


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**Comparative Ecophysiology of Temperate and
Tropical Rainforest Canopy Trees of Australia
In Relation to Climate Variables.**

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ABSTRACT

Rainforests have a discontinuous distribution along the eastern edge of Australia. Therefore, they provide an opportunity to investigate differences in the physiology of temperate and tropical trees within the same vegetation type. Eight rainforest canopy species were chosen to investigate differences between tropical (*Alstonia scholaris*, *Castanospermum australe*, *Heritiera trifoliolata* and *Sloanea woollsii*) and temperate species (*Acmena smithii*, *Eucryphia lucida*, *Nothofagus cunninghamii* and *Tristaniaopsis laurina*). A climate analysis showed the important differences between the climates of the temperate and tropical rainforest species to be the higher temperatures and evaporation rates of the tropical climate, the higher day-to-day and seasonal variability of temperature of the temperate climate, and the shift from winter-dominant precipitation in the temperate climate to summer-dominant precipitation in the tropical climate. A series of glasshouse and controlled environment cabinet experiments were used to test photosynthetic and growth responses of rainforest species to temperature and vapour pressure deficit.

The response of temperate and tropical rainforest species to temperatures was compared in terms of growth and net photosynthesis. The first experiment aim^{ed} to determine the temperatures for maximum growth and net photosynthesis. Seedlings were grown under five different temperature regimes (14°C/6°C, 19°C/11°C, 22°C/14°C, 25°C/17°C, and 30°C/22°C) in controlled environment cabinets for 16 weeks. The temperate species showed maximum net photosynthesis at lower growth temperatures but maintained it over a wider range of growth temperatures than the tropical species. Similarly, the temperate species showed maximum growth at lower temperatures than the tropical species. However, the temperatures for maximum growth were considerably higher than those for maximum net photosynthesis. Furthermore, there was substantial overlap in relative growth rates of the temperate and tropical species at both 14°C and 30°C.

The second experiment investigated differences in the capacity to acclimate photosynthetically to changing temperature regimes. Plants were grown in controlled environment cabinets under a constant temperature regime of 22°C/14°C or a fluctuating temperature regime that was randomly changed daily between 27°C/19°C and 17°C/9°C.

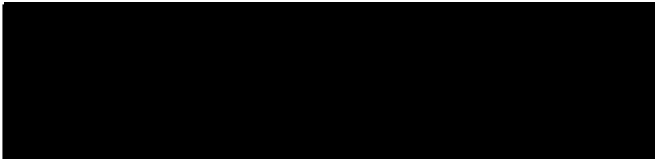
Maximum net photosynthesis of leaves that developed under these conditions was then measured after two weeks acclimation under a series of temperature regimes (14°C/6°C, 18°C/10°C, 22°C/14°C, 26°C/18°C and 30°C/22°C). The temperate species showed an ability to maintain maximum net photosynthesis over a wider range of acclimation temperatures than the tropical species. This ability was improved by development under the fluctuating temperature regime.

The final experiment investigated whether tropical rainforest species show greater reductions in net photosynthesis and growth under high vapour pressure deficit (VPD) than temperate species. Seedlings were grown under ambient conditions or a lowered VPD in glasshouses for a year. The tropical species showed greater reductions in net photosynthesis with increasing instantaneous VPD than the temperate species when grown under a lowered VPD but not when grown under ambient conditions. In contrast, the VPD treatments had no effect on growth rate and biomass allocation of the species.

The greater photosynthetic tolerance of the temperate than the tropical species to temperature and vapour pressure deficit reflects the seasonal variability of the temperate climate. The findings of this study have several implications for the present vegetation-climate models: (i) temperatures for maximum growth can not be implied from photosynthetic responses to temperature, (ii) temperate species have maximum growth at higher temperatures than predicted from their distributions, and (iii) high latitude limits of species may be determined by relative growth rates and not cold tolerance.

DECLARATION

To the best of my knowledge, this thesis contains no material that has been accepted for the award of any other degree or diploma in any university or other institution, and does not contain any material previously published or written by another person, except where due reference has been made in the text.



Shaun Cameron Cunningham

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CHAPTER 1

Introduction

Rainforests cover a wide latitudinal range in Australia from the southern tip of Tasmania to the northern tip of Cape York Peninsula. They have a discontinuous distribution along the eastern edge of Australia (Figure 1.1). Rainforest patches also occur in Arnhem Land and the Kimberley regions of northwestern Australia. Patches of rainforest are typically found as small, wet pockets, which fire rarely penetrates, within the distinctive sclerophyll forests of Australia (Webb & Tracey 1994; Specht & Specht 1999).

The species composition, diversity and structure of Australian rainforests changes with climate. In northeast Australia temperatures are warm with low seasonality and precipitation falls predominantly in summer (Bureau of Meteorology 1989). The tropical rainforests that grow under these conditions are estimated to contain up to 900 rainforest tree species (Unwin & Kriedemann 1990) with up to 60 tree species in a 5 ha plot (Debski *et al.* 2000). These rainforests are characterized by strangler figs, vines, large epiphytes and several strata of trees (Webb & Tracey 1981b). Temperatures decrease with increasing latitude along the east coast of Australia and precipitation changes from summer-dominant to winter-dominant (Bureau of Meteorology 1989). The temperate climate of southern Australia is also characterised by greater seasonal fluctuations in temperature than the tropical climate (Nix 1982). There is a reduction in the structural complexity of rainforests associated with these climate changes. The temperate rainforests of the south are characterized by the presence of commonly less than five canopy tree species and a high diversity of bryophytes (Howard 1981). Within the tropics, reductions in the structural complexity of rainforests are also found with increasing altitude or decreasing precipitation (Webb 1968). Furthermore, many genera with temperate affinities are found on top of tropical mountains (Adam 1992).

Relationships between species distributions and climate, such as those within rainforests, have long been observed (eg. de Candolle 1855; Cain 1944). Many attempts have been made to characterise the vegetation types of the world according to climate (eg. Holdridge 1947; Box 1981). Woodward (1987) proposed a comprehensive vegetation-climate model which delimited world vegetation types according to physiological responses to climate (Figure 1.2). The distribution of vegetation types was explained by the interaction between leaf area and evapotranspiration. The high latitude limits of forest types were explained by differences in cold tolerance and the required length of the growing season. The cost of cold tolerance in these high latitude forest types was then proposed to reduce their competitive ability under the warmer conditions at low latitudes. Recent vegetation-climate models (eg. Box 1995; Neilson 1995) have continued to explain the distribution of forest types through the tolerance of climatic extremes. None of these models adequately explains the delimitation of forest types under moderate climates.

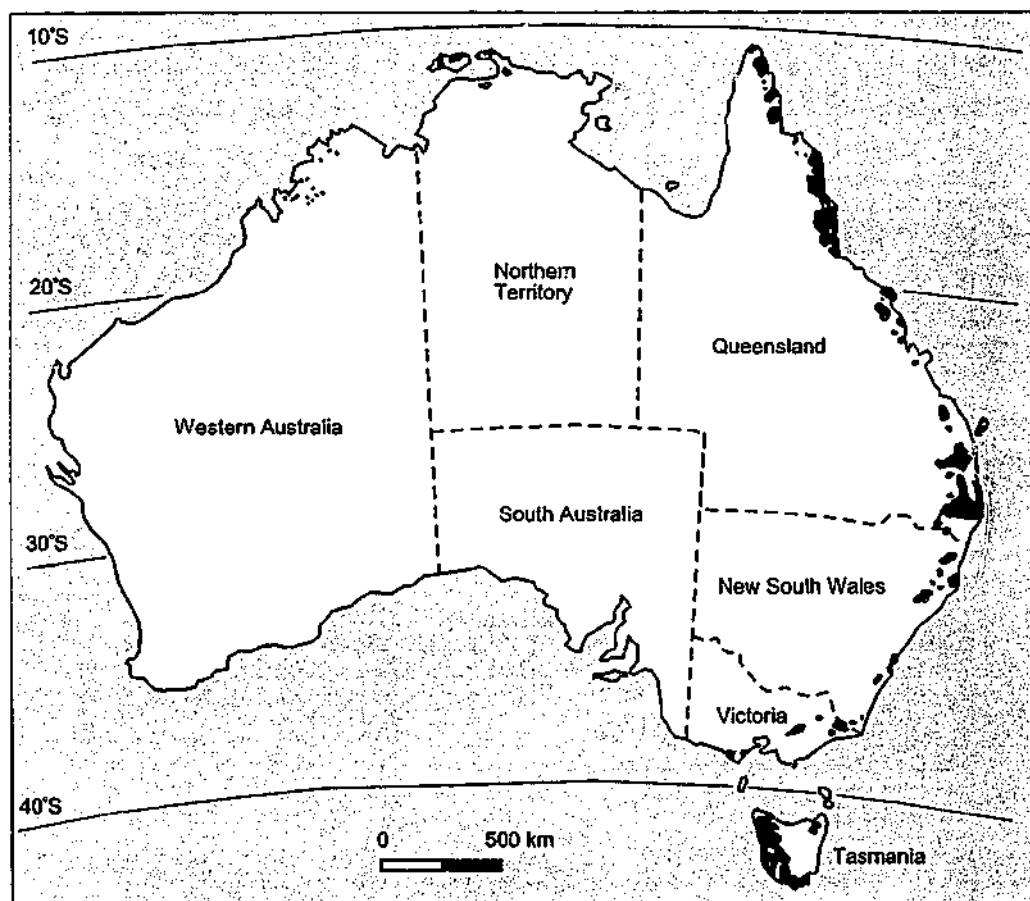


Figure 1.1 Map of rainforest distribution in Australia, showing the main areas in black (adapted from Adam 1992). State borders are included (dashed lines) for later reference.

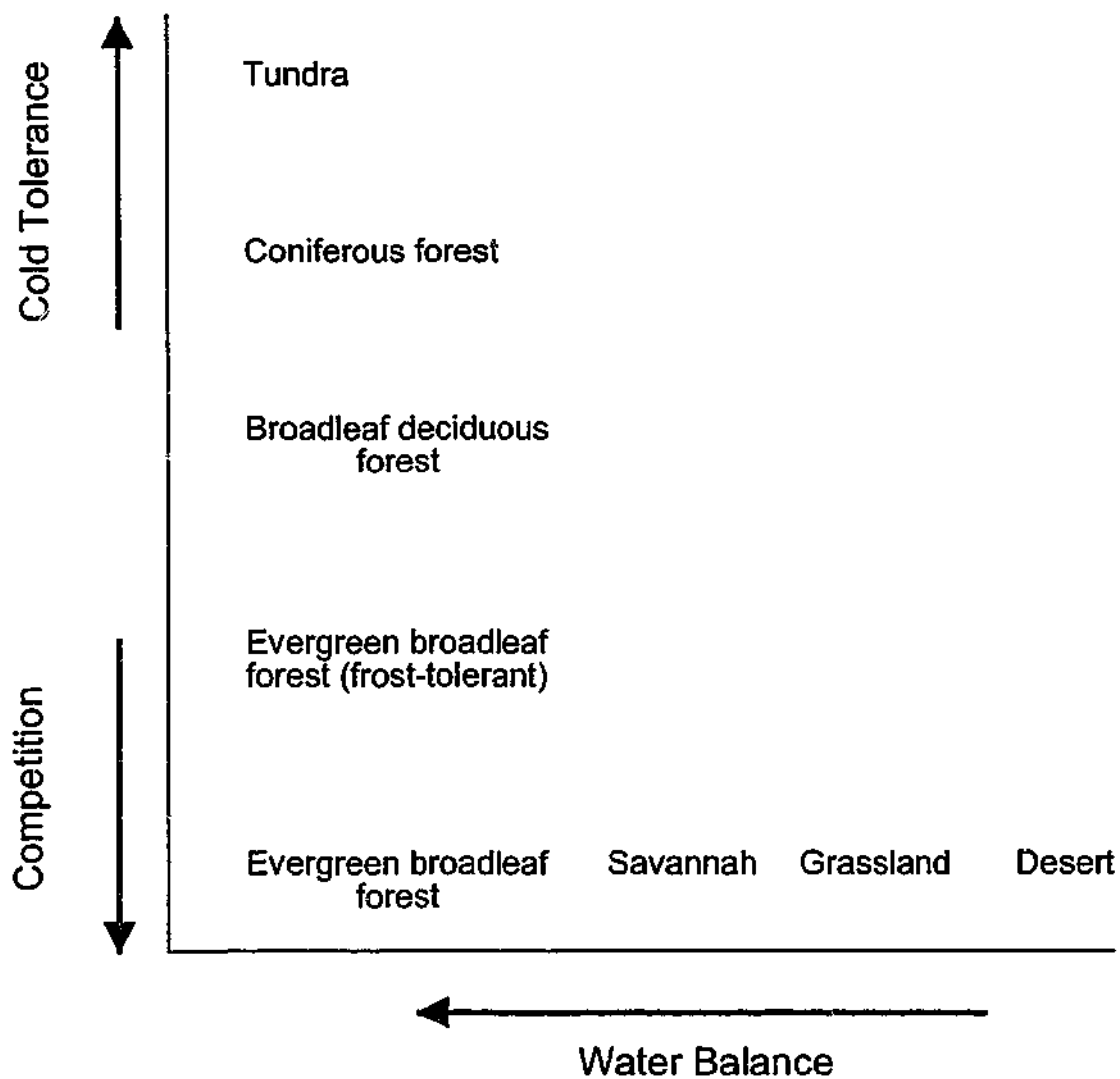


Figure 1.2 Predictions of Woodward's (1987) model for vegetation types and physiognomic types of the world.

Specht (1981) and Nix (1982) proposed similar growth models for Australian vegetation. They, like Woodward (1987), also used water balance to delimit vegetation types. The important difference from the global models is that they used growth responses to temperature to explain the distribution of species within vegetation types. The central proposition of these models was that plants fall into a series of thermal response groups each with a characteristic temperature for maximum growth (Figure 1.3). Nix (1982) predicted that these thermal response groups will dominate regions where the mean annual temperature is close to their temperature for maximum growth. Nix (1991) went on to relate his thermal response groups to the change in rainforest types with latitude. Therefore, he was predicting that the change in the dominant rainforest tree species with latitude is the result of different temperatures for maximum growth.

There is evidence for different physiological responses to temperature among species from different temperature climates. Studies of species from the climatic extremes of alpine, arctic and desert environments have shown a trend for species from colder environments to show maximum net photosynthesis at lower temperatures than species from hotter environments (Berry & Björkman 1980; Larcher 1980). In addition, species from environments that have large temperature fluctuations, such as deserts or mountains, usually show maximum photosynthesis over a greater range of temperatures (Billings *et al.* 1971; Pearcy 1977; Mooney *et al.* 1978a; Björkman 1981a). Studies have shown that temperate tree species have maximum growth over the temperature range of 15°C to 25°C (Brix 1971; Hellmers & Rook 1973; Paton 1980; Schaffer & Andersen 1994a) whereas tropical tree crops have maximum growth at temperatures between 25°C and 35°C (Opeke 1982; Schaffer & Andersen 1994b).

Evidence for competitive exclusion of species with changing temperature conditions has come predominantly from the study of alpine herbaceous species (eg. Woodward & Pigott 1975; Woodward *et al.* 1986). Loehle (1998) presented a weak trend between cold tolerance and reduced height growth of North American trees in support of Woodward's (1987) model. In addition, Loehle (1998) showed a plot of height growth rate of tree species in the United States against temperature (growing degree days) formed a replacement series (Figure 1.4). That is, as conditions become warmer low latitude species have faster growth rates than high latitude species.

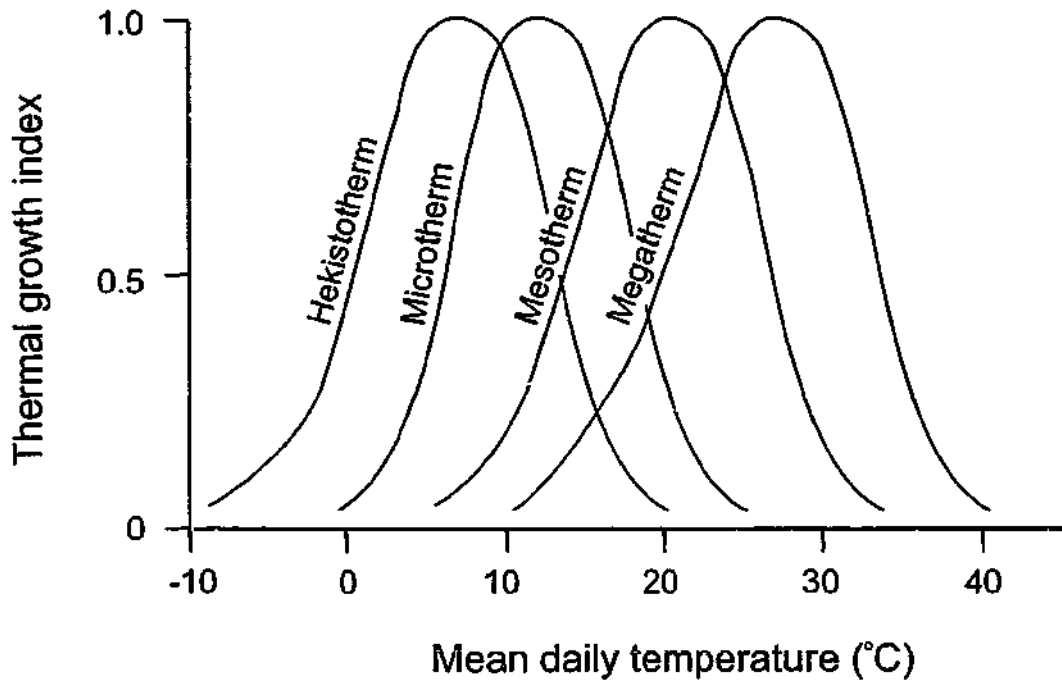


Figure 1.3 Relationship between relative growth of thermal response groups and mean daily temperature proposed in Nix's (1982) model.

