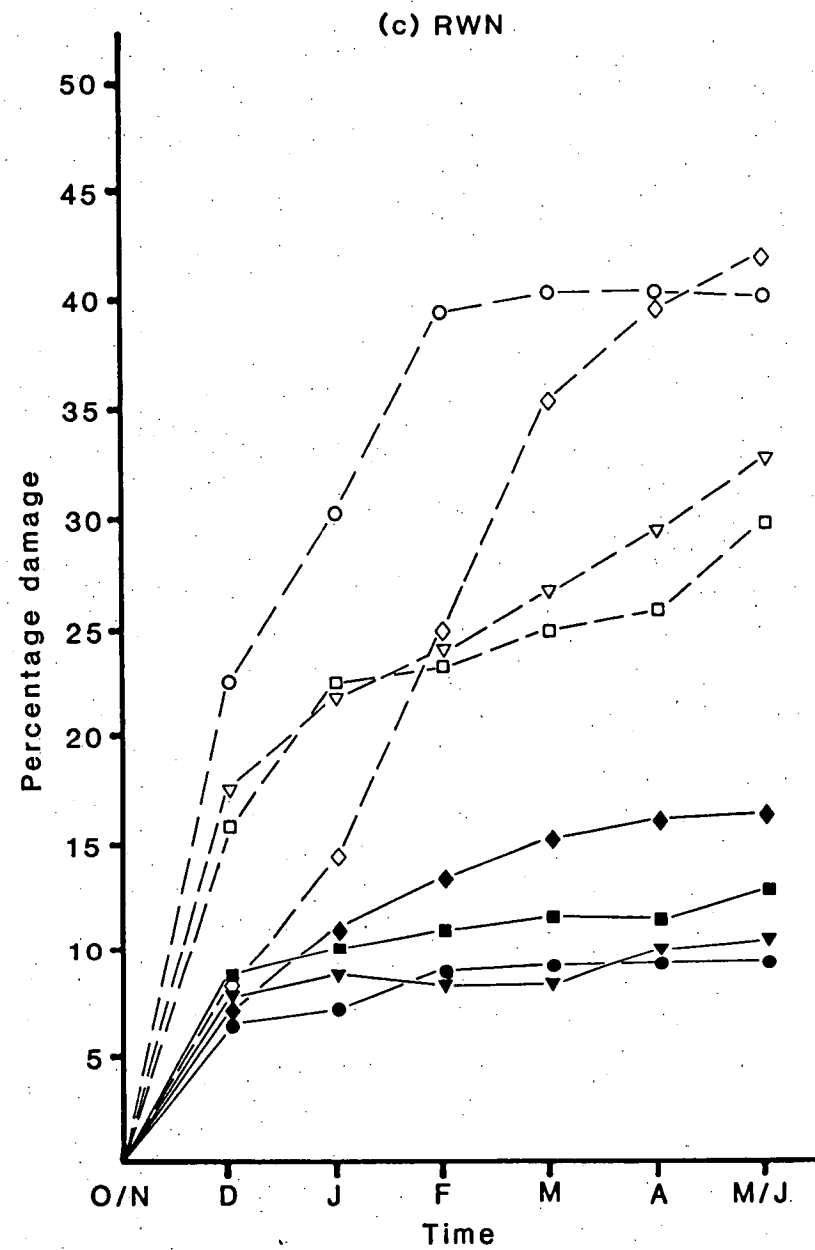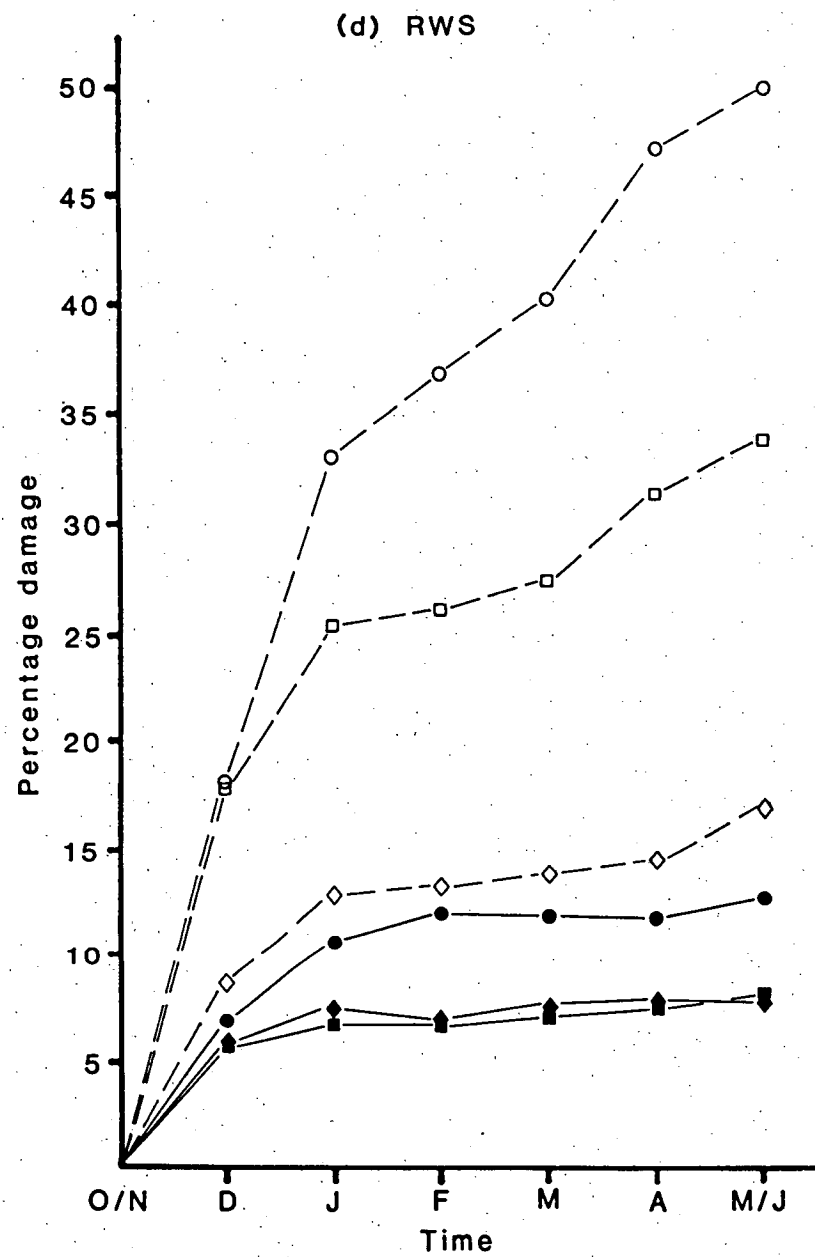
	Mid-December	Mid-January	Mid-February	Mid-March	Mid-April	May/June
CPN			E. pulchella			E. obliqua E. viminalis (adult foliage)
CPS			E. pulchella		E. obliqua E. viminalis (adult foliage)	
RWN					E. obliqua	E. viminalis (adult foliage E. viminalis (juvenile foliage) E. tenuiramis
RWS					E. viminalis (juvenile foliage)	E. obliqua E. viminalis (adult foliage)
	0	0	2	0	4	7
	0	0	15.38%	0	30.77%	53.85%

TABLE 3.6: The month in which each species on the different sites sustain maximum insect damage.

	CPN		CPS		RWN		RWS		SUM OF DAMAGE		MEAN DAMAGE	
	mean % actual damage	mean % total damage	mean % actual damage	mean % total damage	mean % actual damage	mean % total damage	mean % actual damage	mean % total damage	mean % actual damage	mean % total damage	mean % actual damage	mean % total damage
E. obliqua	8.3	33.6	7.2	40.0	9.1	40.1	12.7	50.1	37.3	163.8	9.3	41.0
E. pulchella	7.7	32.8	5.7	27.6					13.4	60.4	6.7	30.2
E. viminalis (adult foliage)	7.6	25.9	6.3	26.2	12.6	29.6	8.0	33.7	34.5	115.4	8.6	28.9
E. viminalis (juvenile foliage)					16.0	41.9	7.5	16.8	23.5	58.7	11.8	29.4
E. tenuiramis					10.4	32.7			10.4	32.7	10.4	32.7

TABLE 3.7: The mean percentage damage (actual and total) sustained by different species of eucalypts on each site.

	Eucalyptus obliqua		Eucalyptus pulchella		Eucalyptus viminalis (adult foliage)		Eucalyptus viminalis (juvenile foliage)		Eucalyptus tenuiramis		Total damage		Mean damage	
	mean % actual damage	mean % total damage	mean % actual damage	mean % total damage	mean % actual damage	mean % total damage	mean % actual damage	mean % total damage	mean % actual damage	mean % total damage	% actual damage	% total damage	% actual damage	% total damage
CPN	8.3	33.6	7.7	32.8	7.6	25.9					23.6	92.3	7.9	30.8
CPS	7.2	40.0	5.7	27.6	6.3	26.2					19.2	93.8	6.4	31.3
RWN	9.1	40.1			12.6	29.6	16.0	41.9	10.4	32.7	48.1	144.3	12.0	36.1
RWS	12.7	50.1			8.0	33.7	7.5	16.8			28.2	100.6	9.4	33.5

TABLE 3.8: The mean percentage damage (actual and total) sustained by a species on different sites.

sampled (*E. pauciflora* and *E. radiata*).

Thus it would appear that my results are generally consistent with those found in other studies. Even so, it seems unusual that species sampled from the same environment over the same period of time sustain similar amounts of damage, when previous research has shown that species growing in the same environment do differ significantly in the amount of damage they incur (Fox and Morrow 1983). The lack of significant results may be partly due to the age of the foliage and/or trees sampled (Section 3.3.1.2). Whatever is the case, these results have interesting implications for the role of insect damage in the establishment and maintenance of mixed stands (see Discussion).

(b) Between-Site Comparison

Of the six comparisons made between the sites in the general analysis only one, the level of damage sustained by RWN compared with CPS, was significantly different (0.01<P≥0.05). However, two other relationships, the percentage damage on RWN compared to CPN and the percentage damage on RWS compared to CPS, just failed to be significantly different from one another (0.05<P≥0.10).

In the species-site analysis no significant relationships were found. Three comparisons just failed to be significant: (1) the amount of damage sustained by *E. obliqua* on RWS was higher than that sustained by the same species on CPN; (2) the amount of damage in *E. viminalis* (adult foliage) on RWN was higher than the amount of damage on CPS and (3) the amount of damage in *E. viminalis* (juvenile foliage) on RWN was higher than the amount of damage on RWS. These differ from the relationships found in the main analysis because of the increased amount of actual damage sustained by *E. obliqua* on RWS and *E. viminalis* (adult foliage) on RWN compared to the other sites, which is obscured when taking the mean actual damage per site in the general analysis.

In all of these relationships the percentage actual damage in the Ridgeway sites is higher than that in the Chimney Pot Hill sites

(see Figure 3.5). This may indicate that actual damage in the small trees occurring in dry sclerophyll forests would be subject to variance between ecologically distinct sites. In fact, other researchers have shown that insect species and insect numbers, and therefore the amount of damage, does vary between ecologically distinct sites. For example, insect species have been shown to vary upon slopes of different aspect (see Chapter one). Carne *et al.* (1974) found that the appearance and disappearance of Christmas beetles (Coleoptera:Scarabaeidae) and the 'timing of maximum' occurrence varied between sites, which they attributed to environmental differences between the sites. Fox and Morrow (1983) found that eucalypts from higher altitudes on more mesic sites were subject to increased levels of insect attack compared with the same species occurring at lower altitudes, whereas Burdon and Chilvers (1974b) found the percentage leaf area loss (and the mean leaf area per shoot, and the numbers of parasites) decreased in *E. pauciflora* as altitude increased. Carne (1965) found the level of infestation by the sawfly *Perga affinis affinis* upon *E. blakelyi* depended upon the environment in which the tree was growing. Trees from low lying mesic sites produced regular amounts of foliage that were highly attractive to the sawflies, whereas trees in the drier upland areas rarely produced foliage that became infested. The results and conclusions from these studies are highly conflicting (see end of chapter).

However, it seems likely that when species are sampled along a wide ecological gradient, differences in the damage sustained by them do occur. Whether these differences are the result of the physical environment restricting the activities (i.e. reproduction and survival) and/or distribution of insect species or whether they are the result of between-tree differences resulting from growth in different environments is a matter for further investigation.

(c) Comparison of Actual Damage Between Untreated and Treated Trees

The percentage actual damage sustained by the untreated trees was significantly higher than that sustained by the treated trees in four of the five between-species comparisons made. (Table 3.9, Figure 3.6).