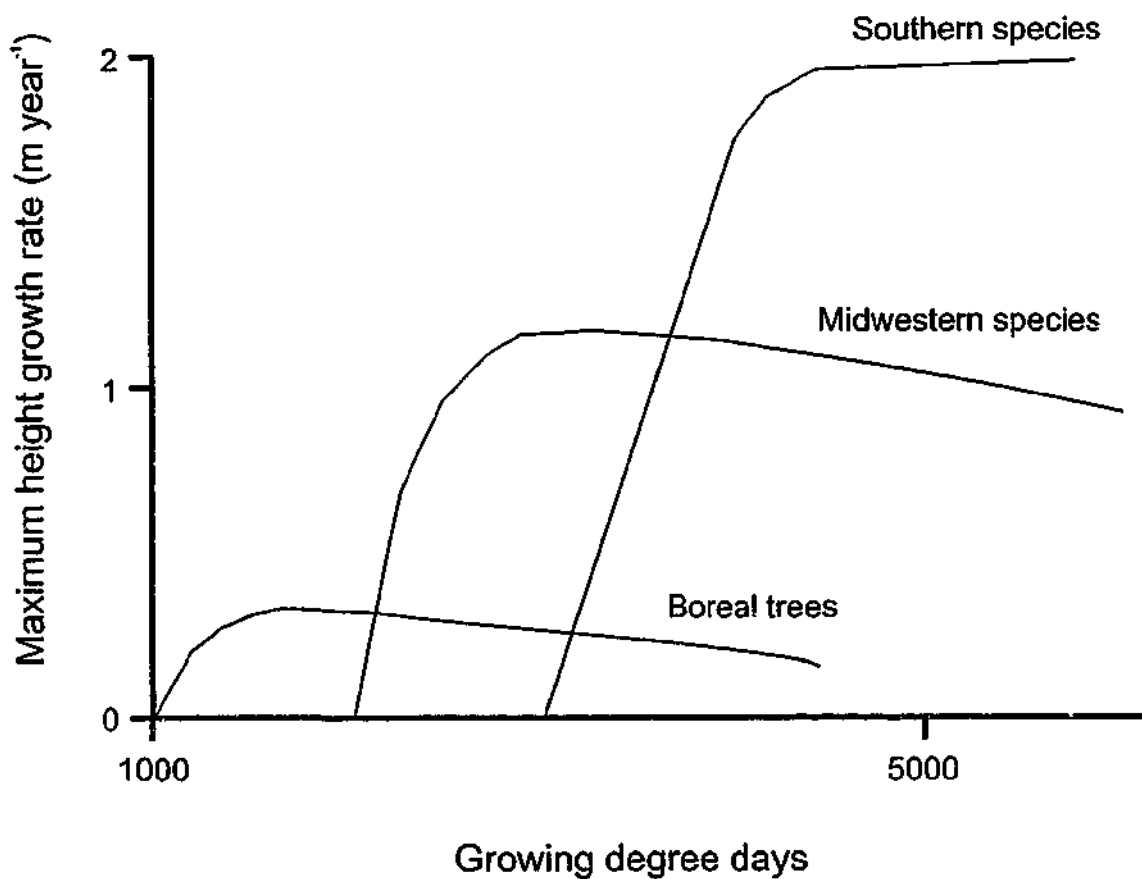


Figure 1.4 Maximum sapling height growth rate for early successional species of regional tree floras of the United States. Adapted from Loehle (1998).

Recent work with Australian rainforest trees has revealed physiological differences among species from different latitudes. A study of temperate rainforest trees found that species from lower latitudes showed maximum photosynthesis at higher temperatures than higher latitude species (Hill *et al.* 1988). In contrast, tropical and temperate species of *Nothofagus* showed little difference in the temperature for maximum photosynthesis (Read 1990). Instead the difference was the ability of temperate species to acclimate to a wider range of temperatures than tropical species. The tropical species of *Nothofagus* were also found to have a higher long-term water-use efficiency (Read & Farquhar 1991) and stomatal sensitivity to leaf water-deficit (Read 1998) compared with the temperate species.

In light of previous findings, temperate and tropical rainforest species of Australia are likely to show differences in the temperatures for maximum net photosynthesis and growth that reflect the difference in temperatures between their climates. However, the difference between the physiology of temperate and tropical rainforest species of Australia may be more than the temperatures for maximum growth predicted by Nix (1991). The temperate rainforest species may maintain maximum net photosynthesis and growth over a wider range of temperatures than tropical rainforest species. In addition, as proposed by Loehle (1998) the tropical rainforest species may simply have faster growth rates than the temperate species under warmer temperatures. Furthermore, the temperate and tropical rainforest species may have different strategies to avoid water stress due to differences in the seasonality of their precipitation.

AIM

The aim of this thesis is to investigate physiological differences in respect to climate variables between temperate and tropical of rainforest canopy trees in Australia.

The main questions to be explored are:

- 1) Do temperate species have lower temperatures for maximum growth and photosynthesis than tropical species?
- 2) Do temperate species maintain maximum growth and photosynthesis over a wider range of temperatures than tropical species?
- 3) Do tropical species show a greater sensitivity of growth and photosynthesis to high vapour pressure deficits than temperate species?

RESEARCH APPROACH

There are two ways of selecting species to test differences between tropical and temperate rainforest species. Firstly, the species selected for comparison can be restricted to a single genus. Studies of physiological responses to climate variables in Australia have investigated trends within the genera *Banksia*, *Eucalyptus* and *Nothofagus* to varying degrees (eg. Groves 1978; Mooney *et al.* 1978b; Ferrar *et al.* 1989; Read 1990). The advantage of these studies is that physiological differences among species can be assumed to be adaptations to their different environments. However, the disadvantage is that the type of difference among species may simply reflect the evolutionary restrictions of that genus. Secondly, species from different climates can be compared across a broad range of families. The advantage of this approach is that general adaptations to environment, due to parallel evolution, can be determined. However, conclusions can be complicated by differences in physiological responses to variables other than those of interest. Direct comparisons of species have concentrated on the climatic extremes of coastal and desert species, arctic and alpine species, and species from different altitudes (eg. Mooney *et al.* 1964; Billings & Mooney 1968; Björkman *et al.* 1980). There is a lack of direct comparisons between

temperate and tropical species. In an attempt to find general trends, temperate and tropical rainforest species were chosen from a broad range of genera.

The interpretation of trends between temperate and tropical rainforest species depends on how the boundaries between vegetation types are defined. Firstly, temperate and tropical rainforest species can be seen as belonging to distinct forest types (*sensu* Clements 1916). Nix (1991) took this approach by separating species into different rainforest types and then relating these types to thermal response groups according to his growth model (Nix 1982). This approach could be taken further by only selecting species from climate extremes, such as humid tropical and cool-temperate rainforests. Secondly, the difference between temperate and tropical species can be seen as a climate gradient (*sensu* Whittaker 1975). This type of approach has been taken by Austin (1990) in their study of temperate eucalypts. Rainforest species of Australia, although forming distinct forest types, show a degree of overlap in their distributions and therefore climate. This thesis will use both types of analysis in order to test the hypothesis of Nix (1991) and to investigate trends in physiological responses across rainforest types with climate.

The first section of this thesis presents preliminary investigations of the study species. The section begins with Chapter 2, which contains a climate analysis that determines the major climatic differences among the species. Multivariate techniques were used to interpret climate data produced for site locations by the program ANUCLIM. Chapter 3 outlines a shading experiment performed to determine the photosynthetic shade-tolerance of the study species and to determine an appropriate irradiance for the main experiments

The second section investigates differences in physiological responses to temperature between tropical and temperate species. In Chapter 4, the plasticity of the photosynthetic response to temperature of the species is determined from leaves developed under several temperature regimes. In Chapter 5, the optimum temperatures for growth of the species are determined. Finally, Chapter 6 investigates the ability of the species to adjust to seasonal changes in temperature. This is determined by measuring the ability of leaves to acclimate their photosynthetic rate to new growth temperatures.

The third section investigates differences in physiological responses to vapour pressure deficit between tropical and temperate species. Chapter 7 investigates the photosynthetic responses to vapour pressure deficit of the species. An investigation of differences in growth strategies under contrasting water vapour pressure deficits follows in Chapter 8.

The final chapter presents a general discussion of what the findings revealed about differences between these tropical and temperate rainforest species. These findings are discussed in relation to the climate and phenology of the species, the evolutionary past of Australian rainforests, differences between temperate and tropical species and the assumptions of present climate models.

SPECIES SELECTION

Eight species was decided as the maximum practical number of species to investigate physiological differences among rainforest trees from different latitudes. Species were selected to represent the broad range of climates in which rainforests occur in eastern Australia. The eight species were selected to be:

(i) canopy dominants.

- This excluded species that never reach the upper canopy and therefore may not be adapted to the macroclimate. Previous research has shown that subcanopy species can have narrower photosynthetic responses to temperature than would be predicted from their macroclimate distribution (Read & Busby 1990).

(ii) found in lowland rainforests (< 500 m).

This excluded low latitude species that are restricted to high altitudes and are therefore exposed only to a cooler climate. In contrast, species that occur over a large range of altitudes were included.

(iii) from different families.

This ensured that similarities between species were not due simply to phylogenetic relatedness.

(iv) from the four broad rainforest types.

Selecting species from each of the rainforest types ensured a good representation of the range of rainforest species that occur in Australia.

(v) broad and narrow in latitudinal distribution.

A species with a broad latitudinal distribution and a species with a narrow latitudinal distribution were chosen within each rainforest type. This was an attempt to sample the range of response types within each rainforest type.

(vi) from similar ecological niches.

An attempt was made to choose species that had similar life strategies. Deciduous species, such as *Toona australis*, were avoided as their leaves are only adapted to the favourable season. Epiphytic species, such as species of *Ficus*, were avoided, as their establishment in the branches of trees means their microenvironment is different to other seedlings. Similarly, a preference was given to shade-intolerant species, which establish in large gaps, as they are exposed to the macroclimate throughout their lives.

The eight species selected meet all but two of these criteria. Attempts to obtain seedlings of more appropriate species from the field, seed stockists and nurseries were unsuccessful. Firstly, the two warm-temperate species used were both from the family Myrtaceae. Secondly, several of the species (*Acmena smithii*, *Castanospermum australe* and *Heritiera trifoliolata*) have been stated as shade-tolerant in the literature. However, only one or none of these shade-tolerant species was included in each rainforest type and all species are dominant species in the upper canopy. Furthermore, a shading experiment was performed to quantify the photosynthetic shade tolerance of each species (see Chapter 3).

Seed or seedlings of each species were collected from a forest where they were canopy dominants. Low altitude forests were chosen to avoid adaptations to cooler mountain climates. Details of the collection sites are given in Table 1.1. The distribution and ecology of the selected species are summarized in the following pages.

Table 1.1 Locations of the collection sites for the eight study species.

species	site	latitude	longitude	altitude
<i>Eucryphia lucida</i>	Stephenson's Rivulet	41° 10'	144° 57'	140 m
<i>Nothofagus cunninghamii</i>	Sumac	41°09'	145°01'	180 m
<i>Acmena smithii</i>	Royd Creek	37°25'	149°49'	200 m
<i>Tristaniopsis laurina</i>	Bull Creek, Mitchell River N. P.	37°42'	147°22'	150 m
<i>Sloanea woollsii</i>	Way Way State Forest	30° 43'	152° 43'	60 m
<i>Heritiera trifoliolata</i>	Bungdoozle Flora Reserve	28° 36'	152° 43'	540 m
<i>Castanospermum australe</i>	Petrie Creek, Nambour	26°38'	153°38'	40 m
<i>Alstonia scholaris</i>	Daintree River	16°13'	145° 52'	20 m

SPECIES DESCRIPTIONS

Eucryphia lucida (Labill.) Baillon

Family: Eucryphiaceae

Common name: Leatherwood

Latitudinal range: 41 - 43.5°S

Altitudinal range: 0 - 1000 m

Eucryphia lucida is a canopy dominant of cool-temperate rainforests in western and southwestern Tasmania (Figure 1.5a). It grows in association with the rainforest trees *Nothofagus cunninghamii*, *Atherosperma moschatum* and *Phyllocladus aspleniifolius* and in rainforests with a eucalypt overstorey (Boland *et al.* 1994; Jarman *et al.* 1994). The genus *Eucryphia* includes seven species, five of which occur at different latitudes in eastern Australia and two of which occur in Chile (Hill & Read 1987).

Mature trees of *E. lucida* can grow to a height of 30 m, with a DBH of 65-80 cm and a maximum stem life of 250 years (Read 1991). However, it is more commonly found as a medium sized canopy tree (height of 10-15 m, DBH of 50-60 cm, Boland, 1994 #584]. Adults leaves are simple, opposite, and 2.5-4.5 × 1.5-2.0 cm in size (Plate 1a, Boland *et al.* 1994). Trees flower predominantly in January and February but may continue into May.

Both vegetative and reproductive regeneration are common. Populations are considered to be continuously regenerating, with seedlings becoming more common on more open sites. Large numbers of seedlings are found in canopy gaps produced by falling trees (Read & Hill 1988b). Seed is winged and born in woody capsules, and is poorly dispersed usually falling one tree height away (Hickey *et al.* 1983; Read 1991; Boland *et al.* 1994).

Eucryphia lucida is found in areas with mild summers (mean^{monthly} maximum temperature^s of 20-22°C), cool winters (mean^{monthly} minimum temperature^s of 2-5°C), high rainfall (1000-2000 mm), poorer soils (fertility and drainage) and low fire frequency (>150 years, Jackson 1968; Boland *et al.* 1994; Read 1995). Therefore, it is difficult to determine the individual importance of these factors (Hill *et al.* 1988). Trees are found

a) *Eucryphia lucida*



b) *Nothofagus cunninghamii*



Plate 1 Foliage of the cool-temperate species. The white scale bar represents 1cm.

over a wide range of topography. Soils range from the intermediate fertility of xanthozems or yellow podsolics to the low fertility of shallow acid peats overlying quartzite or schist (Boland *et al.* 1994).

The physiology of *E. lucida* has been extensively studied in an attempt to explain its distribution in relation to climate and competition with associated trees. The gap requirement for seedling regeneration of *E. lucida* has been supported by reduced growth and photosynthetic capacity under shade conditions (Read 1985). *Eucryphia lucida* shows a greater frost resistance than temperate rainforest trees from lower latitudes (Read & Hiil 1988a;1989), maximum net photosynthesis at 18-21°C (Hill *et al.* 1988; Read & Busby 1990) and plant death after seven days of acclimation to a constant temperature of 32°C (Read & Busby 1990), consistent with its restriction to the cooler climate of western Tasmania. The dominance of *E. lucida* on poorer soils has been associated with poorer relative growth of *Nothofagus cunninghamii* on these soils (Read 1995).

***Nothofagus cunninghamii* (Hook.) Oersted**

Family: Fagaceae

Common name: Myrtle Beech

Latitudinal range: 37 - 43.5°S

Altitudinal range: 0 - 1500 m

Nothofagus cunninghamii is a canopy dominant of cool-temperate rainforest in western and northeastern Tasmania, and in disjunct areas of southern central Victoria (Figure 1.5b). It forms pure stands on optimal sites but usually grows in association with *Atherosperma moschatum*, *Eucryphia lucida* and the conifers *Athrotaxis selaginoides* and *Phyllocladus aspleniifolius*. The genus *Nothofagus* consists of 35 species found in Australia, Chile, New Caledonia, New Guinea and New Zealand reflecting its Gondwanic origin (Hill & Dettmann 1996). In addition to *N. cunninghamii*, only two of these species are found in Australia, *N. gunnii*, a deciduous species restricted to the wet mountains of Tasmania, and *N. moorei*, which is found in disjunct areas from northern New South Wales to southern Queensland (Poole 1987). *Nothofagus cunninghamii* is believed to have evolved from a *N. moorei*-like ancestor as a result of declining temperatures and/or precipitation before glaciation (Hill & Read 1987).

Mature trees of *N. cunninghamii* can grow to a height of 35-40 m, with a DBH of 200-250 cm and a maximum stem life of 400-450 years (Gilbert 1959; Read 1991). However, trees decrease in height with altitude and are found as stunted, spreading shrubs (1.5 m) at high altitude sites exposed to wind (Poole 1987; Boland *et al.* 1994). *Nothofagus cunninghamii* is also commonly found as an understorey tree (6-18 m) in *Eucalyptus* forests (Boland *et al.* 1994). The trunk is slightly buttressed, fluted and often swollen at the base with coppice shoots (Floyd 1989). Adult leaves are simple, alternate, with a bluntly toothed margin and $0.6-1.5 \times 0.4-1.0$ cm in size (Plate 1b, Boland *et al.* 1994). An annual growth flush occurs in spring and a second flush occurs occasionally in autumn (Howard 1973). Trees flower from November to January and fruit are ripe from March to May (Floyd 1989).