(a) *E. obliqua*

(b) *E. pulchella & E. tenuiramis*
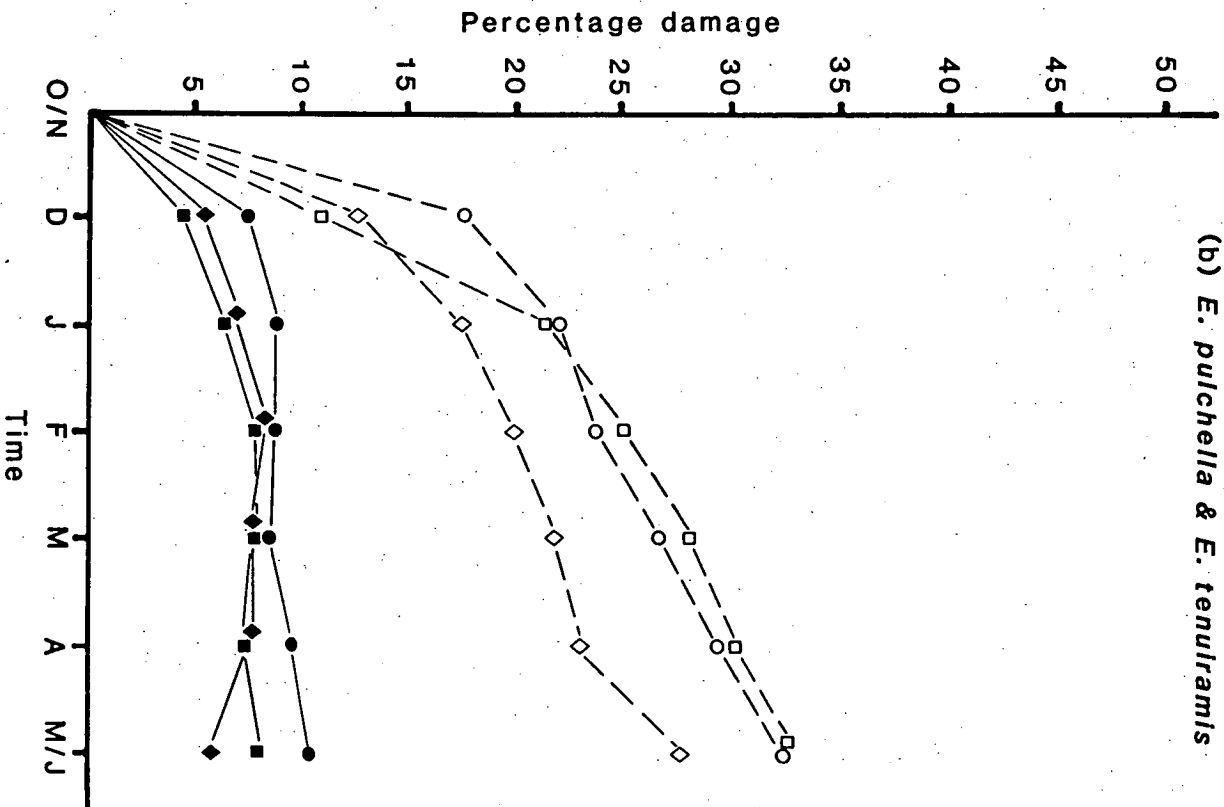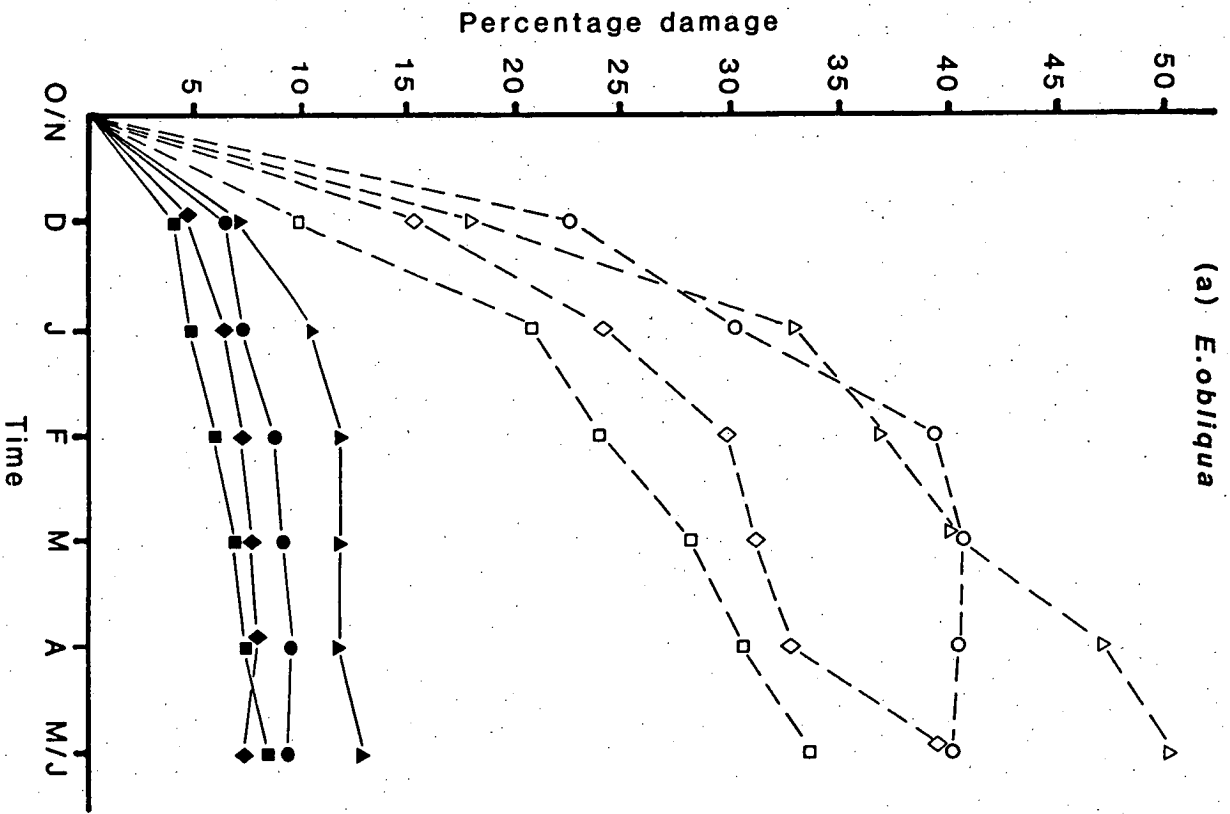
FIGURE 3.5 (continued): (c) on *E. viminalis* (adult foliage);
(d) on *E. viminalis* (juvenile foliage)

(c) *E.viminalis* (adult foliage)

(d) *E.viminalis* (juvenile foliage)

	Eucalyptus obliqua		Eucalyptus pulchella		Eucalyptus viminalis (adult foliage)		Eucalyptus viminalis (juvenile foliage)		Eucalyptus tenuiramis		TOTAL		MEAN	
	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated
CPN	8.3	3.2	7.7	4.6	7.6	4.6					23.6	12.4	7.9	4.1
CPS	7.2	4.2	5.7	2.9	6.3	4.4					19.2	11.5	6.4	3.8
RWN	9.1	6.1			12.6	3.5	16.0	8.0	10.4	5.1	48.1	22.7	12.0	5.7
RWS	12.7	4.3			8.0	6.4	7.5	8.6			28.2	19.3	9.4	6.4

TABLE 3.9: The mean percentage actual damage per shoot on treated and untreated trees per species per site.

	Eucalyptus obliqua		Eucalyptus pulchella		Eucalyptus viminalis (adult foliage)		Eucalyptus viminalis (juvenile foliage)		Eucalyptus tenuiramis		TOTAL		MEAN	
	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated
CPN	33.6	35.7	32.8	24.3	25.9	37.3					92.3	97.3	30.8	32.4
CPS	40.0	31.1	27.6	23.8	26.2	34.0					93.8	88.9	31.3	29.6
RWN	40.1	38.7			29.6	30.5	41.9	28.3	32.7	29.5	144.3	127.0	36.1	31.8
RWS	50.1	37.4			33.7	25.8	16.8	33.0			100.6	96.2	33.5	32.1

TABLE 3.10: The mean percentage total damage per shoot on treated and untreated trees per species per site.

FIGURE 3.6: Histograms showing the percentage actual damage per shoot in treated and untreated trees per species, per site.

▨ = untreated trees;   ☐ = treated trees

E.ob = E.obliqua, E.pu = E .pulchella,
E.va = E.viminalis (adult foliage), E.vj
= E.viminalis (juvenile foliage), E.te =
E.tenuiramis

Only *E. viminalis* (juvenile foliage) failed to show such a relationship. This may have been partly due to the small sample size of the data and partly due to the fact that several of the treated trees showed signs of repeated heavy insect attack in previous years, so that the level of insect activity in these trees would have been high in any case (see Section 3.3.1.3).

In the comparison of the percentage actual damage between all the treated trees and all the untreated trees on one site, the actual damage on the untreated trees in all four sites was significantly higher.

3.3.1.5   Estimates of Total Damage

The percentage of missing leaves and shoots per species per site is shown in Table 3.11. The mean percentage of missing leaves and shoots combined for *E. obliqua*, *E. pulchella*, *E. viminalis* (adult and juvenile foliage) and *E. tenuiramis* is 21.4%, 13.8%, 12.1%, 16.4% and 15.3% respectively. The percentage missing leaves and shoots sustained by *E. obliqua* is very much higher than that in the other species.

Figure 3.4 shows the percentage total damage of the different species by site. Figure 3.5 shows the difference in the level of total damage within one species between different sites.

The mean percentage total damage sustained by each species is 41.0% in *E. obliqua*, 30.2% in *E. pulchella*, 28.9% and 29.4% in the adult and juvenile foliage of *E. viminalis* respectively and 32.7% in *E. tenuiramis* (Table 3.10). These values are significantly higher than the values of actual damage found in each of the species (Section 3.3.1.4).

Journet (1981) incorporated abscission data into his estimate of foliage loss. He found that the (total) damage was 60-70% on *E. blakelyi* occurring in various woodland sites. This estimate is much higher than those found for the eucalypts in the Ridgeway Park Reserve. However, (actual) damage to *E. blakelyi* was very high, being around 40% (see also Fox and Morrow 1983).

	E. obliqua		E. pulchella		E. viminalis (adult foliage)		E. viminalis (juvenile foliage)		E. tenuiramis	
	% missing leaves (%ML)	% missing shoots (%MS)	% ML	% MS	% ML	% MS	% ML	% MS	% ML	% MS
CPN	27.9	4.2	27.4	2.9	20.8	0.0				
CPS	30.8	8.3	22.6	2.1	21.2	3.0				
RWN	35.3	7.7			19.6	2.0	30.9	22.2	24.2	6.3
RWS	43.0	14.0			28.0	1.9	10.1	2.3		

TABLE 3.11: The percentage missing leaves and percentage missing shoots per species per site.

(a)   Between–Species Comparison of Total Damage

In all but two of the eight comparisons made in the general analysis, there was no significant difference between the percentage total damage of the different species.   The two exceptions were the significantly higher total damage sustained by *E. obliqua* compared with *E. viminalis* (adult foliage; 0.01 <P⩾0.001)and *E. pulchella* (0.05<P⩾0.01).   There is an additional significant relationship in the species –site analysis, with *E. obliqua* on RWS having a significantly higher level of total damage than *E. viminalis* (juvenile foliage; 0.05<P⩾0.01).

The 'additional' significant relationship occurs because of the very great differences between the percentage total damage of *E. viminalis* (juvenile foliage) on RWN and RWS (41.9% and 16.8% respectively; see Table 3.7); so that although the level of total damage on RWS was significantly different from that of *E. obliqua*, this relationship was masked in the general analysis because I took the mean score for species over all sites.

The significantly higher percentage of total damage sustained by *E. obliqua* compared with the other eucalypts is due to the higher numbers of missing leaves and missing shoots found in this species (Table 3.11).

(b)   Between–Site Comparison of Total Damage

No significant relationships were found in the between–site comparison of percentage total damage in the general analysis.   However, the level of total damage in the two most ecologically different sites (CPN and RWS) just failed to be significantly different from one another (0.10<P⩾0.05).   Again,the very great difference between the percentage total damage in *E. viminalis* (juvenile foliage), is reflected in the species–site analysis, with the level of total damage sustained on RWN just failing to be significantly different from that on RWS (0.10<P⩾0.05).

The trend for actual damage to be higher on the Ridgeway sites compared with the Chimney Pot Hill sites is not exhibited by the total damage data. However, the results do not preclude the possibility that total damage may be subject to variance along an environmental gradient (see discussion).

Overall the results show that: (1) although there are some between-species differences in the level of total damage on a site (cf. actual damage), in 75% of the comparisons made no such differences existed; (2) total damage did not significantly vary between sites differing in climate and soil type; and (3) percentage total damage is significantly higher than percentage actual damage.

Very high levels of damaged and missing leaves have been found to suppress tree growth and in severe cases cause tree mortality (Bamber and Humphreys 1965; Mazanec 1966, 1967, 1974; Kalman 1971 and Cremer 1973). It is therefore important to establish what proportion of this total damage can be attributed solely to the activities of insects in order that the true amount of insect damage be ascertained. This was partially achieved by a series of experiments excluding insects from the shoots of some trees through the use of insecticide.

(c) Comparison of the Percentage Total Damage in Untreated and Treated Trees

Table 3.10 shows the percentage total damage of treated and untreated trees for each species per site.

There was no significant difference between the level of total damage sustained by the untreated and treated trees in any species, although the total damage in the untreated trees of *E. pulchella* just failed to be significantly higher than that sustained in the treated trees ($0.05 < P \geqslant 0.10$). Neither was there any significant difference between the percentage total damage in the treated and untreated trees on any one site (see Figure 3.7).
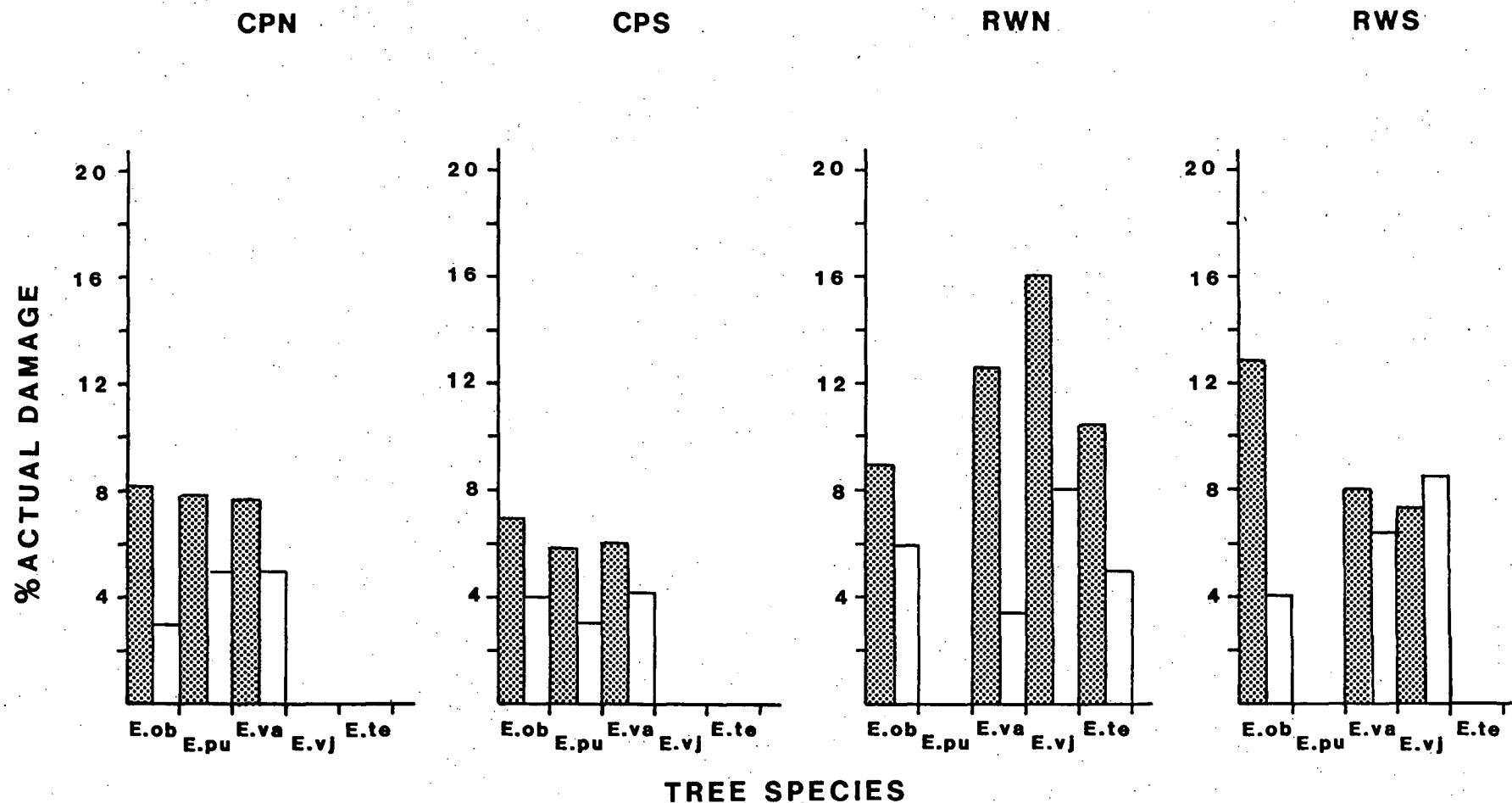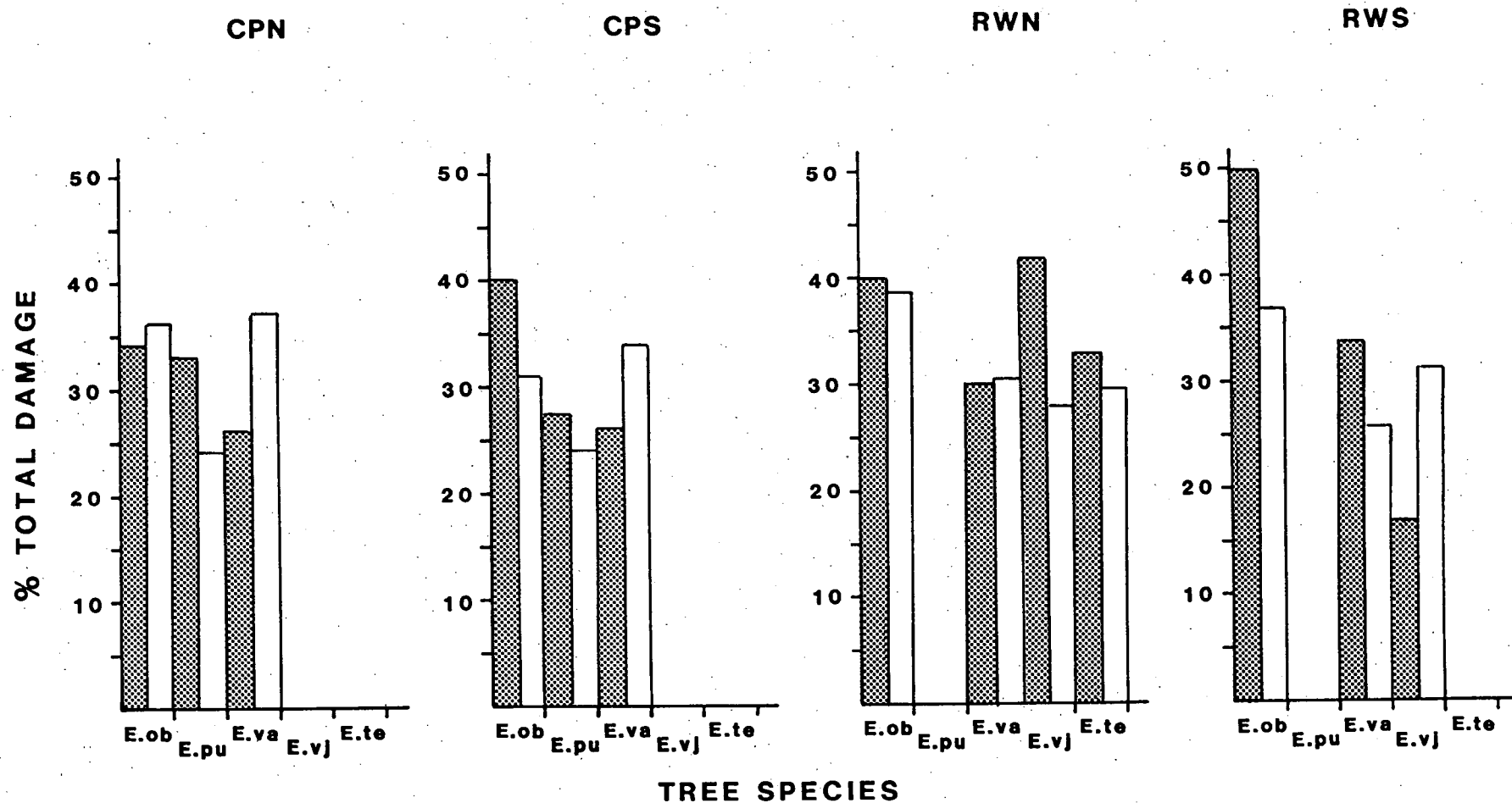
FIGURE 3.7: Histograms showing the percentage total damage in treated and untreated trees per species, per site