Seed is poorly dispersed, landing within one tree height and germinating readily (Hickey *et al.* 1983; Read & Hill 1985; Read 1991). Seedling establishment is successful in canopy gaps (Read & Brown 1996). Regeneration differs between populations in Tasmania and Victoria. In Tasmania, regeneration is from both vegetative shoots and seedlings and populations are considered self-replacing (Read & Hill 1988b). In contrast, the *Nothofagus* forests of Victoria have a lower frequency of seedlings and saplings (Read & Brown 1996). The higher fire frequency in Victoria has maintained structurally immature forests, which are not considered to be continuously regenerating (Howard 1973; Read 1992).

Nothofagus cunninghamii is found in areas with mild summers (mean ^{monthly} maximum temperature^s of 20-25°C), cold winters (mean ^{monthly} minimum temperature^s of 0-5°C), high rainfall (1100-2500 mm), soils of low to moderate fertility and slow fire frequency (>150 years, Jackson 1968; Boland *et al.* 1994). Soils are usually krasnozems, brown or yellowish podsolics, or brown earths developed on a range of parent materials, with best growth on krasnozems developed from basalt (Boland *et al.* 1994). *Nothofagus cunninghamii* is found over a wide range of topography in Tasmania but is restricted to river gullies and south-east facing slopes in Victoria (Howard & Ashton 1973). Fire is an important factor controlling the distribution of *N. cunninghamii* in Victoria with trees more likely to occur in old-growth forest, in gullies and in locations with high summer precipitation (Lindenmayer *et al.* 2000). Similarly, a climate analysis by Busby (1986)

showed the distributional limits of *N. cunninghamii* are correlated with mean summer precipitation. He also suggested that populations are migrating into favourable areas of northeast Victoria.

The physiology of *N. cunninghamii* has been extensively studied to explain its distribution and regeneration patterns. *Nothofagus cunninghamii* showed one of the widest photosynthetic responses to temperature (14-17°C) among the temperate rainforest species that have been studied and showed variation in the responses of different provenances, which may facilitate its wide distribution (Hill *et al.* 1988; Read & Busby 1990). Furthermore, *N. cunninghamii* showed greater frost resistance than *E. lucida* and northern temperate species (Read & Hill 1988a; 1989). Similarly, *N. cunninghamii* showed a higher frost resistance, a similar temperature for maximum photosynthesis but a greater tolerance of extreme temperatures, and a lower long-term water-use efficiency than *Nothofagus* species from New Guinea, which reflect differences in their climates (Read & Hope 1989; Read 1990; Read & Farquhar 1991). The reduced dominance of *N. cunninghamii* on poorer soils has been supported by a reduced relative growth rate of seedlings in the field and glasshouse experiments with declining soil fertility, with rates at low soil fertility similar to other canopy dominants (Read 1995). The canopy gap requirement for establishment of *N. cunninghamii* seedlings has been explained by reduced growth and photosynthetic capacity under shade conditions (Read 1985).

Acmena smithii (Poiret.) Merr. & Perry

(formerly known as *Eugenia smithii*)

Family: Myrtaceae

Common name: Lilly Pilly

Latitudinal range: 16 - 39°S

Altitudinal range: 0 - 1200 m

Acmena smithii is a canopy dominant in warm temperate rainforests of southern Australia whereas in northern Australia it is found scattered in or on the margins of subtropical rainforests (Ashton & Frankenberg 1976, Figure 1.5c). Common associates in warm temperate rainforest include *Elaeocarpus reticulatus*, *Pittosporum undulatum* and *Tristaniopsis laurina* in Victoria and *Ceratopetalum apetalum*, *Doryphora*

sassafras and *Eucryphia moorei* in New South Wales (Boland *et al.* 1994). Three races of *A. smithii* are recognised (typical, minor and rheophytic) according to leaf morphology, however even taxonomists find it hard to assign specimens (Hyland 1980). There are fifteen species of *Acmena* found in Australia, Southeast Asia, Philippines and the Solomon Islands. Six species are endemic to Australia, of which *A. smithii* is the only species found south of northern New South Wales (Floyd 1989; Boland *et al.* 1994).

Mature trees of *A. smithii* can grow up to 30 m tall but are usually medium sized tree of 20 m in mountain forests or reduced to shrubs in coastal areas (Hyland 1980; Boland *et al.* 1994). The trunk is usually up to 50 cm at breast height and generally without buttresses although occasionally on larger trees (Hyland 1980). Adult leaves are simple, opposite, entire, and 5-10 × 2-5 cm in size (Plate 2a, Boland *et al.* 1994). Seasonal growth occurs in a series of flushes commencing in early or midwinter and reaching a maximum in spring (Ashton & Frankenberg 1976). Trees flower between November and February and fruit ripen throughout winter (Boland *et al.* 1994).

Regeneration is from seed or vegetatively from either a lignotuber or coppices. Seed germinates in late spring to midsummer and does not survive summer drought or form a soil seed store. Seedling development is slow and the root system small, resulting in a dependence on reliable spring and summer precipitation or constantly moist soil. The ability to coppice after fire may be related to its occurrence on rainforest margins in New South Wales (Ashton & Frankenberg 1976). *Acmena smithii* is considered to be a climax species of warm temperate rainforests in the absence of disturbances such as fire or flooding (Melick & Ashton 1991).

Acmena smithii has a very wide distribution and therefore grows under a range of environments. Climates range from warm-temperate to tropical (mean maximum temperature of 26-32°C, mean minimum temperature of 5-15°C) with 1000-2000 mm of precipitation annually. However, some areas in Victoria receive as little as 700 mm (Boland *et al.* 1994). *Acmena smithii* shows no preference for any particular soil type, being found on serpentine, trachyte, basalt and sandstone (Hyland 1980). Trees tend to grow along the banks of small streams and rivers (Boland *et al.* 1994).

a) *Acmena smithii*



b) *Tristaniopsis laurina*



Plate 2 Foliage of the warm-temperate species. The white scale bar represents 1 cm.

Physiological work has been restricted to populations in southern Australia, where *A. smithii* is a dominant tree. The optimum temperature range for germination is 20-30°C, which reflects its germination during spring and summer (Ashton & Frankenberg 1976). *Acmena smithii* is considered shade-tolerant, showing low light compensation points for growth and photosynthesis (Ashton & Frankenberg 1976; Melick 1990a). However, *A. smithii* showed less photoinhibition when transferred from low to high light than *Doryphora sassafras*, a late successional species of warm-temperate rainforest (Roden *et al.* 1997). The growth of *A. smithii* shows little response to increasing nutrients, possibly explaining its occurrence over a range of soil types (Melick 1990a). Nine-month old seedlings were found to be resistant to both drought and waterlogging (Melick 1990b; 1990c).

Tristaniopsis laurina (Smith) Peter G. Wilson & Waterhouse
(formerly known as *Tristania laurina*)

Family: Myrtaceae

Common name: Water Gum, Kanuka

Latitudinal range: 25.5 - 38°S

Altitudinal range: 0 - 1000 m

Tristaniopsis laurina is found mainly along watercourses of the east coast and ranges of Australia from southern Victoria to southern Queensland (Figure 1.5d). It occurs as a canopy dominant in warm-temperate forests and also in subtropical rainforests.

Common associates include *Acmena smithii*, *Ceratopetalum apetalum* and *Doryphora sassafras*. *Tristaniopsis* is a genus of around 30 species, which are found in Australia, Burma, Indonesia, New Caledonia, New Guinea, Malaysia, the Philippines and Thailand. Only three of these species are found in Australia, with *T. collina* occurring from southern New South Wales to southeastern Queensland and *T. exiliflora* found along the east coast of Queensland (Boland *et al.* 1994).

Mature trees of *T. laurina* attain a height of 35 m and a stem diameter of 160 cm. Trees are often crooked, with channelled trunks and leaning out over streams. Adults leaves are simple, alternate, entire, and 5-14 cm long (Plate 2b). Trees flower from December to February and fruit is ripe from March to September (Floyd 1989).

Tristaniopsis laurina is able to regenerate vegetatively after flood or fire (Melick 1990c; Melick & Ashton 1991). *Tristaniopsis laurina* dominates flood-disturbed rainforests and is an early coloniser on disturbed riverbanks. In the absence of disturbance, *T. laurina* does not appear to regenerate and is likely to be replaced by more shade-tolerant species like *A. smithii* (Melick & Ashton 1991). Seed is small (5-6 mm long) and winged, shed over a short period in July and August, and remains viable for less than a year (Beardsell 1982; Wilson & Waterhouse 1982).

Tristaniopsis laurina has a similar wide distribution to *A. smithii* and therefore grows under a range of environments. Climates range from warm-temperate to tropical, with the warmest month having a maximum temperature of 25-28°C and the coldest month having a minimum temperature of 3-6°C and an annual precipitation of 1000-2000 mm.

Physiological work on *T. laurina* has involved comparisons with *A. smithii* that attempted to explain its dominance in riparian rainforest. *T. laurina* is considered to be less shade-tolerant than *A. smithii*, showing a higher light compensation point and maximum rate of photosynthesis, reflecting its establishment in high light conditions. Seedlings of *T. laurina* were found to have a higher nutrient demand than *A. smithii* and therefore would be more responsive to the nutrient pulse to river sands after flooding (Melick 1990a). Furthermore, *T. laurina* showed little physiological drought tolerance but greater tolerance of waterlogging than *A. smithii* (Melick 1990c; 1990b).

***Sloanea woollsii* F. Muell.**

Family: Elaeocarpaceae

Common name: Yellow Carabeen

Latitudinal range: 26 - 32°S

Altitudinal range: 30 - 1000 m

Sloanea woollsii is a dominant canopy species of subtropical rainforests along the central east coast of Australia but also occurs in warm-temperate rainforests (Figure 1.6a). Common associates are *Dendrocnide excelsa*, *Dysoxylum fraserianum*, *Toona australis* and *Orites excelsa* (Boland *et al.* 1994). *Sloanea* is a genus of 120 species found in Asia, Australia, and Central and South America (Harden 1990). There are four Australian species, two of which are restricted to Queensland (*S. langii* and

S. macbrydei) and two which are found in both northern New South Wales and Queensland (*S. australis* and *S. woollsii*, Boland *et al.* 1994).

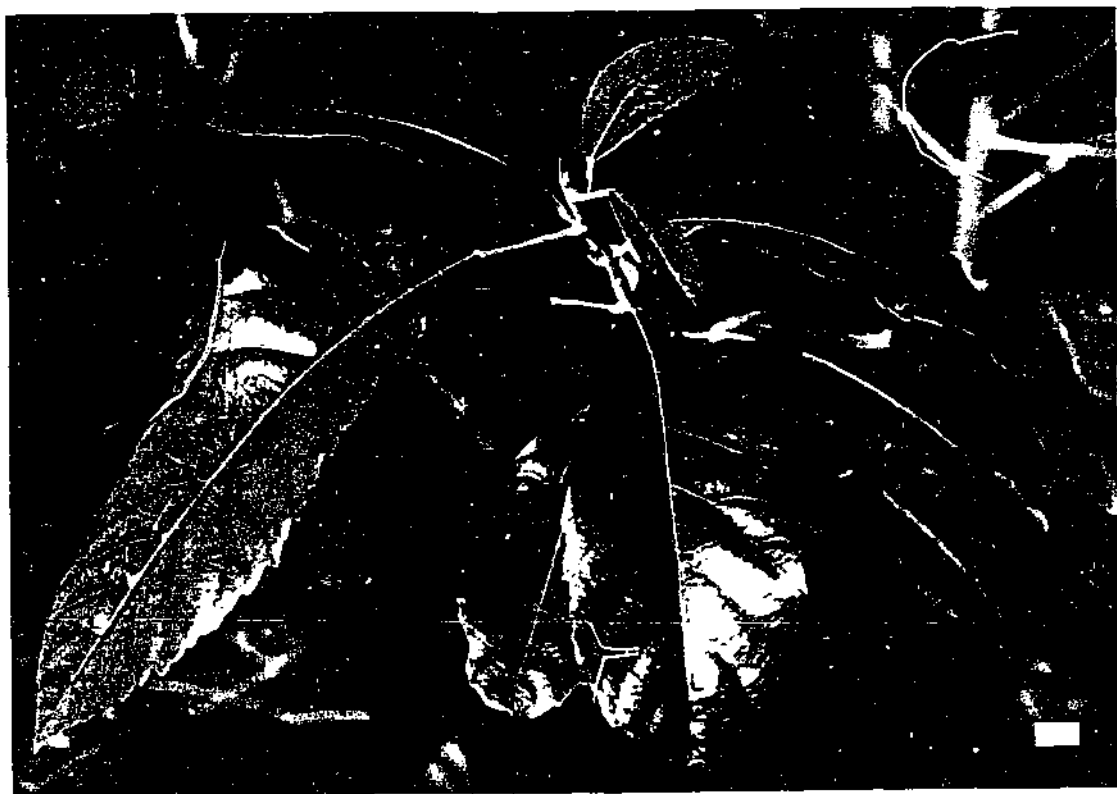
Mature trees are very tall rainforest trees attaining a height of 55 m and a stem diameter of 250 cm. The trunk has large buttresses, which extend 2-5 m up the trunk and are typically convex. Adult leaves are alternate, with toothed margins and $7.5-15.0 \times 2.5-3.0$ cm in size (Plate 3a). Trees flower from September to November and fruit are ripe March to July (Floyd 1989; Boland *et al.* 1994).

Regeneration is only from small seeds (0.6 cm) borne in spiny capsules covered by an aril. Mortality of seedlings was found to be density-dependent (Penfold & Lamb 1999) and saplings are found in lower numbers than adults (Debski *et al.* 2000). Therefore, *Sloanea woollsii* is considered a non-persistent dominant (*sensu* Connell & Lowman 1989) needing a catastrophic disturbance, such as a cyclone, to establish (Debski *et al.* 2000).

Sloanea woollsii is found in areas with warm climates, high rainfall (1000-2000 mm), low fire frequency, and well-drained and fertile soils. The warmest month of its climate has a maximum temperature of 26-30°C and the coldest month has a minimum temperature of 5-8°C. Populations are typically found on krasnozems and red earths derived from basalt and rich alluvium.

The only published work on the physiology of *S. woollsii* appears to be that of Yates (1995) on the foliar uptake of water. They found that detached branches were able to absorb water through their leaves, reducing water potential to saturation levels. This may be an important survival mechanism during the dry season when the foliage is commonly wet from fog or dew.

a) *Sloanea woollsii*



b) *Heritiera trifoliolata*



Plate 3 Foliage of the subtropical species. The white scale bar represents 1 cm.

Heritiera trifoliolata (F. Muell.) Kosterm.

(formerly known as *Argyrodendron trifoliolatum*)

Family: Sterculiaceae

Common name: White Booyong

Latitudinal range: 17 - 30°S

Altitudinal range: 0 - 1100 m

Heritiera trifoliolata occurs throughout lowland subtropical rainforests of northern New South Wales and southern Queensland (Figure 1.6b). Common associates include *Dendrocnide excelsa*, *Ficus microphylla*, *F. watkinsiana*, *Geissois benthamii*, *H. actinophyllum*, *Pseudoweinmannia lachnocarpa*, *Sloanea woollsii* and *Toona australis*. The genus *Heritiera* contains 35 species in tropical regions including Africa, Asia, Australia, the Indian subcontinent and Pacific Islands. The Australian species include five described species (*H. actinophyllum*, *H. littoralis*, *H. peralatum*, *H. polyandrum* and *H. trifoliolata*) and three or four undescribed species.

Trees can reach heights of 45 m and attain stem diameters of 200 cm. The trunk is cylindrical except at the base where it is strongly buttressed. Mature leaves are alternate, pinnate with three leaflets, entire and 7-14 cm long (Plate 3b). Trees flower from July to September and fruits are ripe from October to January (Floyd 1989).

Heritiera trifoliolata is considered to be a late successional species, with seedlings able to persist in narrow canopy gaps (Thompson *et al.* 1992b). Therefore, it is likely to be self-replacing. Fruits have a large wing (3 x 1.5 cm) and may be carried one and a half times the height of the tree (Floyd 1989).

Heritiera trifoliolata is found in areas with subtropical climates, high precipitation (1000-3000 mm) and rich soils (basalt or alluvial). The warmest month of its climate has a maximum temperature of 26-30°C and the coldest month has a minimum temperature of 5-10°C.

Physiological research on *H. trifoliolata* has focused on its ability to adapt to contrasting light environments of narrow canopy gaps and the upper canopy (Thompson *et al.* 1992b; Thompson *et al.* 1992a). This research showed that growth of

H. trifoliolata increased with increasing irradiance (30 to 535 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) and with higher nutrient levels under high irradiance. *Heritiera trifoliolata* showed a strong photosynthetic response to irradiance under all growth conditions and a higher maximum photosynthetic rate when grown under high irradiance (535 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$). In contrast, the photosynthetic response to irradiance was unaffected by nutrient levels (Thompson *et al.* 1992a). Leaf morphology and anatomy was less affected by low irradiance than shade-intolerant species (Thompson *et al.* 1992b).