▨ = untreated trees; ☐ = treated trees

E.ob = E.obliqua, E.pu = E .pulchella,
E.va = E.viminalis (adult foliage), E.vj
= E.viminalis (juvenile foliage), E.te =
E.tenuiramis

As the insecticide has been shown to significantly diminish insect activity on the leaves (see Part (c) of 3.3.1.4 on actual damage), the results from the above analysis would seem to indicate that insect damaging activities do not affect the amount of total damage: i.e., the number of missing leaves and shoots. This phenomenon is further discussed in the section on missing leaves (3.3.2.1).

3.3.2 The Effects of Insects Upon Tree Growth

3.3.2.1 The Percentage of Missing Leaves

Figure 3.8 shows the percentage of missing leaves sustained by untreated and treated trees. In some instances the number of missing leaves was higher in the treated trees.

The mean percentage missing leaves found in *E. obliqua*, *E. pulchella*, *E. viminalis* (adult and juvenile foliage) and *E. tenuiramis* was 34.3%, 25.0%, 22.4%, 20.5% and 24.2% respectively (Table 3.12). The figure of 22.4% for *E. viminalis* (adult foliage) is far greater than the value of 9.0% found by Fox and Morrow (1983) for the same species. However, the range of values for leaf loss is similar to that found by Rogers and Westman (1979) for *E. signata* and *E. umbra* spp. *umbra* (33% and 24.6% respectively) in southern Queensland.

(a) Between-Species Analysis

Of the eight comparisons made between the level of percentage missing leaves among the different species, only two were significantly different and another two just failed to be significant. The percentage missing leaves sustained by *E. obliqua* was significantly higher than that sustained by *E. viminalis* (adult foliage, $P<0.001$) and *E. tenuiramis* ($0.05<P\geqslant0.01$), and just failed to be significantly higher than *E. viminalis* (juvenile foliage; $0.10<P\geqslant0.05$).

% MISSING LEAVES

TREE SPECIES

<u>FIGURE 3.8</u>: Histograms showing the percentage of missing leaves per shoot in treated and untreated
trees per species, per site

= untreated trees; ☐ = treated trees

E.ob = E.obliqua, E.pu = E .pulchella,
E.va = E.viminalis (adult foliage), E.vj
= E.viminalis (juvenile foliage), E.te =
E.tenuiramis

The level of missing leaves in *E. tenuiramis* just failed to be significantly higher than those in *E. viminalis* (adult foliage; $0.05 < P \geqslant 0.10$). These results were reiterated in the species-site analysis. It appears that *E. obliqua* loses more leaves than the other species.

(b) Between-Site Analysis

There were no significant differences in the percentages of missing leaves between the sites in the general analysis. However, in the species-site analysis the level of missing leaves found in *E. viminalis* (juvenile foliage) on RWN was significantly higher than that found on RWS ($0.01 < P \geqslant 0.05$). This is due to the very great difference between the percentage leaf loss of *E. viminalis* (juvenile foliage) on the north compared with the south-facing slope on the Ridgeway site, a difference which is disguised in the general analysis. This partially explains the large difference in percentage total damage between those two slopes (see section 3.3.1.5).

(c) Comparison of the Percentage Missing Leaves in Untreated and Treated Trees

In the comparisons of leaf loss sustained between untreated and treated trees of a species, only one result was significant. The treated trees of *E. viminalis* (adult foliage) lost significantly more leaves than untreated trees ($0.01 < P \geqslant 0.05$). Leaf loss in the untreated trees of *E. pulchella* just failed to be significantly higher than that in the treated trees ($0.05 < P \geqslant 0.10$).

There were no significant relationships to be found in the general analysis between the percentage missing leaves sustained by the treated and untreated trees in each site.

These results would seem to indicate that in *E. viminalis* (adult foliage) either insects stimulate the growth of leaves or the insecticide promoted leaf loss. If insects had stimulated the growth

	Eucalyptus obliqua		Eucalyptus pulchella		Eucalyptus viminalis (adult foliage)		Eucalyptus viminalis (juvenile foliage)		Eucalyptus tenuiramis		TOTAL		MEAN	
	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated
CPN	27.9	33.6	27.4	20.5	20.8	32.5					76.1	86.6	25.4	28.9
CPS	30.8	28.2	22.6	19.3	21.2	30.3					74.6	77.8	24.9	25.9
RWN	35.3	36.4			19.6	27.3	30.9	21.3	24.2	27.9	110.0	112.9	27.5	28.2
RWS	43.0	34.8			28.0	21.3	10.1	21.2			81.1	77.3	27.0	25.8

TABLE 3.12 The mean percentage of missing leaves per shoot on treated and untreated trees per species per site.

	Eucalyptus obliqua		Eucalyptus pulchella		Eucalyptus viminalis (adult foliage)		Eucalyptus viminalis (juvenile foliage)		Eucalyptus tenuiramis		TOTAL		MEAN	
	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated
CPN	78.2	67.5	74.2	63.2	66.4	63.8					218.8	194.5	72.9	64.8
CPS	81.4	73.7	67.7	55.3	74.6	74.7					223.7	203.7	74.6	67.9
RWN	81.3	83.4			96.1	52.6	66.9	65.1	82.5	55.9	326.8	257.0	81.7	64.3
RWS	93.5	74.3			75.5	83.5	65.9	75.1			234.9	232.9	78.3	77.6

TABLE 3.13 The mean percentage of damaged leaves per shoot on treated and untreated trees per species per site.

of leaves, then it would be expected that the number of leaves per shoot on the untreated trees would be higher than that in the treated trees. No such relationship was found (Section 3.3.2.4). Therefore it seems probable that over-spraying with insecticide had a detrimental effect on *E. viminalis* (adult foliage).

In the remaining species, one of two hypotheses would explain the similarity between the number of missing leaves found on untreated and treated trees. Firstly, insects may not affect the number of missing leaves. Secondly, the number of missing leaves caused by stressful environmental conditions (see Methodology) may outweigh the number lost through insect activity to the extent that there is no significant difference between the number occurring in treated and untreated trees.

3.3.2.2 Percentage of Leaves Damaged

The percentage of leaves damaged in each species per site is represented diagrammatically in Figure 3.9. It was found that the mean percentage of leaves damaged in *E. obliqua* was 83.6%, in *E. pulchella* 71.0%, in *E. viminalis* (adult foliage) 78.2%, in *E. viminalis* (juvenile foliage) 66.4% and in *E. tenuiramis* 82.5% (Table 3.13). These percentages are higher than those recorded by Fox and Morrow (1983) who found *E. viminalis* (adult foliage) to have 43% of its leaves damaged and *E. obliqua* 72-73%.

(a) Between-Species Comparison

In all but two of the eight comparisons made there was no significant difference between the percentage of leaves damaged in each species. The two exceptions were the higher levels of damaged leaves on (1) *E. obliqua* compared with *E. viminalis* (juvenile foliage; $0.05 < P \geqslant 0.01$) and on (2) *E. viminalis* (adult foliage) compared with *E. tenuiramis* ($0.05 < P \geqslant 0.01$). The percentage of damaged leaves found for *E. viminalis* (adult foliage) just failed to be significantly higher than that in *E. viminalis* (juvenile foliage; $0.10 < P \geqslant 0.05$).

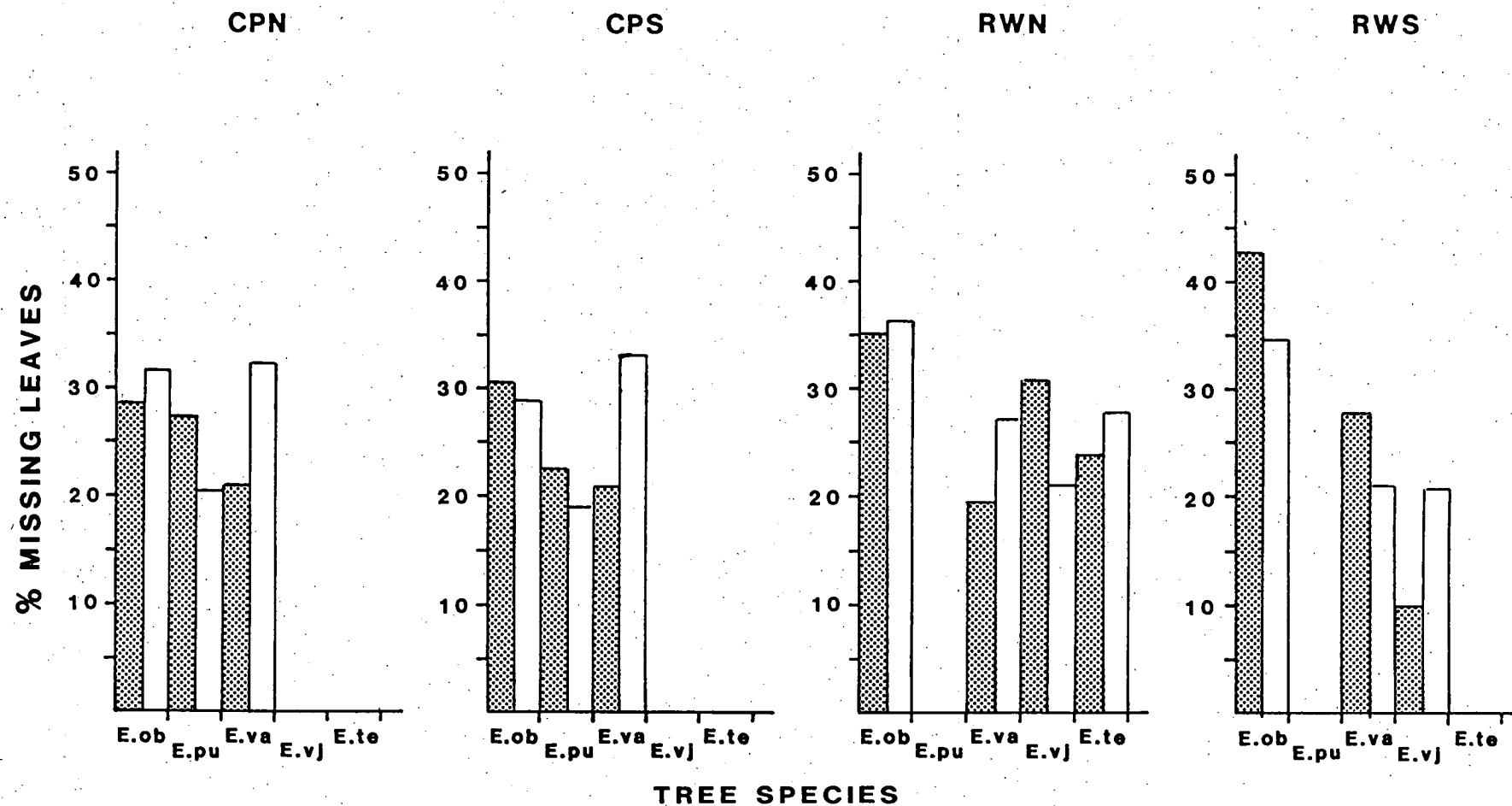FIGURE 3.9: Histograms showing the percentage of damaged leaves per shoot in treated and untreated trees per species, per site

▨ = untreated trees;   ☐ = treated trees

E.ob = E.obliqua, E.pu = E .pulchella,
E.va = E.viminalis (adult foliage), E.vj
▬ E.viminalis (juvenile foliage), E.te =
E.tenuiramis

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In the species-site analysis there were two additional significant relationships: in *E. viminalis* (adult foliage) the amount of damaged leaves was higher than that in *E. obliqua* on RWN (0.01<P⩾0.05), while on RWS the reverse of this relationship was found, with *E. obliqua* sustaining a higher amount of damaged leaves compared to *E. viminalis* (adult foliage); 0.01<P⩾0.05). This reversal of position of the two species accounts for the lack of a significant difference in the General Analysis.

Overall, between-site differences seem to have a greater influence on the number of damaged leaves than between-species differences (see part (b) below).

(b) Between-Site Analysis

There is a trend for the percentage of damaged leaves to be higher on the Ridgeway sites compared with the Chimney Pot Hill sites with RWS and RWN having a higher percentage of damaged leaves than CPN (0.01<P⩾0.05), and the level of damaged leaves on RWN just failing to be significantly different from that on CPS (0.05<P⩾0.1). Moreover, the level of leaf damage sustained by *E. obliqua* on RWS is so high that it is significantly different from that sustained by the species on all other three sites. The higher number of damaged leaves on the Ridgeway sites compared with the Chimney Pot Hill sites is to be expected, since the percentage actual damage exhibits the same trend.

(c) The Percentage of Damaged Leaves in Untreated and Treated Trees

The mean percentage of leaves that were damaged in the untreated trees of *E. obliqua* and *E. pulchella* was, as expected, significantly higher than that in their treated counterparts (0.01<P⩾0.05), while the number of damaged leaves on the untreated trees of *E. viminalis* (adult foliage) and *E. tenuiramis* just failed to be significantly higher than the number of leaves damaged in the treated trees of these species (0.05<P⩾0.10). Only in *E. viminalis* (juvenile foliage) was there no such significant relationship. This is not surprising, since there was no difference in the level of actual damage sustained between the

untreated and treated trees in this species (see section on 3.3.1.4). damage).

In the comparison of the level of damaged leaves between all treated and untreated trees on each site, two of the four comparisons were significant; the untreated trees on CPN and RWN had more damaged leaves than the treated trees on the same site ($0.01 < P \geqslant 0.05$).

3.3.2.3 Mean Shoot Length

Figure 3.10 shows the mean shoot length of treated and untreated trees for every species per site. The mean shoot lengths of *E. obliqua*, *E. pulchella*, *E. viminalis* (adult and juvenile foliage) and *E. tenuiramis* are 9.3 cm, 3.2 cm, 6.7 cm, 7.0 cm and 4.3 cm respectively (Table 3.14).

(a) Between-Species Comparison

Six of the eight comparisons made in the general analysis between the mean shoot length of species were found to be significantly different from one another with the mean shoot length of *E. viminalis* (adult foliage) being significantly higher than that of *E. pulchella* ($P > 0.001$) and *E. tenuiramis* ($0.01 < P > 0.05$), and the mean shoot length of *E. obliqua* being significantly higher than that of *E. viminalis* (adult foliage), *E. pulchella* ($0.001 < P \geqslant 0.01$), *E. viminalis* (juvenile foliage) and *E. tenuiramis* ($0.01 < P > 0.05$). The shoots of *E. viminalis* (juvenile foliage) just failed to be significantly longer than those of *E. tenuiramis* ($0.05 < P \geqslant 0.10$), while there was no difference between the mean shoot lengths of the juvenile and adult foliage of *E. viminalis*.

(b) Between-Site Comparisons

There were no significant between-site differences in the mean shoot length. The change in the environment between the sites therefore had no influence upon the growth of the stems.
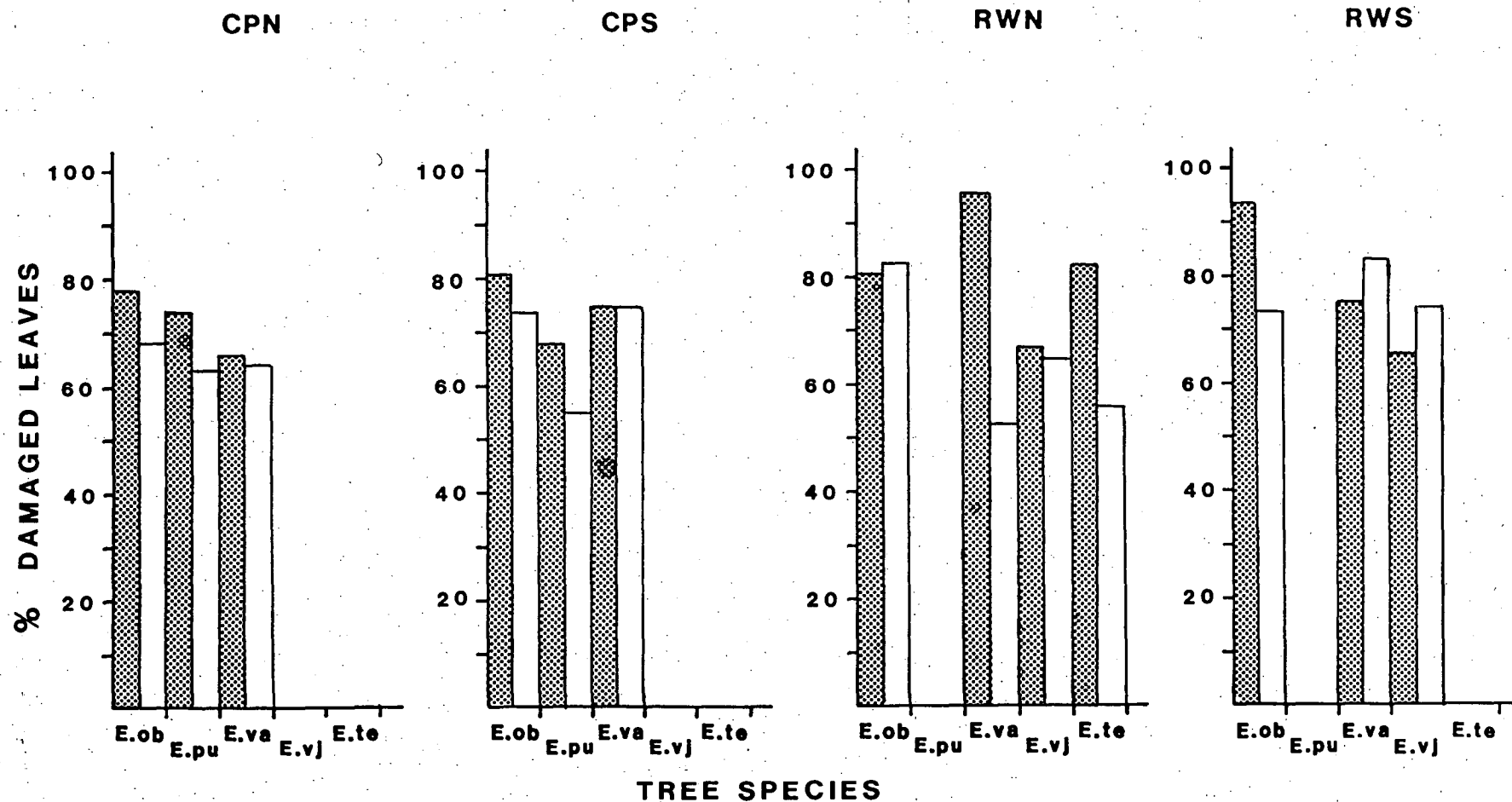
CPN   CPS   RWN   RWS

SHOOT LENGTH (CM)

TREE SPECIES

FIGURE 3.10: Histograms showing the mean length of the shoot in treated and untreated trees per species, per site

▨ = untreated trees;   ☐ = treated trees

E.ob = E.obliqua, E.pu = E .pulchella,
E.va = E.viminalis (adult foliage), E.vj
= E.viminalis (juvenile foliage), E.te =
E.tenuiramis

(c)   Comparison in the Mean Shoot Length Between Untreated and
      Treated Trees

The shoots on the treated trees of *E. pulchella* were significantly
longer than those on the untreated trees (0.01 <P≥0.001) while the
shoots on the treated trees of *E. viminalis* (adult foliage) were signific-
antly shorter than those on the untreated trees (0.05<P≥0.01). There
were no differences, however, in the mean shoot length of the untreated
and treated trees of the species *E. obliqua, E. viminalis* (juvenile
foliage) and *E. tenuiramis.*

There were no significant relationships to be found in the general
analysis between the mean shoot length of all treated and all untreated
trees in each site.

In *E. viminalis* (adult foliage), either insects stimulate the
growth of the shoot, or the insecticide has a detrimental effect on the
physiological processes in this species. Previous evidence suggests the
latter is the most probable explanation (Section 3.3.2.1), although it
has been demonstrated that insects do stimulate plant growth (Lowman
1982b), at least sometimes.

Several hypotheses can be drawn from the results. The first is that
the insecticide failed to protect *E. obliqua, E. viminalis* (juvenile foliage)
and *E. tenuiramis* from insects damaging the shoot tip. This seems unlikely
in view of the fact that the insecticide successfully protected the leaves
from heavy damage (except *E. viminalis*, juvenile foliage), and it is
highly improbable that the insecticide would protect the shoot tip of
some species and not others from insect attack.

The second hypothesis is that the insecticide interfered with shoot
elongation, but not to the extent found in *E. viminalis* (adult foliage).
The third hypothesis is that insects adversely effect the growth of shoot
length in *E. pulchella* and not other species. And finally, insects may
adversely effect the shoot length of all eucalypt species, but it is only
in *E. pulchella* that the shoot is unable to recover by regrowth. As mean
shoot length was measured when all the species bar *E. pulchella* (which
produces new growth all year round) were experiencing a period of rapid

	Eucalyptus obliqua		Eucalyptus pulchella		Eucalyptus viminalis (adult foliage)		Eucalyptus viminalis (juvenile foliage)		Eucalyptus tenuiramis		TOTAL		MEAN	
	untreated (cm)	treated (cm)	untreated (cm)	treated (cm)	untreated (cm)	treated (cm)	treated (cm)	treated (cm)	untreated (cm)	treated (cm)	untreated cm	treated cm	untreated cm	treated cm
CPN	7.4	7.2	3.3	4.1	7.1	6.4					17.8	17.7	5.9	5.9
CPS	9.0	7.8	3.0	3.9	5.8	5.3					17.8	17.0	5.9	5.7
RWN	8.5	7.8			7.5	5.3	6.2	5.1	4.3	6.3	26.5	24.5	6.6	6.1
RWS	12.1	7.1			6.5	4.6	7.7	7.8			26.3	19.5	8.8	6.5

TABLE 3.14: The mean shoot length on treated and untreated trees per species per site.

	Eucalyptus obliqua		Eucalyptus pulchella		Eucalyptus viminalis (adult foliage)		Eucalyptus viminalis (juvenile foliage)		Eucalyptus tenuiramis		TOTAL		MEAN	
	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated	untreated	treated
CPN	5.4	5.1	6.0	9.6	7.1	5.9					18.5	20.6	6.2	6.9
CPS	5.5	5.4	6.5	8.3	5.2	5.0					17.2	18.7	5.7	6.2
RWN	4.9	4.3			5.8	5.0	6.2	6.0	4.9	8.0	21.8	23.3	5.5	5.8
RWS	4.2	4.1			5.1	4.2	7.3	9.3			16.6	17.6	5.5	5.9

TABLE 3.15: The mean number of leaves per shoot on treated and untreated trees per species per site.

regrowth, the final hypothesis may be the most probable.

3.3.2.4 *Mean Number of Leaves Per Shoot*

The mean number of leaves per shoot for each species is represented diagrammatically in Figure 3.11. The mean number of leaves per shoot in *E. obliqua* is 5.0, in *E. pulchella* 6.3, in *E. viminalis* (adult foliage) 5.8, in *E. viminalis* (juvenile foliage) 6.8 and in *E. tenuiramis* 4.9 (Table 3.15).

(a) Between-Species Comparison

The mean number of leaves on the shoots of *E. viminalis* (juvenile foliage) was significantly higher than the mean number of leaves on the shoots of *E. obliqua* ($0.05 < P > 0.01$). This was the only significant relationship in the eight comparisons made between the numbers of leaves per shoot.

(b) Between-Site Comparison

The mean number of leaves per shoot in the species on CPN was significantly higher than the mean number of leaves per shoot on RWS ($0.01 < P > 0.001$). The number of leaves on the shoots of species on CPS just failed to be significantly higher than those on RWS ($0.10 < P \geqslant 0.05$). None of the remaining relationships were statistically significant.

(c) Comparison Between the Mean Number of Leaves Per Shoot in the Untreated and Treated Trees

In the comparison of the mean number of leaves per shoot between the untreated and treated trees of each species only those of *E. pulchella* were significantly different with the treated trees having more leaves per shoot than the untreated trees ($0.05 < P \geqslant 0.01$).
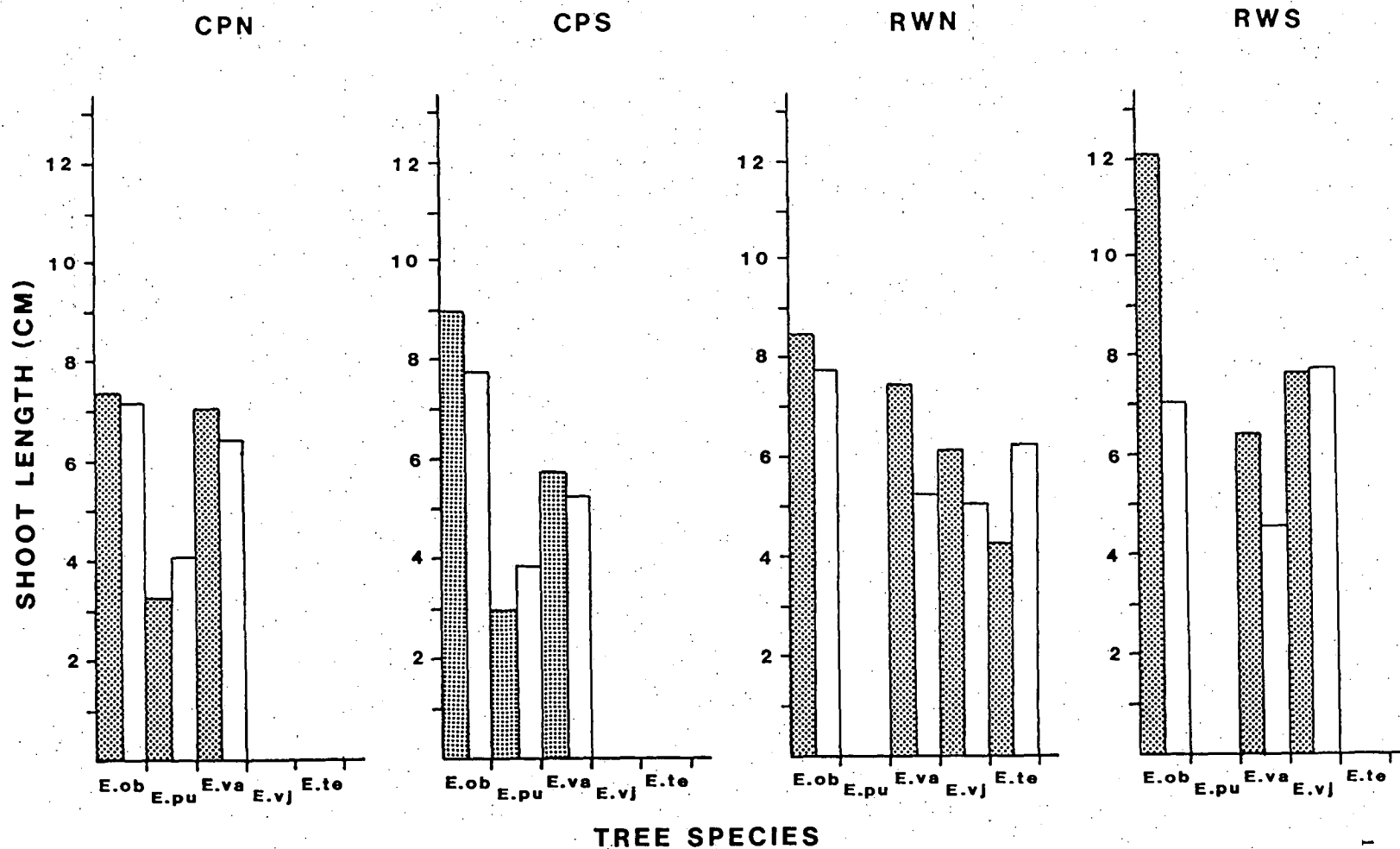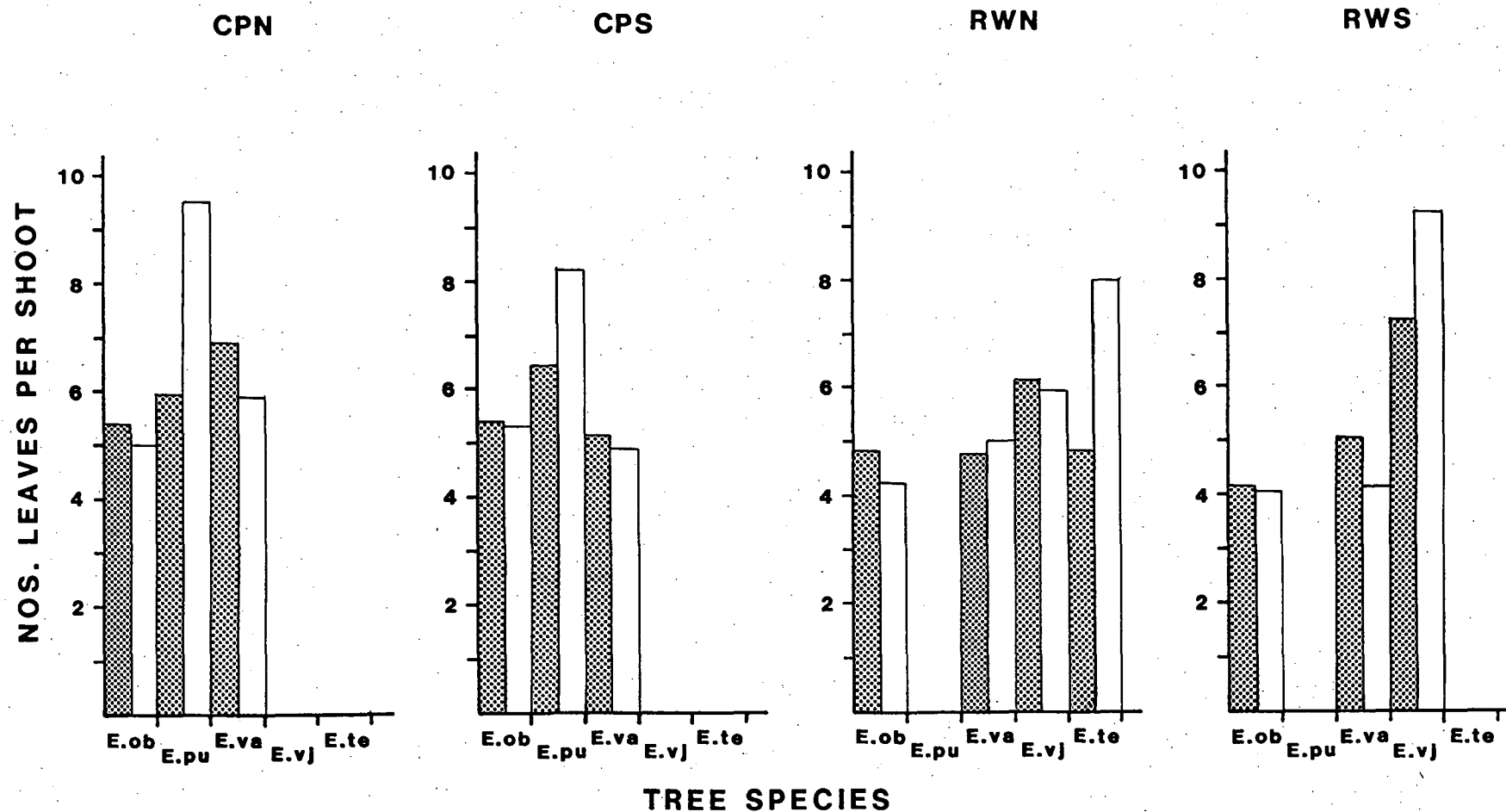
FIGURE 3.11: Histograms showing the number of leaves in treated and untreated trees per species, per site