***Castanospermum australe* Cunn. & C. Fraser ex Hook.**

Family: Papilionaceae

Common name: Black Bean

Latitudinal range: 12.5 - 30°S

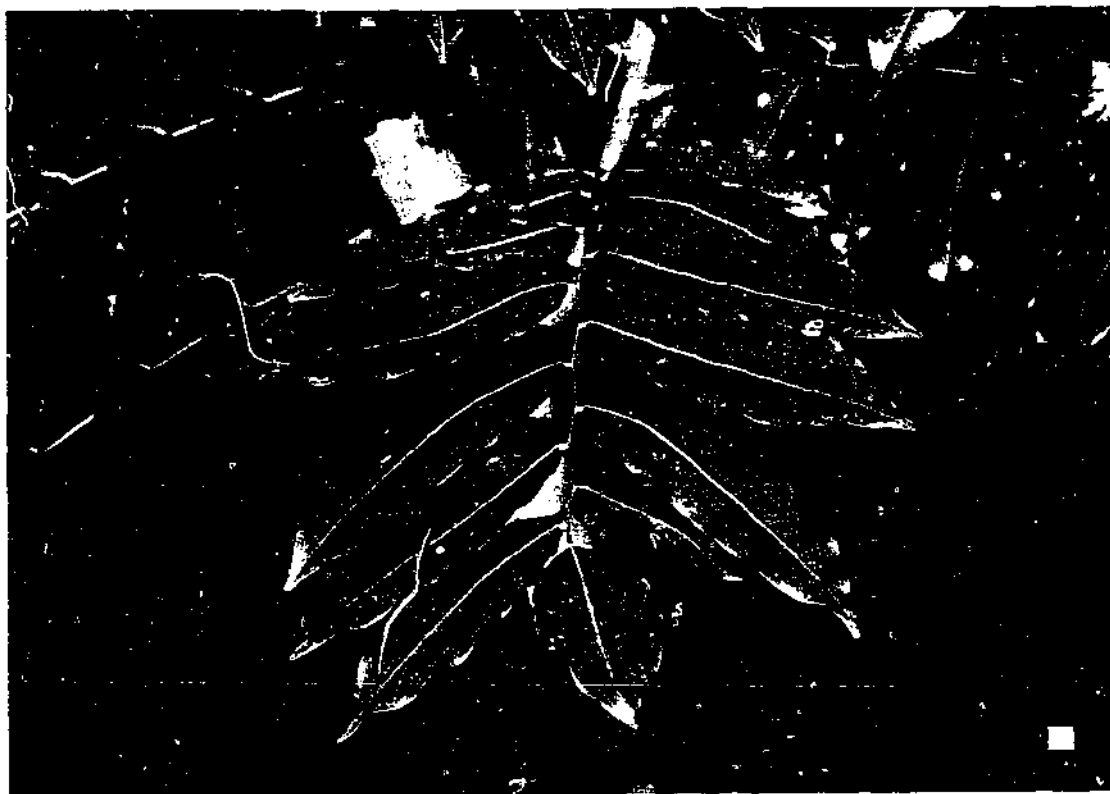
Altitudinal range: 0 - 1150 m

Castanospermum australe occurs in subtropical and tropical rainforests from northern New South Wales to northern Queensland (Figure 1.6c), as well as in New Caledonia and the New Hebrides. Common associates include various *Beilschmiedia obtusiflora*, *Cryptocarya hypospodia*, *Ficus* species, *Gervillea robusta*, *Nauclea orientalis*, *Podocarpus elatus*, *Streblus brunonianus*, *Syzygium floribundum* and *S. paniculatum*. *Castanospermum australe* is the sole species in the genus *Castanospermum* (Boland *et al.* 1994).

Mature trees can attain heights of 40 m with stem diameters of 120 cm. The trunk is cylindrical and not buttressed or flanged. Mature leaves are alternate, pinnate with 11-15 leaflets, entire, narrowly elliptical and 8-15 × 4-5 cm in size (Plate 4a). Flowers arise from leaf scars during October and November and fruits can be ripe throughout the year (Floyd 1989; Boland *et al.* 1994).

Regeneration is from large seeds (4 cm in diameter), which are borne in a large, heavy pod (18-25 × 5 cm). Seed is short-lived (four months) with germination delayed by a hard seed coat (Floyd 1989). Seedlings grow rapidly in the first month attaining a height of 10-20 cm but then slowing off. Survival rate of seedlings is high (57% after sixteen months) in both deep shade and canopy gaps (Osunkjoya *et al.* 1992).

a) *Castanospermum australe*



b) *Alstonia scholaris*



Plate 4 Foliage of the tropical species. The white scale bar represents 1 cm.

Specimens occur throughout the forest from the upper canopy to regenerating seedlings and saplings in the understorey and *C. australe* is therefore considered a climax species (Myers *et al.* 1987; Osunkoya *et al.* 1992).

Castanospermum australe is common along the banks of rivers in riverine rainforest and on level terraces on mountain sides (Floyd 1989). It is found in areas with subtropical to tropical climates, high rainfall (1000-3800) and rich soils. The warmest month of its climate has a maximum temperature of 30-35°C and the coldest month has a minimum temperature of 5-20°C. Soils are rich, consisting largely of river alluvia as well as deep loams on basalt (Boland *et al.* 1994).

The physiology of *C. australe* has been relatively well studied in comparison to other tropical rainforest trees of Australia. In the upper canopy, sun-exposed leaves of *C. australe* show inhibition of quantum yield and maximum net photosynthesis compared with shaded leaves (Pearcy 1986; cited in Osmond 1987). In contrast, leaves of the upper canopy have been shown to have higher maximum rates of photosynthesis than understorey leaves (Pearcy 1987). The photosynthetic response to temperature of leaves is broader, with a lower maximum, when grown under a cooler climate (Swanborough *et al.* 1998). Leaves in the canopy or in open grown trees show greater daily declines in leaf water potential, and lower leaf water and osmotic potentials at full hydration than understorey trees, with similar differences being shown in leaves from different canopy heights (Myers *et al.* 1987). The presence of arbuscular mycorrhiza improves the growth rate and phosphorus content of *C. australe* seedlings (Abu-Zeyad *et al.* 1999). Swanborough (1998) suggested that its wide distribution may be more a result of the food value of the large seed to aboriginals than its wide physiological tolerance.

***Alstonia scholaris* F. Muell.**

Family: Apocynaceae

Common name: White Cheesewood

Latitudinal range: 10.5 - 21.5°S

Altitudinal range: 0 - 1300 m

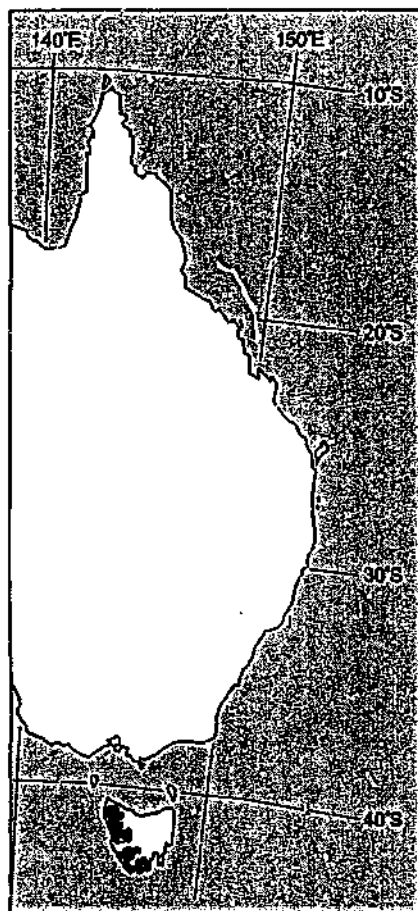
Alstonia scholaris is a very common canopy tree in tropical rainforests from central to northern Queensland in Australia (Figure 1.6d), as well as New Guinea, throughout Southeast Asia, India and Sri Lanka and Africa. It grows in association with a large number of trees, including *Castanospermum australe* (Doran & Turnbull 1997). The genus *Alstonia* consists of about 45 species in Africa, Asia, Australia, Malesia and Melanesia. Six species are found across northern Australia (*A. actinophylla*, *A. constricta*, *A. linearis*, *A. muelleriana*, *A. scholaris* and *A. spectabilis*, Forster 1992).

Mature trees can attain heights of 40 m and a stem diameter of 1 m. The bole is strongly fluted and flanges can extend 10 m up the trunk (Boland *et al.* 1994; Doran & Turnbull 1997). When stems or leaves are broken a milky exudate is released. Mature leaves are formed in whorls of 4-8 leaves, entire and 7.5-15.5 × 3.0-5.0 cm in size (Plate 4b). Trees flower from October to December. Fruits consist of two narrow, pendulous follicles (up to 30 cm long) and seed are 0.5 cm long with a 1 cm long group of fringing hairs (Boland *et al.* 1994).

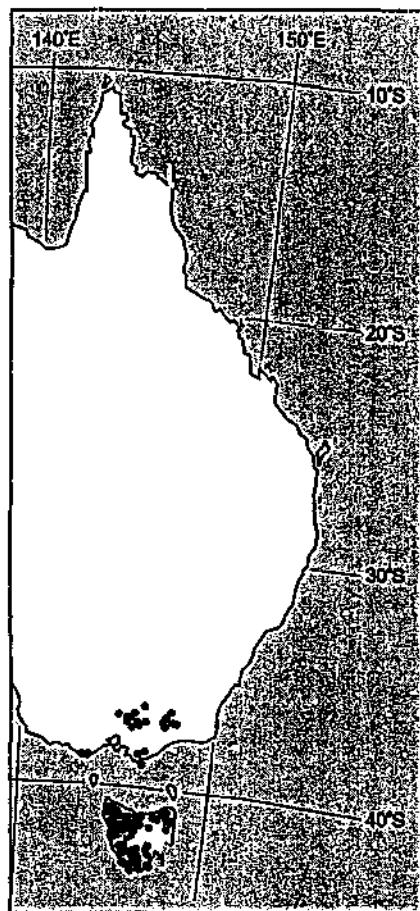
Alstonia scholaris is found areas with tropical climates, high rainfall (1100-3800 mm) and various soils. The warmest month of its climate has a maximum temperature of 30-32°C and the coldest month has a minimum temperature of 12-22°C. Soils range from skeletal to deep well-drained loams on basalt, granite, metamorphic rocks, alluvium and laterite outcrops (Boland *et al.* 1994).

Previous physiological research on *A. scholaris* has not focused on its ecology in rainforests. Instead, studies on *A. scholaris* have been in relation to air pollution (eg. Khan *et al.* 1989; Jabeen & Abraham 1998), the medicinal properties of its alkaloids (eg. Kam *et al.* 1997), pests and diseases that damage its wood (eg. Santhakumaran 1992; Singh *et al.* 1993), its primitive branching pattern (Mueller 1985) and the development of laticifers (Meena *et al.* 1990). In addition, *A. scholaris* has been found to be a fast-growing tree in plantations on various soils types, as long as water is adequate (Doran & Turnbull 1997).

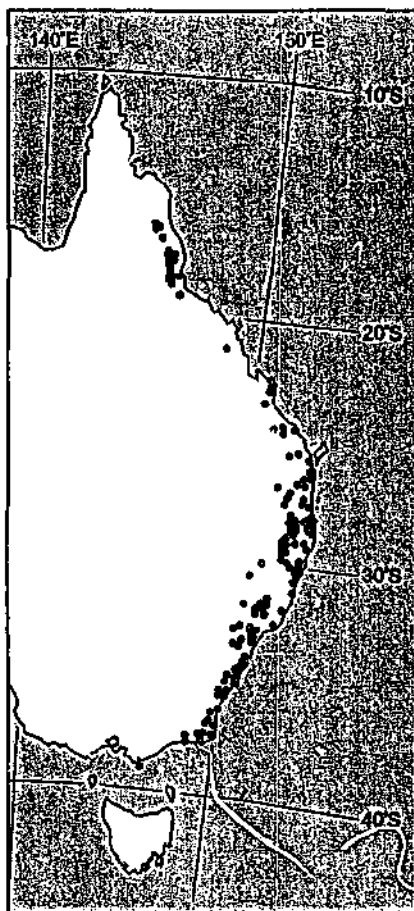
a) *Eucryphia lucida*



b) *Nothofagus cunninghamii*



c) *Acmena smithii*



d) *Tristaniopsis laurina*

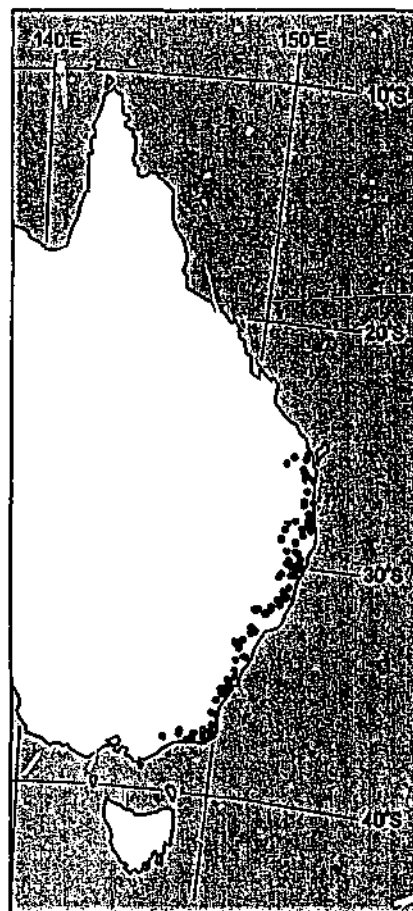
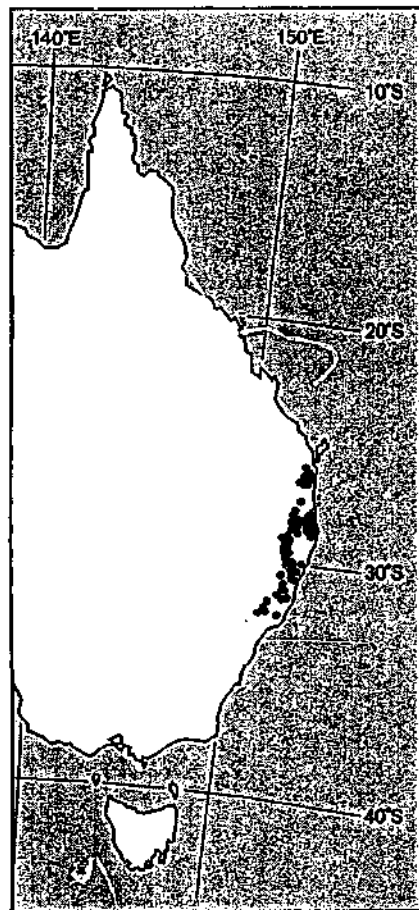
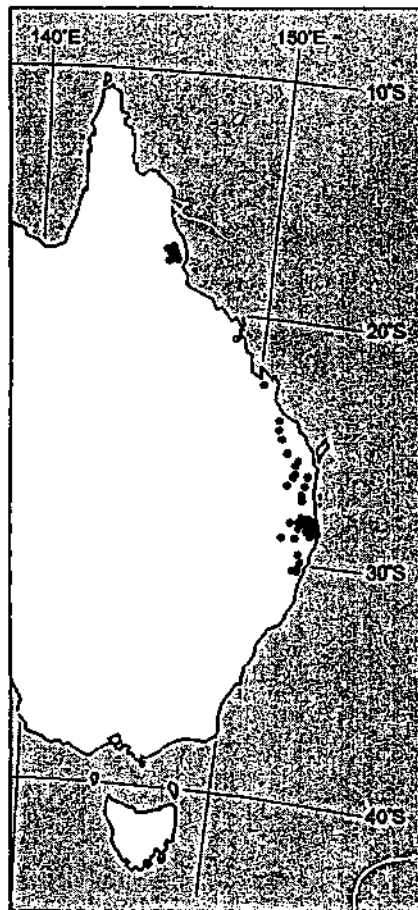


Figure 1.5 Distribution maps for the temperate rainforest species.

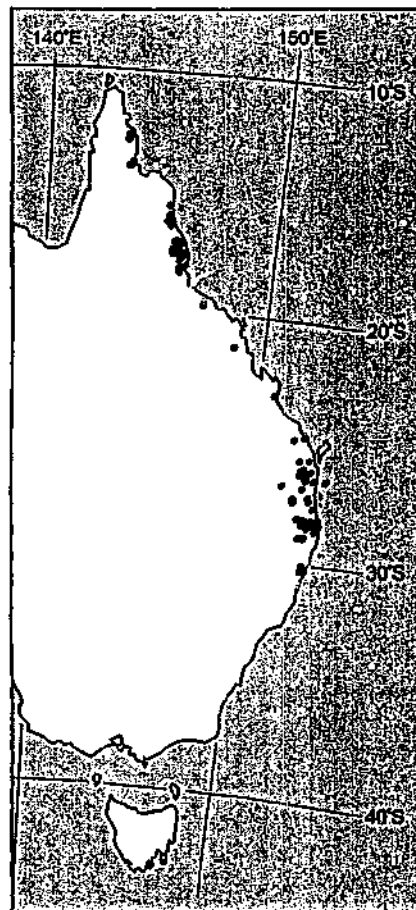
a) *Sloanea woollsi*



b) *Heritiera trifoliolata*



c) *Castanospermum australe*



d) *Alstonia scholaris*



Figure 1.6 Distribution maps for the tropical rainforest species.

Part A

Characterization of species

CHAPTER 2

Climate Analysis

Australian rainforests are found from the humid tropics of the north to the cool-temperate regions of the south. Over this latitudinal range mean annual temperature changes from 27°C in the north to 10°C in the south (Figure 2.1). Topography and cloud cover cause significant lowering of temperatures along the eastern edge of Australia (Adam 1992). Consequently, cooler climates also exist at high altitudes in the tropics. Similarly, the incidence of frost increases with increasing latitude and altitude (Bureau of Meteorology 1989). In addition to lower temperatures at high latitudes, there is also an increase in the seasonality of temperature with increasing latitude (Nix 1982).