▨ = untreated trees;   ☐ = treated trees

E.ob = E.obliqua, E.pu = E .pulchella,
E.va = E.viminalis (adult foliage), E.vj
= E.viminalis (juvenile foliage), E.te =
E.tenuiramis

There was no significant difference between the number of leaves per shoot in treated and untreated trees on any one site.

As in the previous section, these results would also seem to indicate that (1) the insecticide has a differential effect between the species, a hypothesis which has been discounted; or (2), insects inhibit leaf growth in *E. pulchella* only; or (3), insects inhibit leaf growth in all species, but *E. pulchella* is unable to recover as well as the other species (see section 3.3.2.3).

3.3.3 Leaf Damage Studies

3.3.3.1 Leaf Chewers

Figure 3.12 shows the percentage of the total damage caused by leaf chewers in each species per site. The mean percentage of leaf chewing damage is 10.0% (72.7% of the total damage) in *E. obliqua*, 7.1% (73.3% of the total damage) in *E. pulchella*, 9.7% (79.4% of the total damage) and 13.6% (80.8% of the total damage) in the adult and juvenile foliage of *E. viminalis* respectively and 10.3% (84.8% of the total damage) in *E. tenuiramis* (Tables 3.16 and 3.17).

In the general analysis, there was no significant between-species difference in the level of damage caused by leaf chewing insects. The percentage damage inflicted by leaf chewers on *E. viminalis* (adult foliage) just failed to be significantly different from that found on *E. tenuiramis* ($0.10 < P > 0.05$). In the species-site analysis, however, two relationships were significantly different from one another: the proportion of leaf chewing damage found on *E. obliqua* on RWN was significantly lower than that found on *E. tenuiramis* ($0.01 < P \geqslant 0.001$) and *E. viminalis* (juvenile foliage; $0.01 < P \geqslant 0.001$).

In neither the general nor the species-site analysis were there any significant between-site differences in the level of leaf chewing damage.

The proportion of each of the four types of damage in every species were compared with one another in the site-species analyses. In all

FIGURE 3.12: Histograms showing the mean percentage damage (normalised)
caused by each of the four types of insect predation
per species, per site.

1 = Leaf chewers; 2 = Leaf miners and skeletonizers
3 = Leaf distortion; 4 = Miscellaneous damage

species on every site the percentage damage caused by the action of leaf chewers was significantly greater than that caused by any of the other three damage types.

The results show that leaf chewers are responsible for the majority of insect damage, and that the differences between the species and the sites do not affect the amount of this damage type.

3.3.3.2 Leaf Miners and Skeletonizers

The proportion of damage caused by leaf miners and skeletonizers is shown diagrammatically in Figure 3.12. The mean percentage damage caused by these insects in *E. obliqua*, *E. pulchella*, *E. viminalis* (adult and juvenile foliage) and *E. tenuiramis* is 2.0%, 1.7%, 1.0%, 0.7% and 0.8% respectively (Table 3.16; or 15.7%, 19.3%, 6.8%, 4.5%, and 6.4% of the total damage respectively, Table 3.17).

Of the eight between-species comparisons of this type of damage, four were significant. The level of damage caused by leaf miners and skeletonizers in *E. obliqua* was significantly higher than that in *E. viminalis* (adult and juvenile foliage; $P < 0.001$) and *E. tenuiramis* ($0.01 < P > 0.001$). Also, the percentage of this damage type was significantly higher in *E. pulchella* than *E. viminalis* (adult foliage; $0.01 < P \geqslant 0.001$).

When comparing the damage caused by leaf miners and skeletonizers between the different sites, the level of damage on RWN was significantly higher than that in both the Chimney Pot Hill sites ($0.05 < P \geqslant 0.01$).

From the comparison of all four types of damage sustained by the species on each site, the level of damage caused by leaf miners and skeletonizers was significantly higher than that caused by leaf distort-ing insects on: (1) *E. obliqua* on CPN, CPS and RWN; (2) *E. pulchella* on CPN; and (3) *E. viminalis* (adult foliage) on CPS. The level of damage caused by leaf miners and skeletonizers was significantly greater than that caused by miscellaneous damage on (1) *E. obliqua* on RWN; (2) *E. pulchella* on CPN and CPS; and (3) *E. viminalis* (juvenile foliage) on RWS.

	Eucalyptus obliqua				Eucalyptus pulchella				Eucalyptus viminalis (adult foliage)				Eucalyptus viminalis (Juvenile foliage)				Eucalyptus tenuiramis			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
CPN	9.9	1.6	0.1	0.7	7.9	2.1	0.1	0.1	8.0	0.6	0.5	0.9								
CPS	8.2	1.2	0.1	1.7	6.2	1.2	0.3	0.1	7.3	0.8	0.0	0.9								
RWN	9.2	3.0	0.4	1.1					15.0	1.9	0.4	1.9	19.6	0.8	0.2	1.0	10.3	0.8	0.2	0.8
RWS	12.8	2.2	0.8	1.4					8.6	0.6	0.5	1.8	7.5	0.5	1.0	1.2				

TABLE 3.16:   The mean percentage damage caused by each of the four types of insect predation. 1 = Leaf Chewers; 2 = Leaf Miners and Skeletonizers; 3 = Leaf Distortion; 4 = Miscellaneous damage.

Leaf miners and skeletonizers seem to be far more discriminating, compared with leaf chewers, in their choice of host species and environment. *E. obliqua* and *E. pulchella* are the preferred species and RWN the preferred site.

3.3.3.3 *Leaf Distorting Insects*

Figure 3.12 shows the proportion of damage caused by leaf distorting insects. The mean percentage damage is 2.2% (0.4% of the total damage) in *E. obliqua*, 0.2% (2.7% of the total damage) in *E. pulchella*, 0.4% and 0.7% (3.2% and 6.0% of the total damage) in the adult and juvenile foliage of *E. viminalis* respectively and 0.8% (1.9% of the total damage) in *E. tenuiramis* (Tables 3.16 and 3.17).

There were no significant differences in the level of this damage type between the different species. However, there were between site differences, with a significantly higher level of damage found on the Ridgeway sites compared with the Chimney Pot Hill sites. More precisely, the amount of damage from leaf distorting insects was significantly higher on RWS compared with CPS ($0.01 < P > 0.001$) and RWN ($0.05 < P \geqslant 0.01$), and just failed to be significantly higher than that found on CPN ($0.10 < P > 0.05$). In addition, the level of damage from leaf distorting insects on RWN was significantly higher than that on CPS ($0.05 < P \geqslant 0.01$).

The level of damage caused by leaf distorting insects is low compared with the other damage types. While there are no between-species differences there are, however, distinct between-site differences.

3.3.3.4 *Miscellaneous Damage*

Miscellaneous damage includes damage that may not be of insect origin. The proportion of insect initiated damage is unknown. Therefore, care has to be taken when comparing the distribution patterns of this damage type with the others.

	Eucalyptus obliqua				Eucalyptus pulchella				Eucalyptus viminalis (adult foliage)				Eucalyptus viminalis (Juvenile foliage)				Eucalyptus tenuiramis			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
CPN	78.3	14.6	0.8	6.3	76.8	21.6	0.7	1.0	80.5	5.5	6.0	8.1								
CPS	73.0	11.4	1.1	14.5	77.8	16.9	4.7	0.7	81.2	8.5	0.5	9.8								
RWN	65.8	23.2	2.4	8.7					82.5	8.5	1.2	7.9	88.9	4.1	1.3	5.7	84.8	6.4	1.9	6.9
RWS	73.7	13.6	4.3	8.4					73.2	4.7	4.9	17.2	72.6	4.9	10.7	11.8				

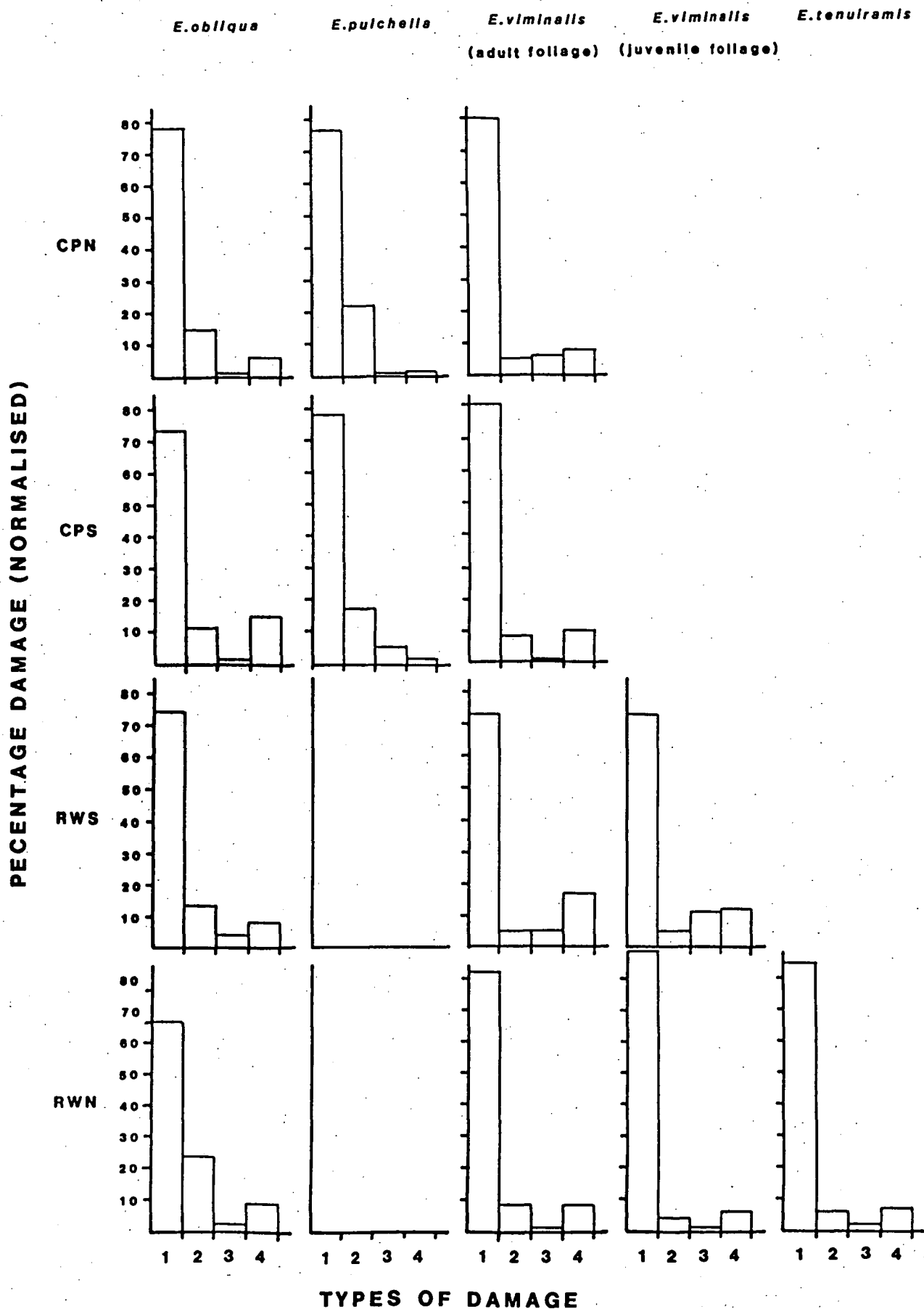TABLE 3.17: The mean percentage damage (normalised) caused by each of the four types of insect predation per species, per site.
1 = Leaf chewers; 2 = Leaf miners and skeletonizers
3 = Leaf distortion; 4 = Miscellaneous damage

Figure 3.12 shows the proportion of miscellaneous damage found on every species per site. The mean percentage of miscellaneous damage is 1.4%, 0.1%, 1.4%, 1.1% and 0.8% (or 9.5%, 0.9%, 10.8%, 8.8% and 6.9% of the total damage) in *E. obliqua*, *E. pulchella*, *E. viminalis* (adult foliage), *E. viminalis* (juvenile foliage) and *E. tenuiramis* respectively (Tables 3.16 and 3.17).

In the general analysis, the amount of miscellaneous damage in *E. viminalis* (adult foliage) was significantly higher than that in (1) *E. pulchella* ($0.01 < P \geqslant 0.001$); (2) *E. viminalis* (juvenile foliage); and (3) *E. tenuiramis* ($0.05 < P \geqslant 0.01$). The level of miscellaneous damage in *E. obliqua* was also significantly higher than that in *E. pulchella* ($P < 0.001$) and just failed to be significantly higher than that sustained by *E. tenuiramis* ($0.10 < P \geqslant 0.05$).

The miscellaneous damage found on RWS was significantly higher than that on CPN ($0.05 < P \geqslant 0.01$). However, the amount of this damage on RWN just failed to be significantly different from that on CPN ($0.10 < P \geqslant 0.05$).

In the comparison of the proportion of each damage type within a species and site, the amount of miscellaneous damage was significantly higher than leaf distortion damage on (1) *E. obliqua* on CPS and RWN; and (2) *E. viminalis* (adult foliage) on CPS.

Like leaf miners and skeletonizers, the miscellaneous damage varies between species and between sites.

3.3.3.5 *The Insect Community and Overall Damage*

Leaf chewers cause the most damage of all taxa followed by leaf miners and skeletonizers. The damage from sapsuckers, psyllids and gall formers is low. It is difficult to translate these figures into a measure of insect abundance. However, it would appear from the very great differences in the proportions of the four damage types, that the insect community is akin to that found in mature forests rather than that found in young trees (Ohmart 1983b). It may be not so much the age

of trees that determines the insect population, but the level of disturbance, since the young trees sampled in other studies (see Ohmart 1983b) come from more highly disturbed environments than those sampled in this research.

3.3.4 Insect Species Occurring in the Canopies of Small Trees

Very few insects were collected, partly because of the method of sampling and partly because of the scarcity of insects during 1982-1983 (see 3.4). Those that were collected are listed in Appendix One.

3.4 DISCUSSION

The results obtained in the present study may be briefly summarized as follows. There were no between-species differences in the actual damage found on six-month-old shoots. However, one-year-old leaves of *E. obliqua* on RWN sustained significantly higher levels of damage than *E. viminalis* (adult foliage) and *E. tenuiramis*. There were no between-species differences in the amount of damage caused by leaf chewing or leaf distorting insects in the general analysis. Nevertheless, between-species differences were found in the following indices of damage (table 3.18): the amount of total damage, leaf loss, damaged leaves, mean shoot length, mean number of leaves per shoot, miscellaneous damage and damage caused by leaf skeletonizers and miners.

There were no between-site differences in the level of total damage, leaf loss, leaf chewing damage, or in the mean shoot length of species in the general analysis. However, the species on the Ridgeway sites sustained significantly higher amounts of actual damage, damaged leaves, miscellaneous damage, leaf distortion, and damage caused by leaf skeletonizers and miners, compared to the Chimney Pot Hill sites. Conversely, the number of leaves per shoot was higher on the Chimney Pot Hill sites than on the Ridgeway sites.

	% total damage	% missing leaves	% leaves damaged	mean shoot length	the amount of miscellaneous damage	mean number of leaves per shoot	damage by leaf miners & skeletonizers	damage by leaf chewers	% actual damage	damage by leaf distorting insects	totals from the general analysis	totals from the species – site analysis
E. obliqua >*E. viminalis (af)*	X	X	RWS	X			X				4	(5)
>*E. viminalis (jf)*	RWS	RWS	X	X			X				3	(5)
>*E. pulchella*	X			X	X						3	(3)
>*E. tenuiramis*		X		X			X				3	(3)
E. viminalis >*E. obliqua*			RWN								0	(1)
(adult >*E. viminalis (jf)*						X					1	(1)
foliage) >*E. pulchella*				X		X					2	(2)
>*E. tenuiramis*			X	X		X					3	(3)
E. viminalis >*E. obliqua*						X		RWN			1	(2)
(juvenile >*E. viminalis (af)*											0	(0)
foliage) >*E. pulchella*											0	(0)
>*E. tenuiramis*											0	(0)
E. pulchella >*E. obliqua*											0	(0)
>*E. viminalis (af)*							X				1	(1)
>*E. viminalis (jf)*											0	(0)
>*E. tenuiramis*											0	(0)
E. tenuiramis >*E. obliqua*								RWN			0	(1)
>*E. viminalis (af)*											0	(0)
>*E. viminalis (jf)*											0	(0)
>*E. pulchella*											0	(0)

E. obliqua	14	(20)
E. viminalis(af)	11	(13)
E. viminalis(jf)	5	(8)
E. pulchella	6	(6)
E. tenuiramis	6	(7)

Results from the general analysis are represented by a cross and those from the species-site analysis by the site in which the relationship is significant (p < 0.05)

af = adult foliage; *jf* = juvenile foliage

TABLE 3.18: Significant between-species differences.

Comparisons between the damage levels for each of the ten variables for the treated trees compared to those which were untreated revealed that: (1) the amount of actual damage in untreated trees was significantly higher than that in treated trees on all sites and in all but one species (*E. viminalis*; juvenile foliage); (2) the number of damaged leaves (the only other variable to show between-site differences) in untreated trees on CPN and RWN was significantly higher than the numbers of damaged leaves in treated trees; (3) there was no significant difference in the percentage total damage, or percentage leaf loss (except in *E. viminalis*; adult foliage) between treated and untreated trees; (4) a significantly higher percentage of missing leaves was found on the treated trees of *E. viminalis* (adult foliage) than on the equivalent untreated trees; (5) the shoots on the treated trees of *E. viminalis* (adult foliage) were significantly shorter than those on the untreated trees; and (6) the treated trees of *E. pulchella* had significantly longer shoots and a higher number of leaves per shoot than present on the untreated trees.

The levels of damage were lower than, or at the lower end of the range of, estimates obtained in other studies (table 3.19). Moreover, the amount of insect damage recorded in the present study may have been overestimated since it included a measurement of miscellaneous damage that may have been caused by other organisms as well as insects. The amount of miscellaneous damage may have in itself been over-estimated since any holes created in very young leaves enlarge as the leaf expands (Reichle *et al.* 1973). However, as miscellaneous damage constitutes only a small proportion of the damage overall the difference contributed by this variance to actual damage totals is probably negligible.

The differences in the estimates for leaf area loss between this research and the study of Fox and Morrow (1983; table 3.19) are in reality even greater, since in the latter work only damage caused by leaf chewing insects is recorded. This fundamental difference in what is recorded as a measurement of insect damage highlights one difficulty involved when comparing results from many studies. Equally, it is difficult to make straightforward comparisons between studies differing with respect to altitude, climate, geology, the age of trees or foliage

Author and time of data collection	Location of site	Description of site	Altitude	Aspect	Level of Disturbance	Species	Age and Height of trees	Age and Type of foliage	% damage	% leaf loss	% damaged leaves
F.M. Marks	S.E. Tasmania	Dry sclerophyll forest on Dolerite	400	North-facing slope	Low	E. obliqua	Young; 2-3m	Young shoots; 6 months old	8.3	27.9	78.2
	"	"	400	"	"	E. pulchella	"	"	7.7	27.4	74.2
	"	"	400	"	"	E. viminalis (adult foliage)	"	"	7.6	20.8	66.4
	"	"	400	South-facing slope	"	E. obliqua	"	"	7.2	30.8	81.4
	"	"	400	"	"	E. pulchella	"	"	5.7	22.6	67.7
	"	"	400	"	"	E. viminalis (adult foliage)	"	"	6.3	21.2	74.6
	"	Dry sclerophyll forest on sandstone	250	North-facing slope	"	E. obliqua	"	"	9.1	35.3	81.3
	"	"	"	"	"	E. viminalis (adult foliage)	"	"	12.6	19.6	96.1
	"	"	"	"	"	E. viminalis (juvenile foliage)	"	"	16.0	30.9	66.9
	"	"	"	"	"	E. tenuiramis	"	"	10.4	24.2	82.5
	"	"	"	South-facing slope	"	E. obliqua	"	"	12.7	43.0	93.5
	"	"	"	"	"	E. viminalis (adult foliage)	"	"	8.0	28.0	75.5
	"	"	"	"	"	E. viminalis (juvenile foliage)	"		7.5	10.1	65.9
	"	"	"	North-facing slope	"	E. obliqua	"	One year old leaves	21.2	-	-
	"	"	"	"	"	E. viminalis (adult foliage)	"	"	16.6	-	-
	"	"	"	"	"	E. tenuiramis	"	"	8.7	-	-
Fox and Morrow (1983) 1975-80	S.E. Australia	Woodlands	>1800	-	Relatively undisturbed	E. obliqua	Different age and height	Damage recorded on current seasons leaves at end of growing season	15.0	-	72.0
	"	Uplands	-	-	"	E. viminalis	"		12.0	9.0	43.0
	"	Woodlands	<300	-	"	E. obliqua	"		7.0	-	73.0
Burdon & Chilvers (1974a)	S.E. Australia	Forest	730	-	Relatively disturbed	E. viminalis	Saplings	Damage recorded on current seasons leaves	13.0	-	-
Kile (1974)	Southern Tasmania	Pure forest stands	-	-	Regrowth forest	E. obliqua	60 years old; 32-34m	Damage recorded on current seasons leaves in mid January	40.0	-	-
		"	-	-	-	"	"	"	22.0	-	-

TABLE 3.19: A comparison of the differences in percentage damage, leaf loss and the percentage of damage leaves in species as the type and age of foliage samples, the age of trees, the level of disturbance and the environment varies between studies.

sampled or the method of assessing leaf chewing damage (table 3.19).
There is also the problem of equating the level of disturbance
between sites. For instance, the vegetation in Ridgeway Park Reserve
has been disturbed, but by the standards of the Australian mainland
it is virtually pristine.

The present study revealed that there may be significant
differences between the amount of actual damage found on old foliage of
E. obliqua compared to that found on the old foliage of other species.
This implies that if a sample of different aged foliage from each
species was compared with every other species, E. obliqua would
sustain slightly higher levels of damage than those present in other
species, although this result would depend on the proportion of young
to old foliage. For instance, in very young trees the proportion of
young to old foliage would be higher than in mature trees. Thus, at
the crucial stage of forest development, E. obliqua may show very little,
if any, difference in the level of damage sustained, when compared with
other species. Furthermore, shoot growth and leaf fall occur at approx-
imately the same time (Jacobs 1955; see Section 3.3.13), as may leaf
loss due to environmental stress. Thus, the tree will, at times, con-
tain a very large percentage of young compared with old leaves.

3.4.1. Patterns of Damage Between the Species

Table 3.18 shows the number of times the level of damage is
significantly higher in one species compared to another. E. obliqua
is involved in the greatest number of significant relationships with
other species, 14 in all (20 in the species-site analysis).

These findings would seem to indicate that E. obliqua is distin-
guished from the other eucalypt species both by its anatomy and its
sensitive response to damage. It is also interesting that there is
some differentiation between the response of the adult and juvenile
foliage of E. viminalis to damage. More especially, the adult foliage
is particularly vulnerable to miscellaneous damage. It was very notice-
able in the field that the juvenile foliage was affected by a leaf spot

that was probably fungal or viral in origin. The extent of the leaf spot was not recorded. However, the indications are that the adult and juvenile leaf form differ in their attractiveness and response to damage forming organisms.

Three of the indices measuring insect damage did not display any between-species variation; (1) damage by leaf distorting insects, (2) leaf chewing damage (see below) and (3) actual damage.

The very low actual damage recorded, and the absence of any between-species differences could be; (1) the norm in eucalypt forests (Ohmart 1983a); see introduction) and/or (2) due to the drought experienced in south-eastern Tasmania from the late 1970's until 1983. Ohmart determined annual leaf consumption from measurements of frass fall. He found that insect activities accounted for the loss of 2 - 3% of annual leaf production. It is not known how accurate these findings are in view of the fact that firstly they are based on estimates of Approximate Digestibility (AD) which are derived from published values of AD for insects feeding on tree foliage since there is no such data available for the majority of the insects found in eucalypt forests. Secondly, the use of frass fall as a surrogate measure for percentage damage to the foliage increases the physical distance between insect and eucalypt and therefore lessens the reliability of this method as a mirror of the impact of insects on eucalypts.

Generally, apart from sampling young trees, the downfalls of measuring percentage damage to foliage as described by Ohmart (see introduction) have been avoided in this research. As expected the values of actual damage found were higher (7 - 12%) than those found by Ohmart for mature trees, but lower than those found in similar aged trees in other studies. However, in view of the limitations in the use of frass fall to determine leaf consumption by insects it would be necessary to undertake further research using and modifying this method before Ohmarts findings could be verified as the norm in eucalypt forests. It is highly conceivable for instance, that the results from Ohmarts work and the findings of this study merely reflect the effect of a period of less than average rainfall on insect populations.

It has been reported that a drop in insect activity and damage occurs during a drought (Kile 1974; Specht and Brower 1975; Fox and Morrow 1983). If insect damage levels are abnormally low, then it is probable that the differences between the damage sustained by species would not be large enough to be statistically significant.

Drought may also partially account for the very high levels of missing leaves, and therefore total damage, especially in *E. obliqua* (see below). Leaves are prematurely abscissed during a drought in order to conserve water (Ohmart *et al*. 1983a). On many trees (especially *E. obliqua* on CPN) whole branches of leaves died during the summer. These factors, and the absence of any differences between leaf loss and total damage on treated and (except in the case of *E. viminalis;* adult foliage) untreated trees, would seem to indicate that insect predation had little effect on the overall level of hidden damage during the period of study. This is especially so since the number of missing shoots may in some cases have been underestimated in treated trees.

The implication is that in a non-drought year the pattern of damage in dry sclerophyll forests may be very different from that found in a drought year. Also, the amount of hidden damage caused by other (often inter-related) variables, such as high winds, plant pathogens etc. (Section 3.2.5.1.2) will vary in time and space, so that total damage may vary between different drought years, and between different non-drought years.

Although many trees showed signs of drought damage especially on CPN, the most xeric site, no between-site differences were found in the level of total damage or leaf loss. This is probably because: (1) there was quite extensive damage on all sites as a result of the activities of larger herbivores and very high winds, and (2) any shoots that were obviously damaged by the effects of drought or high winds etc. (that is where branches or whole sections of the tree had died) were obliterated from the analysis.

Mean shoot length was the only other variable to show just between-species differences. That no between-site variation was found was surprising since changes in the growth along environmental gradients has been demonstrated for tree height, leaf shape, bark thickness and the amount of glaucousness (Barber 1955; Barber and Jackson 1957; Barber 1965). However, the environments under consideration in the aforementioned studies showed a greater range of variation than those displayed between the north and south-facing slopes on Ridgeway compared to Chimney Pot Hill.

3.4.2. The Environmental Gradients Controlling the Patterns of Insect Damage

The environmental gradients that may effect changes in the type and amount of insect damage between the sites include soil moisture availability, soil fertility, humidity, wind speed, temperature and exposure. These physical factors may have an indirect effect on insects through their control of the distribution, structure and composition of forest communities (chapter two) and their influence on the nutritional and chemical composition of the foliage. Direct control of insect populations most probably results from the effects of microclimate. Figure 3.13 illustrates how the integrated effects of the environment may influence plant and insect communities.