Rainforests are commonly found in regions that receive annual precipitation of more than 1500 mm (Francis 1981). However, some rainforest patches are found in areas with precipitation as low as 800 mm per year (Webb & Tracey 1994). Seasonality of precipitation changes with latitude from winter-dominant in the south to uniform at mid-latitudes and summer-dominant in the north (Figure 2.2). There is considerable variability in precipitation among years and few areas of rainforest have escaped intermittent drought during the period of climate records (Adam 1992).

The relationship between climate and the distribution of rainforest species in Australia has been investigated by several authors. Both the structural and floristic classifications of Australian rainforests were found to correspond with thermal regions of Australia (Webb 1959; Webb *et al.* 1984). Nix (1991) related his thermal response groups (Nix 1982) to the structural types of Webb (1959) and consequently proposed that the distribution of rainforest types was explained by differences in growth responses to temperature of their component species. Relationships between these various classifications of Australian rainforest are shown in Table 2.1. Several studies, including that of Nix (1991), have used the BIOCLIM program (Houlder *et al.* 1999) to determine climate profiles of taxa from location data. Studies of climate profiles of

temperate rainforest trees have found their distributional limits are related to summer temperature and precipitation (Busby 1986; Read & Busby 1990). In contrast, studies of tropical rainforests have shown precipitation to be more important than temperature to the distribution of species (Russel-Smith 1991; Mackey 1993a,1993b).

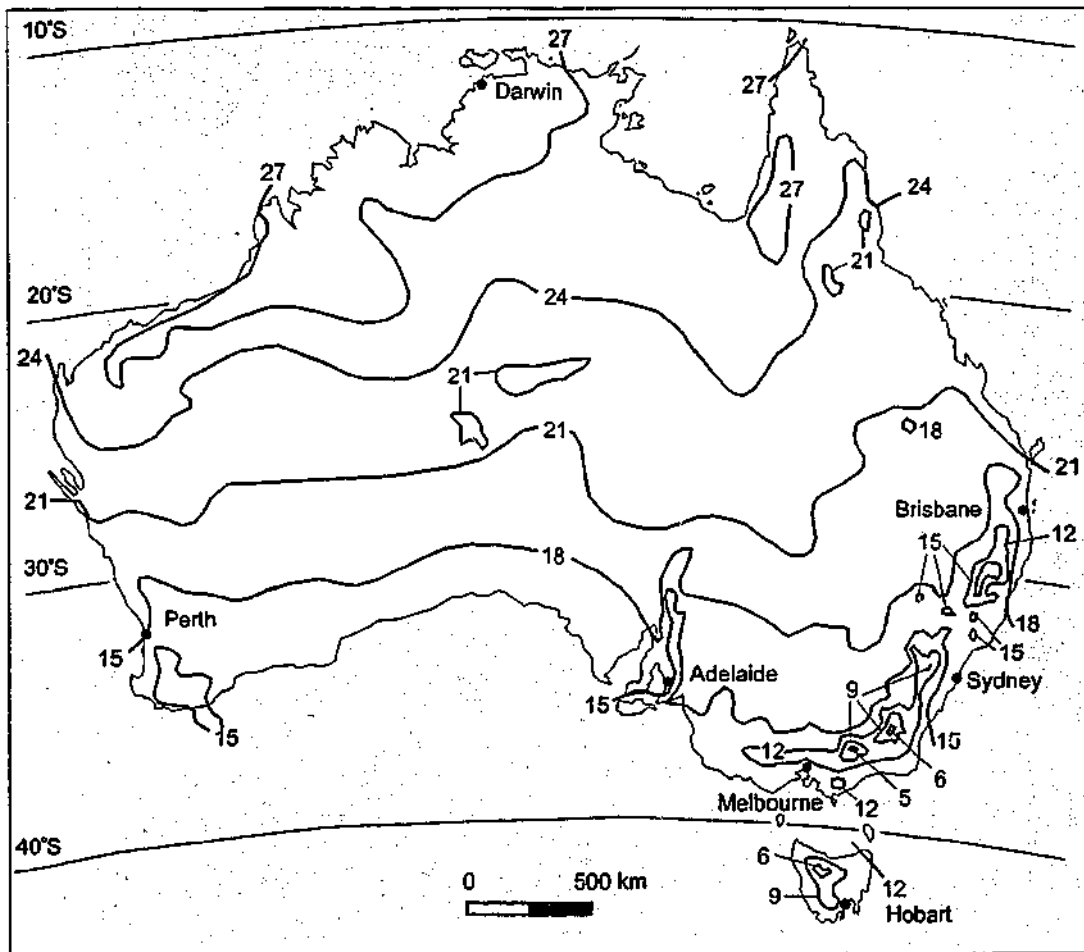


Figure 2.1 Map of mean annual temperature in Australia with isotherms in degrees Celsius (adapted from Bureau of Meteorology 1989).

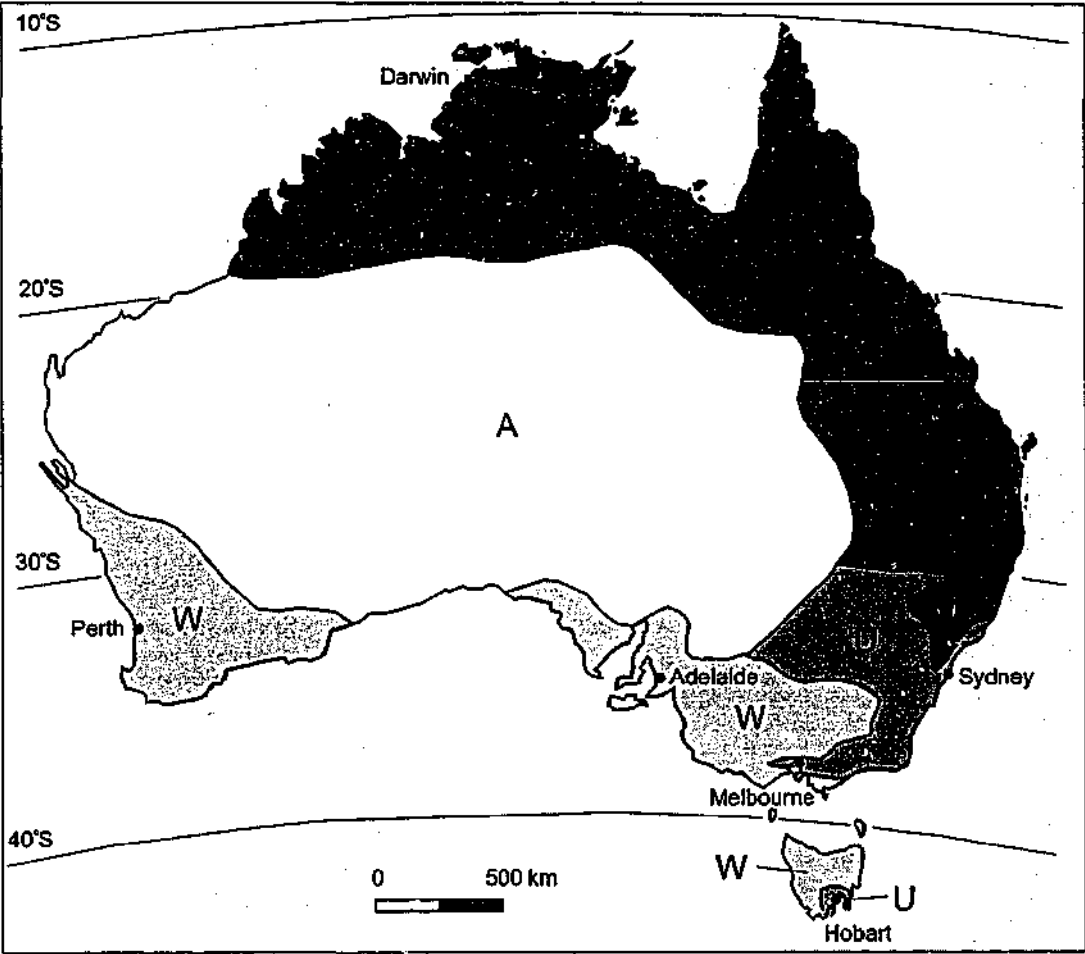


Figure 2.2 Map of the seasonality of precipitation in Australia showing the summer (S), uniform (U), winter (W) and arid (A) rainfall zones (adapted from Bureau of Meteorology 1989).

Table 2.1 Relationships among the various classification systems of Australian rainforest.

Habitat type (Webb 1968)	Structural type (Webb 1968)	Floristic type (Webb <i>et al.</i> 1984)	Thermal type (Nix 1991)
Tropical	evergreen mesophyll vine forest	B ₂	megatherm
	semi-deciduous notophyll/mesophyll vine forest	B ₁	
	deciduous microphyll vine thicket	B ₃	
Subtropical	evergreen notophyll vine forest	A ₁	mesotherm
	evergreen notophyll/microphyll vine forest	C ₁	
	semi-evergreen microphyll vine forest	C ₂	
Warm-temperate	evergreen microphyll fern forest	A ₂	microtherm
Cool-temperate	evergreen microphyll/nanophyll moss forest	A ₃	microtherm

The broad patterns of species distribution across the rainforests of Australia are likely to be determined by climate. Firstly, the broad distribution of rainforest types has been correlated with temperature (Webb 1968). Secondly, precipitation, as well as soils, tend to determine species distributions within thermal regions (Webb 1968; Floyd 1990). By comparison, the current boundary between rainforest and sclerophyll forests in Australia appears to be determined primarily by fire frequency (Bowman 2000). However, fire frequency is determined by interactions among climate, soil fertility and vegetation type (Jackson 1968). Therefore, it is difficult to determine the primary cause of current rainforest boundaries.

The aim of this chapter is to quantify differences in the climates of the study species that may be determining their distributions. The specific aims were:

1. to determine the climate profiles of the species.
2. to determine which climate variables best describe the difference among the climates of the species.
3. to quantify the difference in variability (diurnal, day-to-day and seasonal) of climate between temperate and tropical climates.

The differences in climate among the species will be discussed in relation to other studies and possible physiological mechanisms that determine their distribution.

METHODS

An extensive collection of site locations (latitude, longitude and altitude) was made for each of the study species from the relevant organisations in Australia. Location records were supplied by the Atherton Herbarium, Australian National Herbarium, Australian Tree Seed Centre, National Herbarium of Victoria, National Herbarium of New South Wales, Queensland D.P.I. Forestry Tree Seed Centre, Queensland Herbarium, State Forests of New South Wales, Tasmanian Herbarium and the University of New England Herbarium. For each species, any record within a one-minute grid (latitude \times longitude) and 200 m of altitude of another record was excluded to remove some of the sampling bias in this type of data. The ESOCCLIM subprogram of ANUCLIM 5.0 (previously BIOCLIM, Houlder *et al.* 1999) was then used to obtain monthly averages of several climate variables for each site (variables are listed in Table 2.2). From these climate variables, four additional climate variables (abbreviations given in square brackets) were calculated as follows:

$$\text{mean temperature [MT]} = (\text{MaxT} + \text{MinT}) / 2 \quad (\text{equation 2.1})$$

$$\begin{aligned} &\text{mean VPD [MV]} \\ &= 0.61 e^{(17.27\text{DBT9} / (\text{DBT9} + 237.3))} - 0.61 e^{(17.27\text{DPT9} / (\text{DPT9} + 237.3))} \quad (\text{equation 2.2}) \end{aligned}$$

$$\begin{aligned} &\text{maximum VPD [MaxV]} \\ &= 0.61 e^{(17.27\text{DBT3} / (\text{DBT3} + 237.3))} - 0.61 e^{(17.27\text{DPT3} / (\text{DPT3} + 237.3))} \quad (\text{equation 2.3}) \end{aligned}$$

$$\text{water balance [WB]} = P - E \quad (\text{equation 2.4})$$

Monthly values of the climate variables obtained from ANUCLIM 5.0 and the four variables were used to calculate a series of climate variables. The abbreviations, definitions and calculation of these climate variables are given in Table 2.3. A further climate variable, moisture index, was calculated using BIOCLIM, a subprogram of ANUCLIM 5.0. The moisture index is a measure of soil moisture, which ranges from dry (0) to saturated (1). A detailed explanation of the calculation of the moisture index

is given by Houlder *et al.* (1999). For each species, the mean values of these climate variables across sites were calculated to determine the mean climate profile.

Table 2.2 Climate variables that were obtained from the program ANUCLIM 5.0 with their measurement units and abbreviations.

Variable	Units	Abbreviation
maximum temperature	°C	MaxT
minimum temperature	°C	MinT
precipitation	mm/month	P
evaporation	mm/month	E
raindays	days	RD
dew point temperature at 9AM	°C	DPT9
dew point temperature at 3PM	°C	DPT3
dry bulb temperature at 9AM	°C	DBT9
dry bulb temperature at 3PM	°C	DPT3

Table 2.3 Climate variables used in the climate analysis.

Abbreviation	Description	Calculation
<u>Temperature variables</u>		
MTA	annual mean temperature	\bar{x} (MT)
MTR	annual range of mean temperature	$\max(\text{MT}_i) - \min(\text{MT}_i)$
MTS	seasonality of mean temperature	coefficient of variation (MT)
MTHi	highest monthly mean temperature	$\max(\text{MT}_i)$
MTLo	lowest monthly mean temperature	$\min(\text{MT}_i)$
MTW	mean temperature of wettest month	MT of $\max(P_i)$
MTD	mean temperature of driest month	MT of $\min(P_i)$
MaxTA	annual maximum temperature	\bar{x} (MaxT)
MaxTR	annual range of maximum temperature	$\max(\text{MaxT}_i) - \min(\text{MaxT}_i)$
MaxTS	seasonality of maximum temperature	coefficient of variation (MaxT)
MaxTHi	highest monthly maximum temperature	$\max(\text{MaxT}_i)$
MaxTLo	lowest monthly maximum temperature	$\min(\text{MaxT}_i)$
MaxTW	maximum temperature of wettest month	MaxT of $\max(P_i)$
MaxTD	maximum temperature of driest month	MaxT of $\min(P_i)$
MinTA	annual minimum temperature	\bar{x} (MinT)
MinTR	annual range of minimum temperature	$\max(\text{MinT}_i) - \min(\text{MinT}_i)$
MinTS	seasonality of minimum temperature	coefficient of variation (MinT)
MinTHi	highest monthly minimum temperature	$\max(\text{MinT}_i)$
MinTLo	lowest monthly minimum temperature	$\min(\text{MinT}_i)$
MinTW	minimum temperature of wettest month	MinT of $\max(P_i)$
MinTD	minimum temperature of driest month	MinT of $\min(P_i)$
<u>Moisture variables</u>		
PA	annual mean precipitation	\bar{x} (P)
PR	annual range of precipitation	$\max(P_i) - \min(P_i)$
PS	seasonality of precipitation	coefficient of variation (P)
PH	precipitation of hottest month	P of $\max(\text{MaxT}_i)$
PC	precipitation of coldest month	P of $\min(\text{MaxT}_i)$
PHi	highest monthly precipitation	$\max(P_i)$
PLo	lowest monthly precipitation	$\min(P_i)$
PSW	summer / winter precipitation	$\sum(P_1, P_2, P_{12}) / \sum(P_6, P_7, P_8)$
PTOT	total annual precipitation	$\sum(P_i)$
RDA	annual mean raindays	\bar{x} (RD)
RDR	annual range of raindays	$\max(\text{RD}_i) - \min(\text{RD}_i)$
RDS	seasonality of raindays	coefficient of variation (RD)
RDH	raindays of hottest month	RD of $\max(\text{MaxT}_i)$
RDC	raindays of coldest month	RD of $\min(\text{MaxT}_i)$
RDHi	highest monthly raindays	$\max(\text{RD}_i)$
RDL o	lowest monthly raindays	$\min(\text{RD}_i)$
RDSW	summer raindays / winter raindays	$\sum(\text{RD}_1, \text{RD}_2, \text{RD}_{12}) / \sum(\text{RD}_6, \text{RD}_7, \text{RD}_8)$
RDTOT	Annual total raindays	$\sum(\text{RD}_i)$

Table 2.3 (cont.) Climate variables used in the climate analysis.