Table 3.20 shows the probable ordering of sites with respect to the relative advantage of each environmental gradient to plants (see Chapter two) and insects. It was thought highly probable that, due to the drought, soil moisture availability would be the most limiting factor and therefore have the greatest influence on the level of insect damage. Drought has been associated with an overall decline in insect activity (see earlier in discussion). It may also influence insects in an indirect manner by effecting changes in the chemical and nutritional composition of the foliage (section 3.1). Very little work has been done on the interplay between moisture and the concentration of nutrients and allelochemics in eucalypts (Landsberg and Wylie 1983), however, it has been reported that on sites which experience high water stress
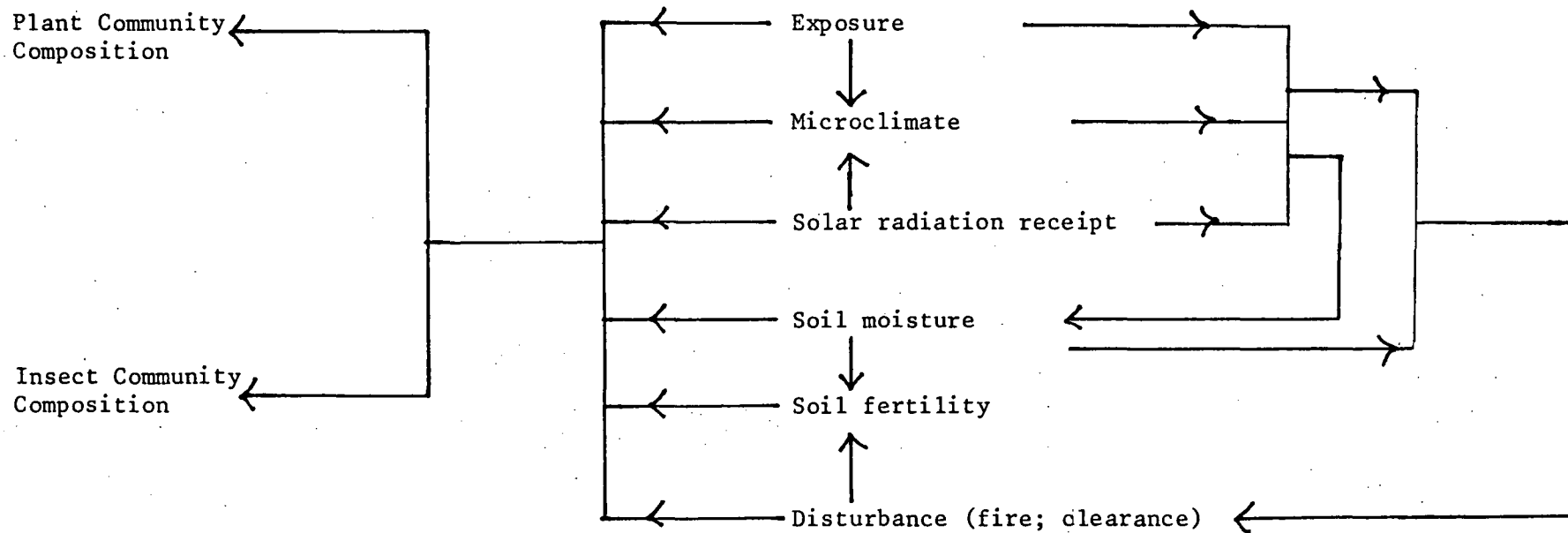
Figure 3.13: The relationships between environmental variables, plants and insects.

site increasingly advantageous

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to flora and insect fauna

Soil Moisture Availability	CPN	RWN	CPS	RWS
Temperature	CPS	CPN	RWS	RWN
Humidity	CPH		RW	
Wind Speed	CPH		RW	
Exposure	CPH		RW	
Effect of Soil Fertility on Plant Communities	RW		CPH	
Effect of Soil Fertility on Insect Communities	CPH		RW	

CPN   North-facing slope at Chimney Pot Hill
CPS   South- "   " "   "   "   "
CPH   Both north and south-facing slopes at Chimney Pot Hill
RWN   North-facing slope at Ridgeway
RWS   South- "   "   "   "
RW   Both north and south-facing slopes at Ridgeway.

Table 3.20: The ordering of sites along environmental gradients

increased insect activity may result (Mattson and Addy 1975;
Landsberg and Wylie 1983). If soil moisture availability does affect
insect activity in this manner it is to be 'expected' that trees on
the most drought prone site (CPN; see chapter two) would experience
more damage than those on RWS, the most mesic site. This was
generally not the case (since so little is known of how insects and
eucalypts respond to changes in the amount of available water it
should be emphasized that although actual damage did not appear to be
influenced by the drought in the 'expected' manner, this does not
altogether preclude the possibility that drought may influence insect
activity). Three variables differed significantly between these two
sites (table 3.21); only one (the number of leaves per shoot) was
significantly higher on CPN, while the other two (the amount of mis-
cellaneous damage and the percentage of damaged leaves) were signifi-
cantly higher on RWS.

The number of leaves per shoot, is a product of the genetics of
the species and the percentage damage (insect or otherwise). The
significantly higher number of leaves on CPN compared with RWS does not
seem to be a product of the differences in leaf and shoot loss between
sites, since leaf loss and total damage did not vary. It seems para-
doxical that a site more readily experiencing moisture stress and
exposure to hot dry winds should have a high number of leaves, when the
tendency appears to be for the trees to discard their foliage in such
circumstances. It may be that the trees on the more drought-prone site
have produced more, but smaller and therefore more drought resistant,
leaves.

Miscellaneous damage comprises damage caused by insects and other
organisms. Therefore, it is not unduly surprising that the amount of
this type of damage is not seemingly related to water availability.

The difference in the percentage of damaged leaves per shoot
between the sites may have been unrelated to the direct effects of
water stress as described above however, moisture availability may
indirectly affect insect abundance by stimulating greater leaf production
on the more mesic (Ridgeway) sites. It is conceivable that a greater

	RWN >CPS	RWN >CPN	RWS >CPS	RWS >CPN	CPN > RWS	CPN > RWN	CPN > RWS	CPS > RWN
General Analysis	% actual damage leaf miners & skeleton-izers leaf dis-torting insects	% damaged leaves leaf miners & skelton-izers	leaf distort-ing insects	% damaged leaves miscellan-eous damage	mean no. of leaves per shoot			
Species-site analy-sis	% damaged leaves (E. vimin-alis; af)		% damaged leaves (E. obliqua)					
	RWN >RWS	RWS >RWN						
General Analysis		leaf dis-torting insects						
Species-site analysis	% missing leaves (E. vimin-lis; vj)	% damaged leaves (E. obliqua)						

TABLE 3.21: Significant between-site differences ($P < 0.05$) RWN > CPS = damage on RWN significantly greater than that on CPS etc.
af = adult foliage; jf = juvenile foliage

density of foliage attracts relatively higher numbers of insects and
therefore increased damage (Carne 1965).

It may be that the percentage of damaged leaves is higher on RWS
compared with CPN simply because the mean number of leaves per shoot
is significantly less in the former site. The proviso would be that
insect abundance (and/or the amount of foliage consumed by the particular
insect community at each site, if different) did not differ significantly
between the two sites, or as is more likely from the results was higher
on RWS (due to the greater density of new foliage and/or other factors;
see below). Two further relationships would seem to indicate that the
differences in the number of leaves damaged may be explained by the
differences in the mean number of leaves per shoot between sites,
especially in one species; *E. obliqua*. Firstly, the number of
E. obliqua leaves damaged on RWS was significantly higher than those
damaged on CPS, which may be explained by the greater number of leaves
per shoot on CPS compared with RWS, a relationship that just failed to
be significant $(0.05 < P \geqslant 0.10)$. Secondly, the percentage of damaged
leaves on *E. obliqua* at RWS was significantly higher than the percen-
tage of damaged leaves at RWN. At RWN the number of leaves per shoot
on *E. obliqua* was higher than the number at RWS, although not signifi-
cantly so. This explanation for the changing number of damaged leaves
between sites however, does not account for the significantly higher
levels of damage on; (1) RWN compared to CPN and (2) on RWN compared
to CPS in the foliage of *E. viminalis* (adult foliage). It would seem
therefore, that the amount of leaves damaged depends on the influence
of an environmental variable instead of, or as well as being influenced
by the number of leaves per shoot (see below).

It is interesting that the percentage of damaged leaves should
demonstrate between-species variation, as well as between-site varia-
tion, whilst the percentage actual damage did not do so (Table 3.18).
It is conceivable that the numbers of leaves damaged by insects is
relatively high, even if absolute damage levels are not. Moreover,
large numbers of larvae may begin feeding on leaves, only to die of
dessication in abnormally hot, dry conditions.

Many of the other forms of insect damage considered (i.e. the percentage of actual damage and the damge by leaf miners and skeletonizers and leaf distorting insects) were also found to be higher on either one or both of the Ridgeway sites compared with one or both of the Chimney Pot Hill sites (table 3.21). It is conceivable that the particular forms of insect damage are influenced by the variation in microclimate between Ridgeway and Chimney Pot Hill resulting mainly from differences in altitude and exposure between the two sites. Temperatures on Chimney Pot Hill are reduced relative to those at Ridgeway because it is some 100 metres higher a.s.l. Furthermore, windspeed is higher at the former site, exposure to the hot dry winds of summer and cold winds of winter greater and the level of humidity reduced. Overall therefore, the microclimate at Ridgeway, and especially RWN, is more favourable to insects (chapter one). For example, the damage by leaf miners and skeletonizers was significantly higher on RWN compared to CPN and CPS. This may represent the preference of these insects for the superior microclimate at Ridgeway and their dislike of the cold, more exposed Chimney Pot Hill sites.

It is also probable that the insect population is affected by the soil fertility gradient (table 3.20). Mattson and Addy (1975) review a number of studies that show insect damage increases as soil fertility declines.

While soil fertility and microclimate may act in combination to influence the amount and type of insect damage, they may alternatively have no effect at all. Factors such as the particular composition of species in the under and overstorey may have a greater influence over the abundance and/or particular species of insects and therefore the overall level of damage (Burdon and Chilvers 1974b).

In addition to the significant relationships between the level of damage by leaf distorting insects on CPS compared with RWN and RWS, these insects also appear to distinguish between the environments at RWN and RWS. This would seem to indicate that another underlying factor is influencing the distribution of these insects at Ridgeway. Further- more, in contrast to the findings in this study, Burdon and Chilvers (1974b) found that leaf galls were more prevalent at higher altitudes.

Although gall formers comprise only part of the total number of leaf
distorting insects it might be expected that any altitudinal differ-
ences in their distribution would be borne out in the results. The
fact that the lower altitude sites bore significantly more damage by
leaf distorting insects than those at higher altitudes gives further
credence to the assertion that another, overriding factor is responsible
for the differences in the amount of damage between RWN and RWS.
Such a factor may be the age of the trees or the level of disturbance.
Despite the effort to minimize between tree differences, the trees
sampled on RWS were younger than those on the other three sites. This
fact may influence the abundance of leaf distorting insects (Ohmart *et al.*
1983b). RWS is also the most highly disturbed of the four sites with
roads passing across the top of it and cleared land to one side
(Figure 2.2).

The amount of leafloss in *E. viminalis* (juvenile foliage) also
varied significantly between RWN and RWS (table 3.21). It is difficult
to ascertain the significance of this result when it is based on such
a small sample size.

In all but one instance, the level of insect damage is higher
on the Ridgeway sites. This has variously been attributed to the effects
of microclimate (as influenced by exposure and altitude) and/or soil
fertility and/or the indirect effects of a soil moisture gradient.
Where insects were able to differentiate between the north and south-
facing slopes at a site, it did not seem to be on the basis of the
inherent physical environment on these slopes but on other factors such
as the level of disturbance. Other as yet unconsidered 'biotic' factors
(i.e. predation, inter- and intra-specific competition) which may in
themselves be modified by the physical environment, may also act on the
distribution, composition and abundance of insects.

In contrast to the nine variables thus far discussed, leaf chew-
ing damage did not vary significantly between either the sites or
species in the General Analysis. Leaf chewers cause the most damage in
all species on all sites. If the different types of chewing damage
could have been attribted to the activities of certain insects, then

perhaps some differentiation in the amount of damage between the
sites and species may have been found. Even so, the overall levels
of insect damage might have been too low during the period of study
for any relationships to be evident.

The indication is that the relationship between insect and environ-
ment is complex. In all probability a combination of factors influences
the type and amount of damage. This combination may vary between
species, in space and time.

3.4.3.   Insects as a Control of Forest Community Patterns

One line of research in insect-eucalypt relations has considered
the role of insects in the formation of mixed stands (Chilvers 1972;
Burdon and Chilvers 1974; Chilvers and Brittain 1972; Duff *et al*.1983;
Rogers and Westerman 1979). Pryor (1953, 1959) noted that eucalypt
species from different subgenera tended to grow together in (mixed)
stands. That is two or more species unable to interbreed share the
same resources and the same niche (cf. Austin *et al*. 1983).
Insects have been considered as part of the mechanism by which
eucalypt species from different subgenera can occur together in a forest,
despite the trees utilizing identical resources.

Chilvers and Brittain (1972) developed a model which was later
extended by Burdon and Chilvers (1974), in which differential parasite
(i.e. Phytophagous insects, fungi and galls) attack between tree species
resulted in two tree species coexisting. Basically, of the two tree
species occurring on a site, the more abundant/dominant one would be
subjected to higher levels of insect damage and therefore reduced
productivity. The model presupposes amongst other things that insect
damage is high enough to affect plant primary productivity.

Most trees on Chimney Pot Hill and Ridgeway study sites were
from the subgenus Monocalyptus. However, there was no difference
between the actual damage sustained by the young shoots in these
species and that sustained by *E. viminalis* (from the subgenus
Symphyomyrtus). Overall, the foliage of *E. obliqua* may be more heavily
damaged than *E. viminalis* (adult foliage). However, the younger the
tree the less likelihood that this relationship is significant (see
earlier in Discussion). More importantly, however, the levels of
damage sustained by <u>all</u> species are not large enough to substantially
affect plant productivity (Mattson and Addy; cited by Ohmart *et al.* 1983a).

It would appear from these results that young trees, and for that
matter mature trees (Ohmart *et al.* 1983a) do not sustain sufficiently large
amounts of actual damage to place the Monocalyptus species at a dis-
advantage compared with the Symphyomyrtus species, or for that matter
any one species at a disadvantage compared to another.

However, the level of total damage sustained by the trees may
be high enough to affect plant primary production. Where insect
damage levels exceed 40% then losses in primary production may be
proportional to foliage losses, between 5 - 30% they have not been found
to adversely affect plant primary production (Mattson and Addy 1975;
cited by Ohmart *et al.* 1983a). Three tree species, all from the sub-
genus Monocalyptus, had mean total damage levels of more than 30%;
E. obliqua (41.0%), *E. tenuiramis* (32.7%) and *E. pulchella* (30.2%).
The values of 28.9% and 29.4% for *E. viminalis* (adult and juvenile
foliage respectively), from the subgenus Symphyomyrtus, although below
30% are so close to the aforementioned values (excepting *E. obliqua*) it
is unlikely that there is any great difference in their impact on plant
productivity. However, it does seem that *E. obliqua* sustaining 41.0%
total damage is disadvantaged compared to all the other species.