Abbreviation	Description	Calculation
Moisture variables (cont.)		
EA	annual mean evaporation	\bar{x} (E)
ER	annual range of evaporation	$\max(E_i) - \min(E_i)$
ES	seasonality of evaporation	coefficient of variation (E)
EH	evaporation of hottest month	E of $\max(\text{MaxT}_i)$
EC	evaporation of coldest month	E of $\min(\text{MaxT}_i)$
EHi	highest monthly evaporation	$\max(E_i)$
ELo	lowest monthly evaporation	$\min(E_i)$
ESW	summer evaporation / winter evaporation	$\sum(E_1, E_2, E_{12}) / \sum(E_6, E_7, E_8)$
MVA	annual mean VPD	\bar{x} (MV)
MVR	annual range of mean VPD	$\max(MV_i) - \min(MV_i)$
MVS	seasonality of mean VPD	coefficient of variation (MV)
MVH	mean VPD of hottest month	MV of $\max(\text{MaxT}_i)$
MVC	mean VPD of coldest month	MV of $\min(\text{MaxT}_i)$
MVHi	highest monthly mean VPD	$\max(MV_i)$
MVLo	lowest monthly mean VPD	$\min(MV_i)$
MaxVA	annual mean maximum VPD	\bar{x} (MaxV)
MaxVR	annual range of maximum VPD	$\max(\text{MaxV}_i) - \min(\text{MaxV}_i)$
MaxVS	seasonality of maximum VPD	coefficient of variation (MaxV)
MaxVH	maximum VPD of hottest month	MaxV of $\max(\text{MaxT}_i)$
MaxVC	maximum VPD of coldest month	MaxV of $\min(\text{MaxT}_i)$
MaxVHi	highest monthly maximum VPD	$\max(\text{MaxV}_i)$
MaxVLo	lowest monthly maximum VPD	$\min(\text{MaxV}_i)$
WBA	annual mean water balance	\bar{x} (WB)
WBR	annual range of water balance	$\max(\text{WB}_i) - \min(\text{WB}_i)$
WBS	seasonality of water balance	coefficient of variation (WB)
WBH	water balance of hottest month	WB of $\max(\text{MaxT}_i)$
WBC	water balance of coldest month	WB of $\min(\text{MaxT}_i)$
WBHi	highest monthly water balance	$\max(\text{WB}_i)$
WBLo	lowest monthly water balance	$\min(\text{WB}_i)$
MIA	annual mean moisture index	calculated using the BIOCLIM subprogram of ANUCLIM 5.0
MIR	annual range of moisture index	
MIS	seasonality of moisture index	
MIHQ	moisture index of hottest quarter	
MICQ	moisture index of coldest quarter	
MIHi	highest quarterly moisture index	
MILo	lowest quarterly moisture index	

Multivariate analysis

Multivariate analyses were performed on the climate variables calculated for the site locations of the species. These analyses were performed on three different data sets:

- (1) all climate variables listed in Table 2.3.
- (2) temperature variables (descriptors of mean temperature, maximum temperature and minimum temperature).
- (3) moisture variables (descriptors of precipitation, evaporation, raindays, mean VPD, maximum VPD, water balance and moisture index).

For each of these data sets, a similarity matrix was calculated. The similarity coefficients recommended for quantitative descriptor variables, such as climate data, are Manhattan metric and Euclidean distance (Legendre & Legendre 1998). The Gower metric was used as it was recommended (P. R. Minchin, pers. comm.) and has been used for climate data previously (Kohlmann *et al.* 1988). The Gower metric is the Manhattan metric applied to data in which each variable has been standardized to range from zero to one. As each climate variable has different units, this standardization is essential to avoid the analysis being dominated by those variables that have the largest values (P. R. Minchin, pers. comm.). The RELATE procedure described by Clarke and Ainsworth (1993), which involves calculating a matching coefficient (ρ) and a simple permutation test was used to measure the agreement between the similarity matrices produced from the three data sets.

The Analysis of Similarity procedure (Clarke 1988) was used to determine if differences in the climatic composition of sites existed among groups. The groups analyzed were the individual species, rainforest types and climatic groups as defined in Table 2.4. Groups were considered significantly different when both the R statistic was greater than 0.05 and the chance of getting a random R statistic greater than the observed was less than 5% ($p < 0.05$). This is because when a large number of replicates are used, as in this analysis ($n > 60$), it is possible to get an R statistic significantly different from zero yet inconsequently small (Clarke & Warwick 1994).

Table 2.4 Groupings of the rainforest species used in data analysis.

Climate group	Rainforest type	Species
Temperate	Cool-temperate	<i>Eucryphia lucida</i> <i>Nothofagus cunninghamii</i>
	Warm-temperate	<i>Acmena smithii</i> <i>Tristaniaopsis laurina</i>
Tropical	Subtropical	<i>Sloanea woollsii</i> <i>Heritiera trifoliolata</i>
	Tropical	<i>Castanospermum australe</i> <i>Alstonia scholaris</i>

The similarity matrices were used to create ordination plots of the site locations using non-metric multi-dimensional scaling (NMDS). Studies that have compared ordination methods have recommended the use of NMDS over other techniques, such as principal coordinates analysis (PCA), due to a lack of distortion of environmental gradients and a lack of assumptions about these gradients (Kenkel & Orloci 1986; Minchin 1987). Rotational correlations (Dargie 1984) were used to assist in the interpretation of the NMDS ordination plots. Firstly, each climate variable was regressed against the coordinates of the two-dimensional ordination using the following equation:

$$V = ax + by + c \quad (\text{equation 2.5})$$

where V is the variable, x and y are the coordinates of sites within the NMDS plots, and a , b and c are fitting parameters. The $r^2_{\text{corrected}}$ values from the regressions were used to determine which variables were most highly-correlated with the NMDS ordination plot.

The angle of rotation (α) needed to rotate the ordination configuration to maximum correlation with V is then given by:

$$\alpha = \tan^{-1} (b/a) \quad (\text{equation 2.6})$$

The values of α were used to show the direction of increase for these variables.

Climate variability within years

To estimate the differences in day-to-day variability of the different climates experienced by rainforest species of Australia, daily climate data were obtained for six different locations (Table 2.5). The weather stations were chosen to be evenly spaced latitudinally. However, two stations were chosen around the latitude of 37-38°S to represent the differences between the continental (Nocjee) and maritime (Merimbula) climates in which rainforests grow in this region. The data obtained from the Bureau of Meteorology consisted of daily measurements of maximum temperature, minimum temperature, precipitation, dry bulb temperature at 3PM, and dew point temperature at 3PM for the years 1995 and 1996. From these data, the additional variable of maximum daily VPD was calculated using equation 2.3. The day-to-day variation in several of these climate variables was calculated as the weekly standard deviation of daily values (WSD). The mean values of WSD for each year or each season of each year were then used in one-way ANOVA to compare the locations.

The diurnal variation in temperature was also calculated from the monthly values of maximum and minimum temperature obtained from ANUCLIM 5.0. The mean values of diurnal temperature range for each species were regressed against their mean latitudinal origin.

Table 2.5 Locations selected to represent the variability in climate experienced by rainforests at different latitudes.

Location	Latitude	Longitude	Altitude
Strahan	42°09'S	145°20'E	7 m
Noojee	37°54'S	145°58'E	270 m
Merimbula	36°55'S	149°54'E	2 m
Coffs Harbour	30°19'S	153°07'E	21 m
Rockhampton	23°23'S	150°30'E	10 m
Cairns	16°52'S	145°45'E	2 m

RESULTS

Mean climate profiles

The mean climate profiles of the species are shown in Table 2.6. Most of the variables describing mean, maximum and minimum temperatures increased from the species with highest mean latitude (*Eucryphia lucida*) to the species with the lowest mean latitude (*Alstonia scholaris*, Table 2.6). However, the annual range of maximum temperature was smallest in the tropical species whereas the annual range of minimum temperature was smallest in the cool-temperature species. Furthermore, the seasonality of temperature experienced by the species was largest in the cool-temperate species.

The climate profiles of all the species showed high annual precipitation (>1000 mm), with *E. lucida* and *A. scholaris* showing the highest annual precipitation (~2000 mm), and the warm-temperate species *Acmena smithii* and *Tristaniopsis laurina* showing the lowest annual precipitation (~1300 mm, Table 2.6). The tropical species showed the greatest range of monthly precipitation, the greatest seasonality of precipitation and the highest monthly precipitation among the species. The amount of precipitation in summer compared with winter increased with the decreasing latitude of the species. The cool-temperate species (*E. lucida* and *Nothofagus cunninghamii*) were the only species to show a mean winter-dominant precipitation. However, the distribution of all the temperate species included locations that have winter-dominant precipitation. There were many similarities between the trends in raindays and precipitation (Table 2.6). For example, the tropical species showed greater seasonality in raindays and the cool-temperate species were the only species to show a greater amount of raindays in winter than summer. In contrast to the trends in precipitation, the cool-temperate species showed the greatest annual number of raindays, the greatest number of raindays in a month and a similar range of raindays to the tropical species.

The majority of the evaporation variables increased with decreasing latitudinal origin of the species (Table 2.6). In contrast, the seasonality of evaporation increased with increasing latitudinal origin of the species. The highest ranges of evaporation were shown by the warm-temperate species. All species showed a proportionally higher evaporation during summer than winter. However, the cool-temperate species showed

the greatest proportional increase in evaporation from winter to summer. The trends in variables of mean VPD and maximum VPD were similar to those of evaporation, with the tropical species showing greater values than the temperate species (Table 2.6). In addition, the cool-temperate species showed greater seasonality in mean VPD and maximum VPD than the other species.

The cool-temperate species showed the highest annual mean water balance among the species (Table 2.6). In addition, the cool-temperate species showed the highest values of water balance during the coldest month reflecting their winter dominant precipitation. The cool-temperate species showed the highest values of the moisture index annually, for the lowest month and during the coldest quarter (Table 2.6). The tropical species showed the greatest range and seasonality of the moisture index.

The seasonal differences in the moisture climates of the species are shown by linear regressions of the mean values of the moisture variables during winter and summer against the mean latitude of the species (Figure 2.3). The tropical species receive higher precipitation during summer whereas the temperate species receive higher precipitation during the winter. The tropical species experience higher evaporation rates and vapour pressure deficits than the temperate species throughout the year. Water balance is higher for the temperate species than the tropical species in winter whereas it is the reverse in summer. In contrast, values of the moisture index are higher for the temperate species than the tropical species in winter but temperate and tropical species cover a similar range during summer.

Table 2.6 Mean climate profiles for the species derived from output of ANUCLIM 5.0. Values are means of n sites with standard errors in brackets. Species are presented in order from highest to lowest latitudinal origin from left to right.

Variable	<i>E. lucida</i> ($n = 112$)	<i>N. cunninghamii</i> ($n = 354$)	<i>T. laurina</i> ($n = 137$)	<i>A. smithii</i> ($n = 291$)	<i>S. woollsii</i> ($n = 140$)	<i>H. trifoliolata</i> ($n = 98$)	<i>C. australe</i> ($n = 123$)	<i>A. scholaris</i> ($n = 61$)
Mean temperature (°C)								
annual mean	9.3 (0.1)	9.2 (0.1)	16.2 (0.2)	16.4 (0.1)	15.8 (0.2)	18.3 (0.2)	20.7 (0.2)	23.0 (0.3)
annual range	8.1 (0.1)	9.3 (0.1)	10.8 (0.1)	10.6 (0.1)	11.1 (0.1)	9.7 (0.1)	8.7 (0.2)	7.3 (0.2)
seasonality	0.33 (0.01)	0.38 (0.01)	0.25 (0.00)	0.25 (0.00)	0.27 (0.00)	0.20 (0.00)	0.16 (0.00)	0.12 (0.00)
highest month	13.5 (0.1)	14.0 (0.1)	21.2 (0.2)	21.2 (0.1)	20.9 (0.2)	22.7 (0.2)	24.5 (0.2)	26.2 (0.2)
lowest month	5.4 (0.2)	4.7 (0.1)	10.4 (0.2)	10.7 (0.2)	9.8 (0.2)	13.0 (0.2)	15.9 (0.3)	18.9 (0.3)
wettest month	5.8 (0.2)	5.4 (0.1)	19.2 (0.4)	19.8 (0.2)	20.5 (0.1)	22.0 (0.2)	23.9 (0.2)	25.5 (0.2)
driest month	13.4 (0.1)	13.9 (0.1)	12.9 (0.2)	13.0 (0.2)	11.9 (0.2)	15.7 (0.3)	18.1 (0.3)	20.9 (0.3)
Maximum temperature (°C)								
annual mean	13.6 (0.2)	13.5 (0.1)	21.8 (0.2)	21.7 (0.1)	21.6 (0.2)	23.7 (0.2)	25.9 (0.2)	27.5 (0.2)
annual range	10.2 (0.1)	11.7 (0.1)	10.2 (0.1)	10.5 (0.1)	10.6 (0.1)	9.1 (0.1)	8.1 (0.1)	7.1 (0.2)
seasonality	0.27 (0.01)	0.33 (0.00)	0.18 (0.00)	0.18 (0.00)	0.18 (0.00)	0.14 (0.00)	0.12 (0.00)	0.10 (0.00)
highest month	18.8 (0.1)	19.5 (0.1)	26.4 (0.2)	26.5 (0.1)	26.4 (0.1)	27.7 (0.2)	29.5 (0.2)	30.7 (0.2)
lowest month	8.7 (0.2)	7.8 (0.1)	16.3 (0.2)	16.0 (0.2)	15.9 (0.2)	18.6 (0.2)	21.4 (0.3)	23.5 (0.3)
wettest month	9.3 (0.2)	8.8 (0.2)	24.1 (0.4)	24.7 (0.2)	25.6 (0.1)	26.5 (0.2)	28.3 (0.2)	29.4 (0.2)
driest month	18.7 (0.1)	19.4 (0.1)	19.1 (0.3)	18.8 (0.2)	18.3 (0.2)	21.8 (0.3)	24.1 (0.3)	26.0 (0.3)
Minimum temperature (°C)								
annual mean	5.0 (0.1)	4.9 (0.1)	10.6 (0.2)	11.0 (0.2)	10.0 (0.2)	13.0 (0.2)	15.5 (0.3)	18.5 (0.3)
annual range	6.0 (0.0)	6.9 (0.1)	11.6 (0.1)	10.9 (0.1)	12.0 (0.1)	10.6 (0.2)	9.5 (0.2)	7.7 (0.2)
seasonality	0.49 (0.2)	0.59 (0.01)	0.42 (0.01)	0.40 (0.01)	0.47 (0.01)	0.32 (0.01)	0.25 (0.01)	0.16 (0.01)
highest month	8.1 (0.1)	8.5 (0.1)	16.1 (0.2)	16.2 (0.1)	15.7 (0.2)	17.9 (0.2)	19.8 (0.2)	22.0 (0.3)
lowest month	2.2 (0.1)	1.6 (0.1)	4.5 (0.2)	5.3 (0.2)	3.7 (0.2)	7.3 (0.3)	10.3 (0.4)	14.3 (0.4)
wettest month	2.4 (0.1)	2.1 (0.1)	14.2 (0.4)	14.8 (0.2)	15.4 (0.2)	17.5 (0.2)	19.6 (0.2)	21.6 (0.2)
driest month	8.1 (0.1)	8.4 (0.1)	6.7 (0.3)	7.2 (0.2)	5.4 (0.2)	9.6 (0.4)	12.1 (0.4)	15.9 (0.4)

Table 2.6 continued Mean climate profiles for the species derived from output of ANUCLIM 5.0.

Variable	<i>E. lucida</i>	<i>N. cunninghamii</i>	<i>T. laurina</i>	<i>A. smithii</i>	<i>S. woollsii</i>	<i>H. trifoliolata</i>	<i>C. australe</i>	<i>A. scholaris</i>
Precipitation (mm)								
annual mean	172.7 (4.3)	139.5 (2.3)	109.8 (2.8)	110.0 (2.0)	116.2 (2.3)	145.9 (5.3)	137.9 (5.0)	164.8 (7.8)
annual range	122.7 (3.3)	106.5 (2.1)	122.5 (5.9)	141.9 (5.9)	151.4 (3.7)	234.7 (12.5)	274.5 (12.6)	388.2 (15.0)
seasonality	0.24 (0.00)	0.25 (0.00)	0.36 (0.01)	0.42 (0.01)	0.45 (0.00)	0.55 (0.02)	0.73 (0.02)	0.93 (0.01)
highest month	228.1 (5.4)	188.3 (3.1)	177.9 (6.1)	194.5 (5.7)	201.1 (4.3)	286.0 (13.5)	311.6 (13.3)	421.3 (17.3)
lowest month	102.4 (2.6)	81.8 (1.3)	55.4 (1.1)	52.6 (0.9)	49.8 (0.9)	51.3 (1.8)	37.1 (1.8)	33.2 (2.8)
hottest month	102.6 (2.6)	84.3 (1.2)	143.7 (4.5)	140.5 (2.3)	164.2 (2.9)	180.6 (4.7)	181.2 (8.2)	231.2 (16.1)
coldest month	225.2 (5.4)	184.2 (3.1)	74.8 (1.8)	68.8 (1.3)	76.5 (1.5)	84.4 (3.2)	55.5 (2.9)	44.1 (3.6)
summer/winter	0.59 (0.01)	0.58 (0.01)	1.95 (0.06)	2.49 (0.12)	2.44 (0.03)	2.91 (0.12)	6.60 (0.75)	8.78 (0.98)
annual total	2072 (52)	1674 (28)	1318 (34)	1320 (24)	1395 (27)	1750 (64)	1655 (59)	1978 (94)
Raindays (days)								
annual mean	19.5 (0.2)	16.7 (0.2)	10.8 (0.1)	10.9 (0.1)	10.8 (0.1)	11.6 (0.2)	11.5 (0.2)	11.7 (0.3)
annual range	11.1 (0.1)	11.0 (0.1)	6.7 (0.2)	7.0 (0.2)	7.3 (0.1)	9.1 (0.2)	11.0 (0.3)	12.8 (0.2)
seasonality	0.17 (0.00)	0.21 (0.00)	0.21 (0.00)	0.22 (0.00)	0.23 (0.00)	0.28 (0.00)	0.36 (0.01)	0.43 (0.01)
highest month	23.8 (0.2)	21.4 (0.2)	14.1 (0.1)	14.5 (0.1)	14.7 (0.1)	16.5 (0.3)	17.6 (0.2)	19.0 (0.3)
lowest month	12.8 (0.1)	10.4 (0.1)	7.5 (0.1)	7.5 (0.1)	7.4 (0.1)	7.4 (0.1)	6.5 (0.1)	6.2 (0.3)
hottest month	12.8 (0.1)	10.5 (0.1)	12.3 (0.2)	12.4 (0.1)	12.9 (0.1)	13.3 (0.1)	12.9 (0.2)	13.3 (0.4)
coldest month	23.8 (0.2)	20.9 (0.2)	8.0 (0.1)	8.0 (0.1)	7.5 (0.1)	8.0 (0.2)	8.0 (0.2)	7.9 (0.3)
summer/winter	0.69 (0.00)	0.63 (0.00)	1.45 (0.03)	1.50 (0.02)	1.67 (0.01)	1.74 (0.02)	1.96 (0.05)	2.24 (0.11)
annual total	233.8 (1.9)	200.3 (1.8)	130.0 (1.0)	130.6 (0.9)	130.2 (0.9)	139.6 (2.0)	138.0 (1.9)	140.4 (3.3)

Table 2.6 continued Mean climate profiles for the species derived from output of ANUCLIM 5.0.

Variable	<i>E. lucida</i>	<i>N. cunninghamii</i>	<i>T. laurina</i>	<i>A. smithii</i>	<i>S. woollsii</i>	<i>H. trifoliolata</i>	<i>C. australe</i>	<i>A. scholaris</i>
Evaporation (mm)								
annual	68.3 (0.6)	73.2 (0.6)	124.2 (0.9)	124.8 (0.6)	120.4 (0.7)	125.8 (1.0)	140.3 (1.6)	156.5 (2.1)
range	106.8 (0.7)	120.2 (0.9)	137.3 (1.6)	135.5 (1.3)	127.1 (0.9)	114.2 (1.3)	110.8 (1.2)	106.0 (1.6)
seasonality	0.55 (0.00)	0.58 (0.00)	0.38 (0.01)	0.37 (0.00)	0.36 (0.00)	0.31 (0.00)	0.28 (0.00)	0.24 (0.00)
highest month	128.7 (1.0)	141.8 (1.0)	196.6 (1.2)	196.8 (1.0)	186.6 (0.9)	185.3 (1.2)	199.0 (1.9)	212.4 (2.6)
lowest month	22.0 (0.4)	21.6 (0.3)	59.3 (1.0)	61.4 (0.8)	59.6 (0.7)	71.1 (1.1)	88.2 (1.9)	106.4 (2.1)
hottest month	112.6 (0.9)	123.6 (0.9)	181.3 (1.3)	181.4 (0.8)	181.4 (1.0)	179.8 (1.2)	189.6 (1.7)	198.5 (2.6)
coldest month	24.5 (0.4)	24.9 (0.3)	67.0 (1.0)	69.1 (0.8)	66.2 (0.7)	78.6 (1.2)	99.5 (2.5)	121.3 (2.9)
summer/winter	4.45 (0.04)	4.88 (0.04)	2.54 (0.05)	2.42 (0.03)	2.35 (0.02)	1.99 (0.03)	1.71 (0.03)	1.44 (0.03)
Mean Vapour Pressure Deficit (kPa)								
annual	0.24 (0.00)	0.28 (0.00)	0.55 (0.01)	0.57 (0.01)	0.56 (0.01)	0.61 (0.01)	0.70 (0.01)	0.79 (0.02)
range	0.31 (0.00)	0.37 (0.01)	0.56 (0.01)	0.57 (0.01)	0.56 (0.01)	0.59 (0.01)	0.64 (0.01)	0.62 (0.02)
seasonality	0.49 (0.01)	0.48 (0.0)	0.36 (0.01)	0.36 (0.00)	0.35 (0.01)	0.35 (0.01)	0.34 (0.01)	0.30 (0.01)
highest month	0.41 (0.00)	0.48 (0.01)	0.84 (0.01)	0.87 (0.01)	0.85 (0.01)	0.92 (0.01)	1.07 (0.01)	1.16 (0.02)
lowest month	0.09 (0.00)	0.11 (0.00)	0.28 (0.01)	0.30 (0.01)	0.29 (0.01)	0.34 (0.01)	0.43 (0.01)	0.54 (0.02)
hottest month	0.36 (0.00)	0.44 (0.01)	0.74 (0.01)	0.78 (0.01)	0.80 (0.01)	0.84 (0.01)	0.96 (0.01)	1.01 (0.03)
coldest month	0.09 (0.0)	0.12 (0.00)	0.32 (0.01)	0.33 (0.01)	0.33 (0.01)	0.37 (0.01)	0.46 (0.01)	0.56 (0.02)
Maximum Vapour Pressure Deficit (kPa)								
annual	0.45 (0.01)	0.52 (0.01)	1.04 (0.02)	1.10 (0.01)	1.10 (0.02)	1.17 (0.02)	1.35 (0.02)	1.41 (0.04)
range	0.54 (0.01)	0.72 (0.02)	0.63 (0.03)	0.77 (0.02)	0.72 (0.02)	0.62 (0.02)	0.75 (0.03)	0.75 (0.05)
seasonality	0.43 (0.01)	0.50 (0.01)	0.19 (0.01)	0.22 (0.00)	0.20 (0.01)	0.17 (0.01)	0.19 (0.01)	0.19 (0.01)
highest month	0.75 (0.01)	0.94 (0.02)	1.36 (0.03)	1.51 (0.02)	1.48 (0.03)	1.49 (0.03)	1.76 (0.03)	1.84 (0.06)
lowest month	0.21 (0.01)	0.21 (0.00)	0.73 (0.02)	0.73 (0.01)	0.76 (0.01)	0.87 (0.02)	1.01 (0.01)	1.08 (0.03)
hottest month	0.74 (0.01)	0.93 (0.02)	1.27 (0.03)	1.40 (0.02)	1.41 (0.03)	1.41 (0.03)	1.63 (0.03)	1.67 (0.06)
coldest month	0.22 (0.01)	0.22 (0.00)	0.82 (0.02)	0.83 (0.01)	0.85 (0.01)	0.97 (0.02)	1.15 (0.02)	1.20 (0.03)

Table 2.6 continued Mean climate profiles for the species derived from output of ANUCLIM 5.0.

Variable	<i>E. lucida</i>	<i>N. cunninghamii</i>	<i>T. laurina</i>	<i>A. smithii</i>	<i>S. woollsii</i>	<i>H. trifoliolata</i>	<i>C. australe</i>	<i>A. scholaris</i>
<u>Water Balance (mm)</u>								
annual	104.4 (4.5)	66.3 (2.6)	-14.4 (3.1)	-14.8 (2.1)	-4.2 (2.6)	20.1 (5.6)	-2.3 (4.9)	8.3 (8.0)
range	215.7 (3.3)	212.4 (1.9)	163.1 (3.7)	188.5 (5.6)	133.8 (4.0)	237.5 (14.8)	302.9 (15.3)	442.2 (15.3)
seasonality	0.85 (0.05)	2.33 (1.44)	1.93 (1.02)	0.98 (1.72)	-5.74 (4.95)	-0.59 (3.06)	-0.37 (1.21)	-0.00 (1.44)
highest month	201.2 (5.4)	160.3 (3.2)	70.2 (4.8)	86.8 (5.3)	63.8 (4.7)	152.8 (14.1)	174.3 (13.3)	275.9 (17.2)
lowest month	-14.4 (3.5)	-52.1 (2.3)	-92.9 (2.6)	-101.8 (1.8)	-69.9 (1.4)	-84.6 (3.2)	-128.7 (4.5)	-166.3 (4.2)
hottest month	-10.1 (3.0)	-39.2 (1.9)	-37.6 (4.9)	-41.0 (2.7)	-17.2 (3.6)	0.8 (5.4)	-8.3 (8.9)	32.7 (17.6)
coldest month	200.7 (5.4)	159.3 (3.2)	7.8 (2.1)	-0.3 (1.7)	10.4 (1.6)	5.8 (3.6)	-44.0 (4.6)	-77.2 (5.1)
<u>Moisture Index</u>								
annual	0.99 (0.00)	0.94 (0.00)	0.81 (0.01)	0.80 (0.01)	0.87 (0.01)	0.85 (0.01)	0.74 (0.01)	0.69 (0.02)
range	0.07 (0.01)	0.23 (0.01)	0.44 (0.02)	0.47 (0.01)	0.30 (0.01)	0.38 (0.02)	0.62 (0.02)	0.77 (0.02)
seasonality	0.03 (0.00)	0.10 (0.00)	0.20 (0.01)	0.22 (0.01)	0.13 (0.00)	0.18 (0.01)	0.36 (0.02)	0.48 (0.03)
highest month	1.00 (0.01)	1.00 (0.00)	0.97 (0.01)	0.97 (0.00)	0.97 (0.01)	0.97 (0.01)	0.97 (0.01)	0.99 (0.01)
lowest month	0.93 (0.01)	0.77 (0.01)	0.53 (0.02)	0.50 (0.01)	0.66 (0.01)	0.58 (0.02)	0.35 (0.02)	0.21 (0.02)
hottest quarter	0.96 (0.01)	0.83 (0.01)	0.72 (0.02)	0.72 (0.01)	0.84 (0.01)	0.86 (0.01)	0.82 (0.01)	0.83 (0.02)
coldest quarter	1.00 (0.00)	1.00 (0.00)	0.94 (0.01)	0.93 (0.01)	0.95 (0.01)	0.92 (0.02)	0.75 (0.02)	0.66 (0.04)

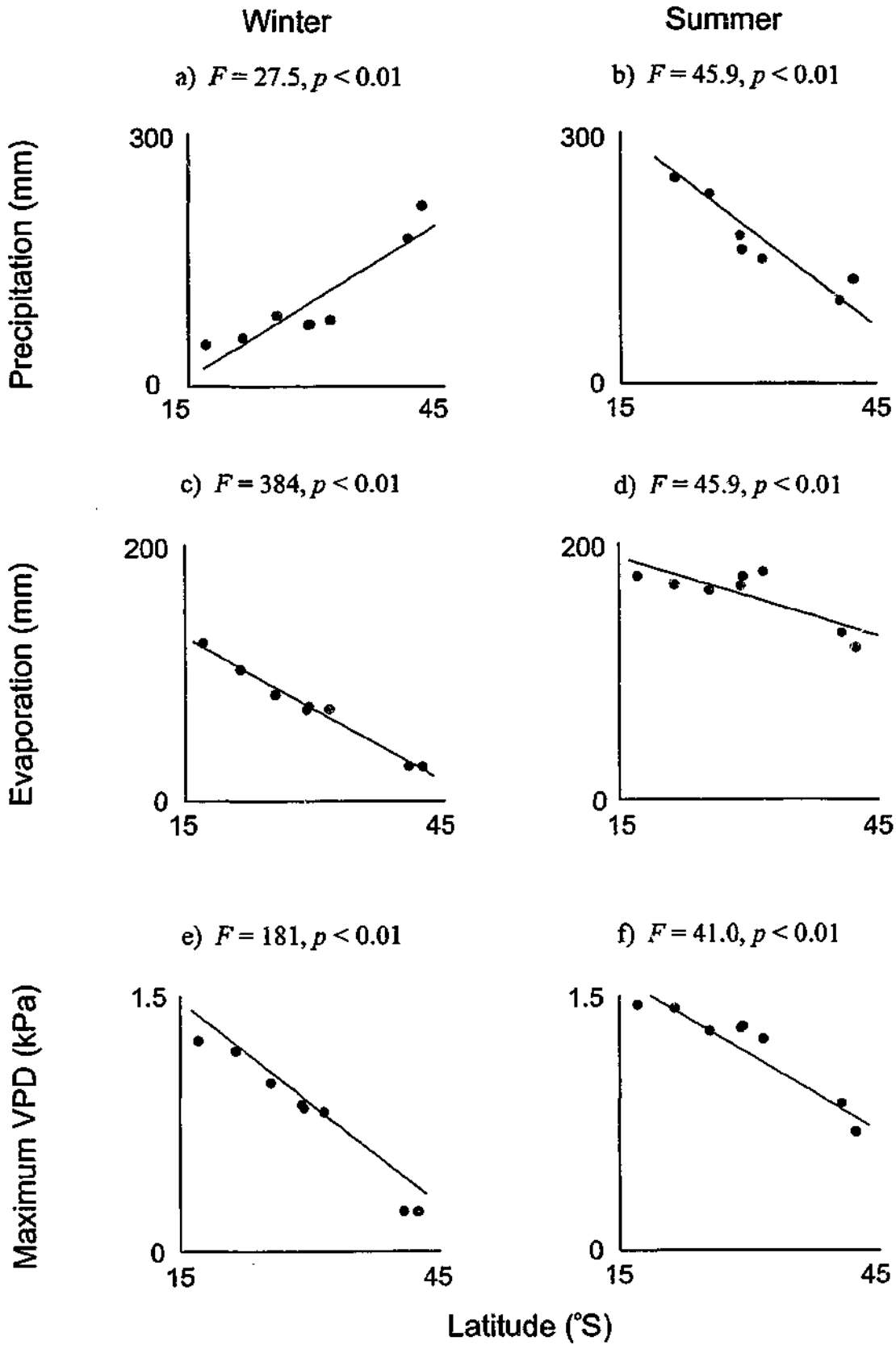


Figure 2.3 a-f Relationships between mean monthly values of moisture variables and the mean latitude of species winter (a, c, & e) and summer (b, d, & f). The line of best fit was derived by linear regression. Points are means for individual species.

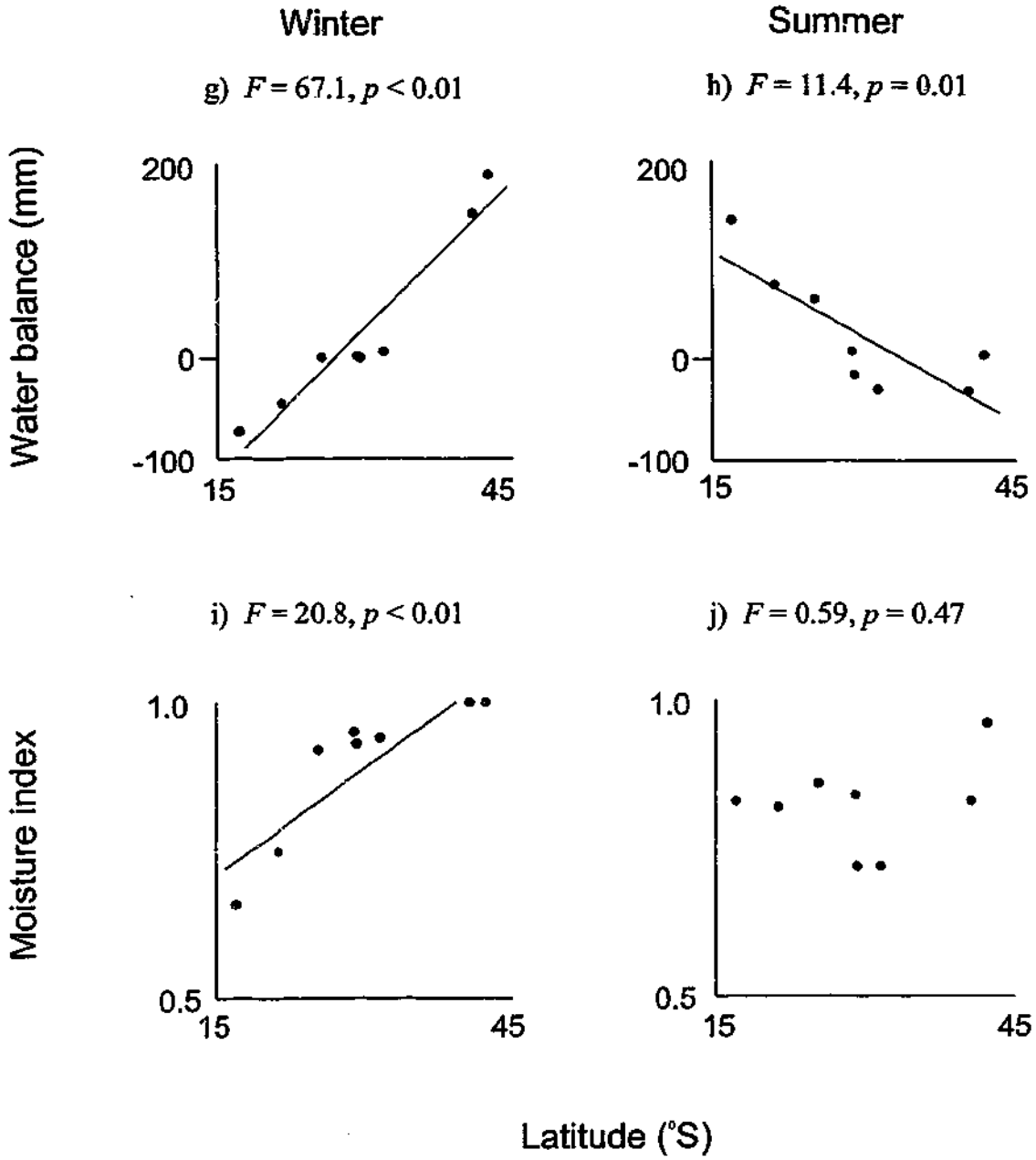


Figure 2.3 g-j Relationships between mean monthly values of moisture variables and the mean latitude of species winter (g & i) and summer (h & j). The line of best fit was derived by linear regression. Points are means for individual species.