Insect activities may affect the forest community composition,
but only as part of a web of inter-relationships that varies between
tree species and sites.

Figure 3.14 a - b model the distribution of three tree species along the moisture gradiant, in the absence and presence of differential total damage by insects. The diagrams could be further modified to take into account between-site differences in total damage. All three tree species (*E. obliqua, E. pulchella* and *E. viminalis*) are subject to some damage. However, *E. obliqua* sustains significantly higher levels of actual (i.e. old + young foliage) and total damage compared with the other species. Hence, the range of *E. obliqua* may be significantly reduced (see below).

E. obliqua dominates those environments in the middle of its ecological range because of its relatively fast growth rate (see section 3.3.2.3.). Its leaves, which were not found to differ significantly in the number per shoot from other species, have a large surface area compared to *E. pulchella, E. tenuiramis and E. viminalis*.

However, *E. obliqua* is particularly susceptible to water stress, not being able to open and close its stomata in accordance with climatic conditions (Sinclair 1980). Thus transpiration continues when most other eucalypts have closed their stomata to prevent water loss. *E. obliqua* therefore requires large amounts of water from the soil. As a consequence of this characteristic, at the margins of its distribution along a soil moisture gradiant the effects of water stress (i.e. the drought) may cause the death of leaves and shoots. The level of hidden damage caused by climatic/environmental stress, in conjunction with that resulting from insect activities and plant pathogens etc. (the magnitude of each variable varying dependently or independently of each other in time and space) may reduce productivity of the tree species to such an extent that a particular individual could be outcompeted by other tree species in an area where it formerly occurred.

It would seem that the margins of a species distribution may be subject to cyclical oscillations depending partly on environmental conditions, together with the amount of insect damage the tree species incurs.
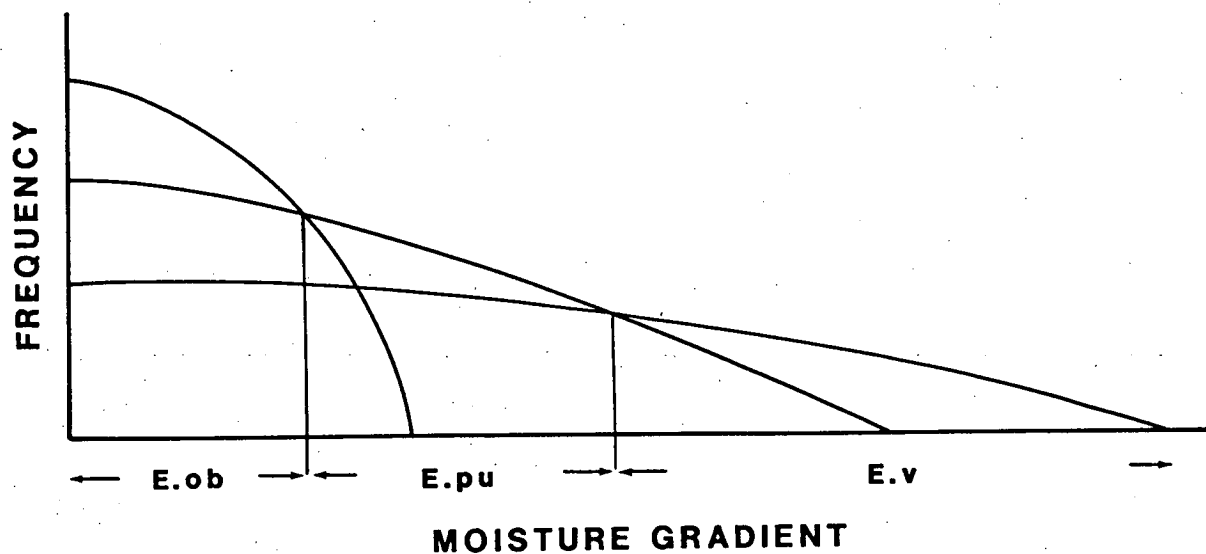
(a)
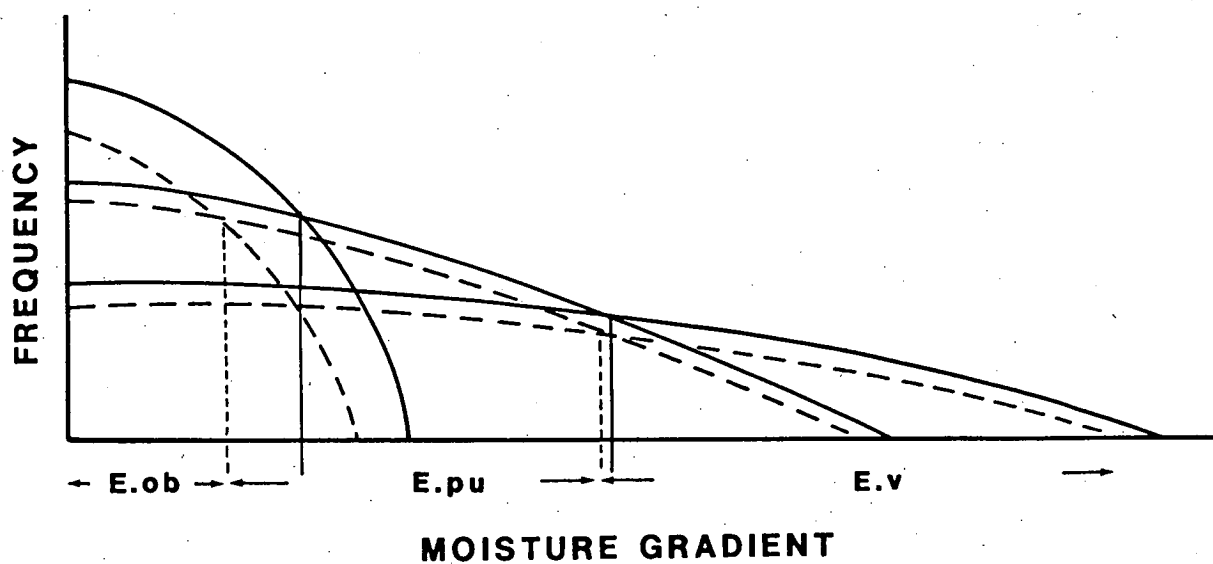
(b)

FIGURE 3.14   The range of *E. obliqua*, *E. pulchella* and *E. viminalis*
in (a) the absence and (b) the presence of total damage.
Curves are accentuated for the sake of clarification.

E.ob= E.obliqua, E.pu= E.pulchella, E.v= E.viminalis

E. *viminalis* (adult foliage) is less susceptible to soil moisture
stress than the other species (Kirkpatrick and Marks, in press).
Therefore, during years of drought it is at a competitive advantage
compared with other tree species because of (1) its tolerance to water
stress and (2) the slightly lower levels of total damage sustained.

E. *pulchella* does not gain a competitive advantage under particular
climatic conditions (cf. E. *obliqua* and E. *viminalis*) but is competitively
superior at some times of the year.

E. *pulchella* differs from the other species in that it bears new
growth all the year round (cr. bimodal growth patterns of the other
species), indicating that it is in the middle of its climatic range,
although growth may cease when temperature and soil moisture stresses are
very high, as in mid-summer, or when temperatures and insolation are very
much reduced, as in winter. Thus, E. *pulchella* avoids intense competition
for nutrients and water during spring and autumn when most trees are
experiencing a growth flush. Furthermore, by not concentrating growth in
one or two limited periods, E. *pulchella* may avoid the very heavy foliage
losses caused by insects which emerge to coincide with the growth of new
shoots. Thus, E. *pulchella* may avoid large losses of new foliage at times
when starch reserves, and therefore the ability to refoliate, are at a
minimum, usually after periods of rapid growth (Mazanec 1967; Morrow 1977).
The fact the new growth is available all the time does not necessarily mean
that the foliage is heavily attacked in the absence of new growth on
other species. For most of the year the young foliage on E. *pulchella*
would be hard to find amongst the foliage of other trees; i.e. it is
less apparent and much of the growth occurs when insects are quiescent
(Feeny 1975; Rhoades and Cates 1975).

E. *pulchella* sustains its maximum insect damage during February.
This may be because water retention is most important during this period
and growth may have been inhibited by unfavourable weather conditions.
It seems then the loss of leaf area through the activity of insects may
in fact be beneficial.

Another effect of insects on *E. pulchella* was to reduce the length and number of leaves per shoot. These may have been reduced in all other species too, this effect having been masked by the time of sampling, which coincided with the period of new growth. This fact is important because it means that the damaging effects of insects may disadvantage a species only at certain times during the year and advantage it at other times. Thus a particular species may be at a competitive advantage or disadvantage compared with another over a period of time ranging from one month to several years or more (cf. Gill and Ashton 1968).

CHAPTER 4   DISCUSSION

Changes in the structure, composition, distribution and physiology of plant communities were reflected by changes in the receipt of radiant energy. Further investigation of this phenomenon showed that incident radiation was controlling changes in soil moisture availability and that in all probability variations in the amount of soil moisture available to plants was an important determinant of forest community patterns.

The effects of soil moisture availability were examined by looking at the changes in the distribution of species across three soil types in relation to specific values of incident radiation and more generally to the differences in water availability between the different soils. It was found that the amount of moisture available to plants in each of the three soils could not be determined from just a straightforward compilation of the effects of rainfall, interception, run-off, evapo-transpiration and soil water capacity under the direct and indirect control of solar radiation, since structural and textural differences between the soils caused subtle variations in the amount of available moisture.

The influence of insect grazing (actual damage) on forest community patterns was found to be negligible. Whether the low damage levels recorded represent the 'normal' state in eucalypt forests (Ohmart *et al.* 1983a) or whether they were the result of decreased insect activity during drought conditions (Kile 1974; Specht and Bower 1975) is unknown. In all probability the effect of the drought did cause a reduction in the level of insect grazing. However, it is unlikely that even during a non-drought year the amount of defoliation by insects would increase to the extent that it could influence the composition, structure and distribution of plant communities.

Conversely, it was found that the levels of total damage, compris-

ing damage from the effects of adverse climatic conditions (i.e.
drought, high winds), insects and other sources (Fungi, herbivorous
animals etc.), may have been large enough (if it is accepted that damage
exceeding 30% may seriously affect plant productivity) to disadvantage
at least one species (*E. obliqua*).

It was hypothesized that species of *Eucalyptus* are particularly
vulnerable to the effects of insects and/or drought at the margins of
their environment range, where their balance with the environment becomes
increasingly precarious.

The importance of soil moisture availability versus insect
predation as a major cause of changes in the forest community varies in
time and space. For the majority of all plant species the primary con-
trol of forest community patterns is the availability of soil water and
less importantly factors such as soil nutrient status and the level of
disturbance. The effect of these gradients is on-going and continual.
Insect predation of the magnitude required to impinge upon and override
the control of the aforementioned environmental gradients may occur in
cycles, at time intervals of several years or more (Varley *et al.* 1973;
Ohmart *et al.* 1983a). It has been reported that heavy infestations of
insects can, depending on the severity, frequency, timing and extent of
the outbreaks, potentially alter the composition and structure of the
forest (Mattson and Addy 1975).

On the north-facing slope of the dolerite site where the combined
effects of water availability, fire and shallow soils most probably
determine the nature of the plant community (grassy woodland with few
mature trees), it is difficult to conceive how insect grazing even at
outbreak proportions has or will override the influence of the afore-
mentioned environmental variables to effect changes in the composition
and abundance of the tree species. However, on slopes where these
environmental variables are not so limiting, insect grazing may have
some impact by attacking the most physiologically vulnerable individuals
or species (i.e. *E. obliqua*) thereby reducing their competitiveness.
From this short term study it is difficult to determine whether soil
moisture availability or insect grazing has the greater ecological
impact overall.

After a fire, the severity, incidence and overall effect of
which varies between the three sites, there may be an increase in the
amount of young foliage and in the number of young trees. Hence, the
competitive advantage of those species in which only the young foliage
is grazed, over others in which foliage is continually grazed throughout
its lifespan, is diminished if not obliterated.

The interplay if any between the insect population of the shrub
layer and tree canopy has not been considered in this research (see
Springett 1978). It may be that insect activity severely weakens the
shrub layer in space and time giving the advantage to the trees and
vice versa. Some insects spend the various stages of their life cycle
in different parts of the forest and hence under the influence of
different environment controls (see below).

Insect grazing would appear to be at least partially controlled
by environmental factors. The extent of this control versus that of
biotic factors most likely varies in space and time.

Whether changes in the composition and distribution of insect
communities are attributable to the effects of solar radiation in itself
or to other environmental variables that are controlled by solar
radiation, were to be investigated directly from the results of insect
sampling and indirectly from a comparison of the levels of insect
damage on the north- and south-facing slopes at Ridgeway and Chimney Pot
Hill over the 1982/83 season. Unfortunately the method of insect
collection was rendered inadequate, and consequently unusable, as a
result of the overall reduction in insect numbers during the period of
study. Any future attempt to test the hypothesis that incident
radiation controls the insect population would have to utilize another
more exacting method of insect collection and extend the sampling in
time and space.

There was a major problem in using a surrogate measure (the amount
of damage to the foliage) to determine the gradients controlling insect
populations in that it was not known how closely patterns of insect

damage reflected changes in the composition, distribution and abundance of insects.

From the results it was impossible to isolate one environmental gradient as being responsible for the overall control of insect populations and in fact in all probability a combination of gradients determined the distribution and composition of insect communities.

The topographically-induced variations in radiant energy on north and south-facing slopes did not appear to influence insect populations. It could be that on the slopes at Ridgeway and Chimney Pot Hill the magnitude of these variations was not large enough to affect insect abundance or community composition. Conversely, it is also possible that variations in the receipt of radiation did affect insects but that: (1) this was overidden at Ridgeway by the effects of disturbance and/or differenes in tree age, and at Chimney Pot Hill by the relatively inhospitable climate; or (2) the effect of these variations on insects were not adequately reflected in the patterns of insect damage.

Insects however, generally did differentiate between the two sites indicating that they were under the overall control of a gradient/s that varied between one or other or both of the slopes at Ridgeway compared with one or other or both of the slopes at Chimney Pot Hill. Such a gradient/s could be the result of variations in soil nutrient status, the abundance of new foliage or microclimate (as influenced by altitude and exposure) between the sites. Observation would seem to suggest that of these microclimate had the most influence on insect populations i.e. it was not so much the direct and indirect effect of differences in the radiant energy between slopes but differences in exposure and altitude between the sites that controlled insect community composition and species distribution. Further research is required to verify these conclusions.

Although one effect of the drought may have been to diminish insect activity overall, the availability of soil moisture as determined by incident radiation levels did not appear to have the same control over insect communities as it had over plant communities.

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APPENDIX 1

Nomenclature follows 'The Insects of Australia' (CSIRO 1970):

Order HEMIPTERA

Suborder HOMOPTERA

Machaerotidae

Chaetophyes sp.

Psyllidae

Suborder HETEROPTERA

Coreidae

Amorbus obscuricornis

Gelonus tasmanicus

Pentatomidae

Order COLEOPTERA

Suborder POLYPHAGA

Scarabaeidae

Heteronyx sp.

Cantharidae

Chauliognathus lugubris

Lycidae

Metriorrhynchus sp.

Coccinellidae

Cleobora mellyi

Tenebrionidae

Lagriidae

Lagria sp.

Chrysomelidae

Curculionidae

Gonipterus sp.

Order   LEPIDOPTERA

Suborder DITRYSIA

Psychidae

   Clania sp.

Geometridae

Lymantriidae

   Acyphas leucomelas

Arctiidae