Multivariate analysis

The RELATE analysis showed that the similarity matrix derived using only the moisture variables was strongly in agreement with the similarity matrix derived using all the climate variables (Table 2.7). The similarity in these two matrices is likely to be because the moisture variables make up 72% of the climate variables.

Table 2.7 Matching coefficients (ρ) for pairwise tests of similarity matrices (calculated from different combinations of climate variables) derived using the RELATE procedure.

	all	temperature	moisture
all	-		
temperature	0.88 (<0.01)	-	
moisture	0.98 (<0.01)	0.79 (<0.01)	-

All climatic variables

Overall, there were significant differences in the climate profiles for site locations among species (Global $R = 0.61$, $p < 0.01$). However, the climate profiles for sites of *E. lucida* and *N. cunninghamii* were not significantly different (Table 2.8). In addition, the site climate profiles of *A. smithii* were not significantly different to those of *Tristaniopsis laurina* and *Sloanea woollsii* (Table 2.8). At the level of rainforest type, the climate profiles of site locations tended to be significantly different among rainforest types (Global $R = 0.69$, $p < 0.01$). Only the warm-temperate and subtropical rainforest types did not show significant differences in their climate profiles (Table 2.9). The climate profiles of site locations were significantly different between climate groups (Global $R = 0.26$, $p < 0.01$).

Table 2.8 *R* values, with unadjusted *p*-values in brackets, for pairwise tests of species derived using ANOSIM on a similarity matrix calculated using all climate variables for the site locations.

	<i>E. lucida</i>	<i>N. cunninghamii</i>	<i>A. smithii</i>	<i>T. laurina</i>	<i>S. woollsii</i>	<i>H. trifoliolata</i>	<i>C. australe</i>	<i>A. scholaris</i>
<i>E. lucida</i>	-							
<i>N. cunninghamii</i>	0.04 (0.03)	-						
<i>A. smithii</i>	0.94 (<0.01)	0.88 (<0.01)	-					
<i>T. laurina</i>	0.98 (<0.01)	0.88 (<0.01)	0.02 (0.19)	-				
<i>S. woollsii</i>	0.99 (<0.01)	0.90 (<0.01)	- 0.03 (0.95)	0.12 (<0.01)	-			
<i>H. trifoliolata</i>	0.98 (<0.01)	0.95 (<0.01)	0.13 (<0.01)	0.18 (<0.01)	0.24 (<0.01)	-		
<i>C. australe</i>	0.96 (<0.01)	0.97 (<0.01)	0.35 (<0.01)	0.35 (<0.01)	0.43 (<0.01)	0.10 (<0.01)	-	
<i>A. scholaris</i>	1.00 (<0.01)	1.00 (<0.01)	0.75 (<0.01)	0.85 (<0.01)	0.93 (<0.01)	0.60 (<0.01)	0.14 (<0.01)	-

Table 2.9 *R* values, with unadjusted *p*-values in brackets, for pairwise tests of rainforest types derived using ANOSIM on a similarity matrix calculated using all climate variables for the site locations.

	cool-temperate	warm-temperate	subtropical	tropical
cool-temperate	-			
warm-temperate	0.90 (<0.01)	-		
subtropical	0.93 (<0.01)	0.03 (0.02)	-	
tropical	0.98 (<0.01)	0.50 (<0.01)	0.42 (<0.01)	-

The two-dimensional NMDS of the site locations using all the climate variables, with the lowest stress, is presented in Figure 2.4. The pattern of sites forms a distinct 'V' pattern with greater scatter towards the positive side of axis one. The rotational correlations showed that 18 of the 75 climate variables were highly correlated ($r^2_{corrected} > 0.90$) with the pattern of the two-dimensional NMDS plot (Table 2.10). The ten climate variables most highly-correlated with the pattern of the NMDS plot included both evaporation (ELo, EC and EA) and temperature variables (MTA, MaxTA, MaxTLo, MTLo, MTHi, MinTA and MinTHi). All these variables increased towards the right-hand arm of the 'V' (Figure 2.4). The patterns of site locations for the individual species show that the cool-temperate species (*E. lucida* and *N. cunninghamii*) make up the left-hand arm of the 'V' (Figures 2.5a & b). The climate profiles of the sites representing *E. lucida* essentially form a subset of those for *N. cunninghamii*. There is a lot of overlap between the climate profiles of the warm-temperate and subtropical species (Figures 2.5b-f). The tropical species show some overlap with these two groups but also show a majority of sites with distinct climate profiles (Figures 2.5 g & h). Overall, the NMDS plot, with the rotational position of the most highly-correlated variables (Figure 2.4), shows a picture of increasing temperature and evaporation from the cool-temperate species through to the tropical species.

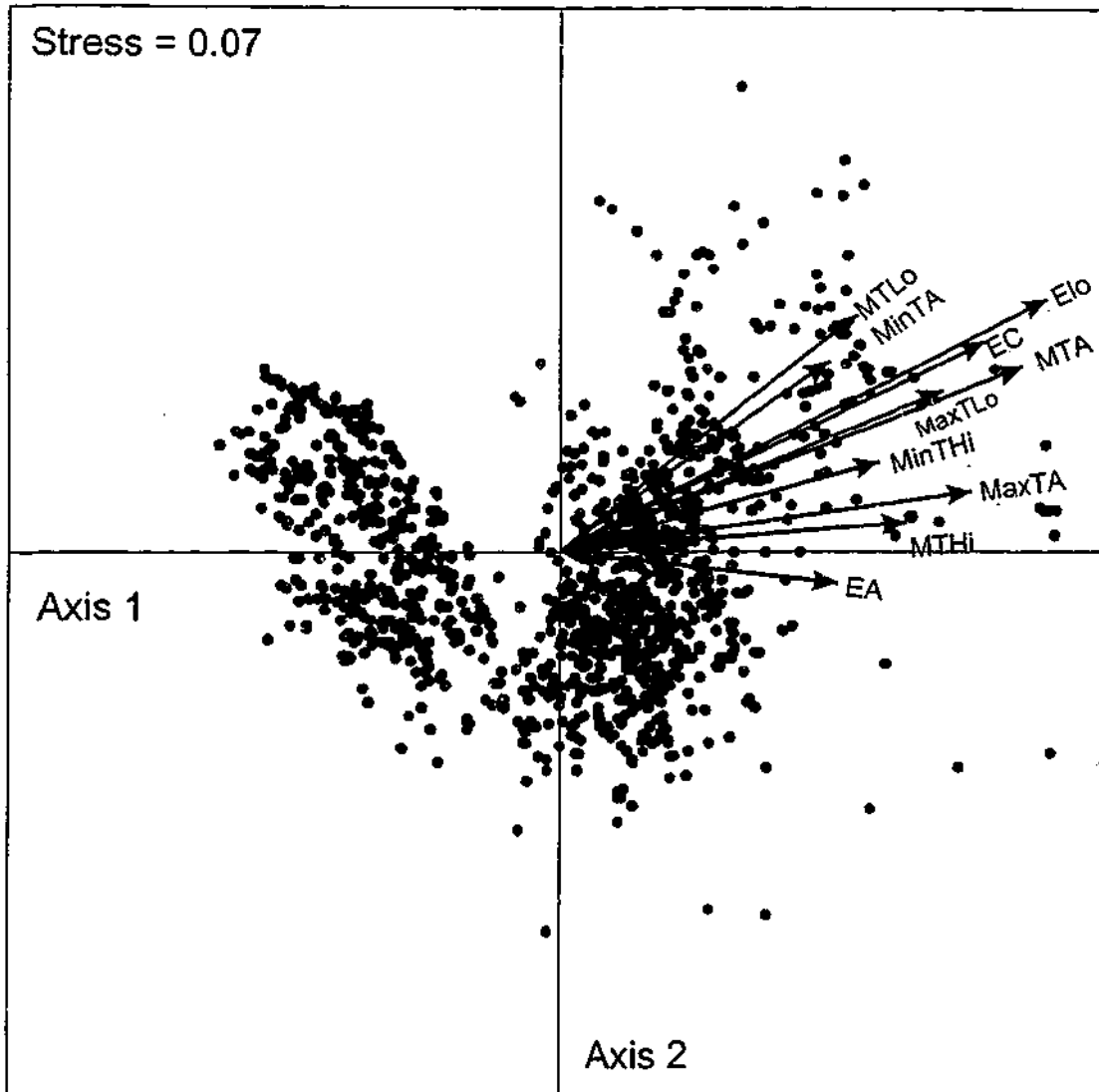


Figure 2.4 Non-metric MDS ordination of the climates of species locations, including all the climate variables. The rotational positions of the ten climate variables most highly-correlated with the ordination are shown. For each variable, the value of $r^2_{corrected}$ is represented by the radius length.

Table 2.10 Rotational correlation parameters for linear trends surfaces fitting MDS coordinates to the various climate variables. See Table 2.3 for explanations of the variable abbreviations.

Variable	Rotation angle	$r^2_{corrected}$	Variable	Rotation angle	$r^2_{corrected}$
ELo	27.5	0.976	PA	-82.5	0.782
MTA	21.9	0.970	PTOT	-82.6	0.782
EC	26.4	0.967	RDSW	11.6	0.781
MaxTA	8.3	0.960	PS	49.9	0.775
MaxTLo	22.9	0.960	WBHi	-86.1	0.769
MTLo	38.7	0.956	MTS	41.7	0.754
MTHi	4.8	0.952	PLo	-42.0	0.749
MinTA	35.3	0.950	ER	-87.3	0.730
MinTHi	15.7	0.950	MVR	-45.0	0.713
EA	-6.5	0.944	MaxVHi	-37.5	0.675
MaxVC	3.3	0.936	MaxTR	67.8	0.666
MVHi	-12.7	0.929	WBLo	-31.3	0.654
ES	25.6	0.924	MTR	-88.7	0.645
MaxTHi	-7.2	0.923	MinTR	-67.2	0.641
WBC	-22.6	0.922	MIo	-28.1	0.638
MVA	-4.6	0.917	MaxVH	-40.9	0.630
MinTW	13.1	0.915	MIA	-44.0	0.622
MaxVLo	3.8	0.914	MaxVS	11.1	0.595
MTW	2.9	0.902	WBR	81.4	0.590
RDA	-54.8	0.902	MIR	-17.4	0.589
RDTOT	-54.8	0.902	MIS	-8.2	0.584
WBA	-65.6	0.899	PH	64.5	0.538
EH	-31.1	0.884	RDS	46.3	0.520
MaxTW	-6.1	0.881	MinTD	74.9	0.493
MVH	-15.6	0.881	MIHQ	-76.5	0.488
ESW	18.8	0.875	MTD	69.2	0.477
MinTLo	54.7	0.873	WBH	87.7	0.463
MaxVA	-20.7	0.871	MinTS	47.8	0.434
EHi	-38.6	0.865	MaxTD	60.9	0.427
PC	-40.5	0.855	PSW	34.5	0.419
RDC	-35.5	0.854	RDR	-84.8	0.411
MVC	19.9	0.844	MVS	25.9	0.383
RDLo	-43.4	0.840	MICQ	-4.1	0.361
MVLo	25.3	0.822	RDH	79.2	0.352
PR	73.4	0.817	MaxVR	-81.4	0.228
PHi	81.0	0.814	MIHi	-75.4	0.215
MaxTS	27.8	0.784	WBS	-74.5	0.001
RDHi	-67.4	0.783			

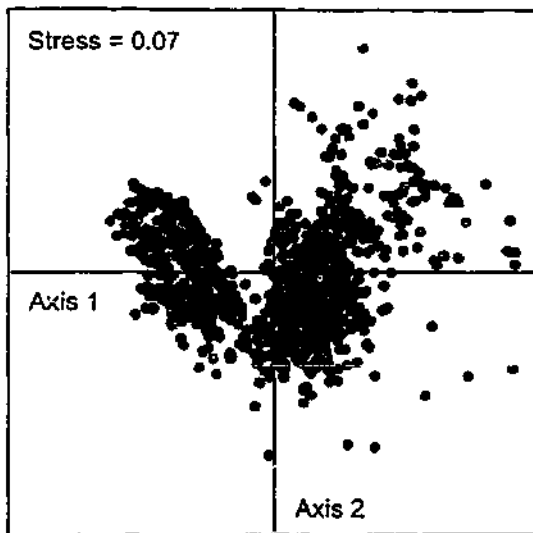
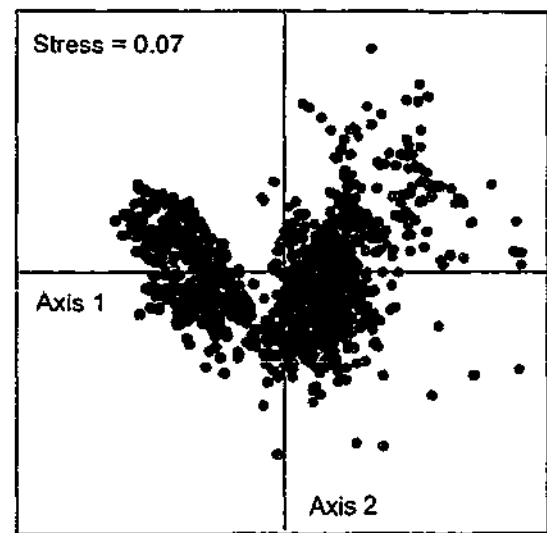
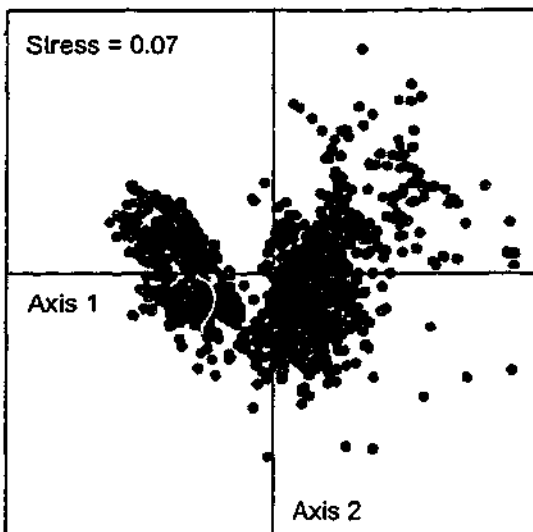
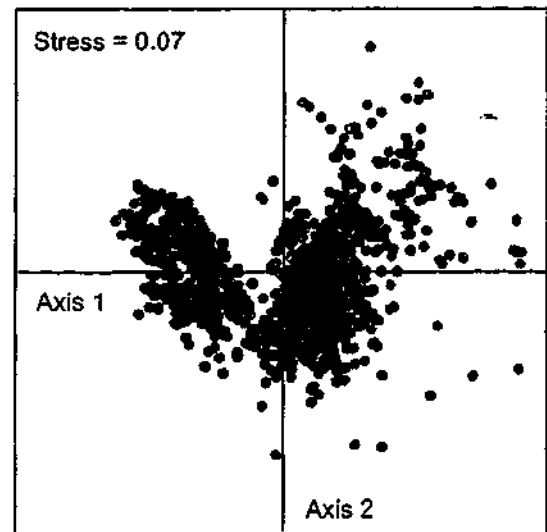
a) *Eucryphia lucida*b) *Nothofagus cunninghamii*c) *Acmena smithii*d) *Tristaniopsis laurina*

Figure 2.5 a-d Non-metric MDS ordination of the climates of site locations, including all the climate variables. The site locations of individual species are overlaid (black) over all the sites in the ordination.

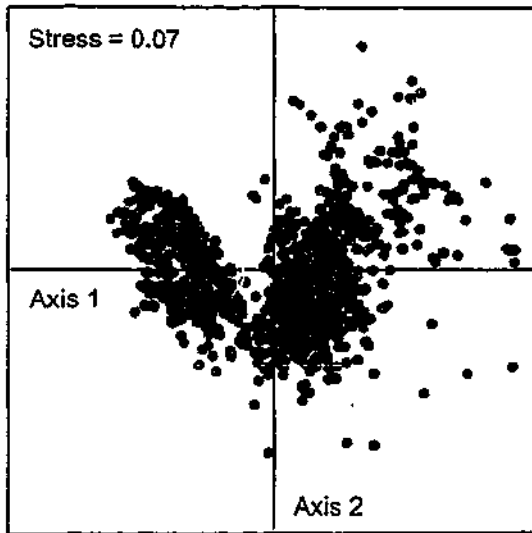
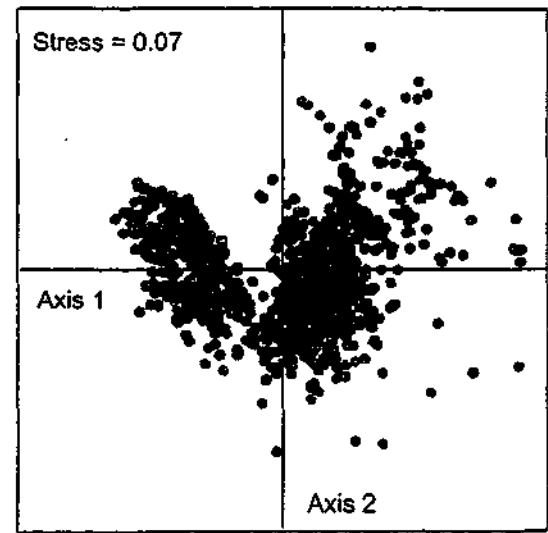
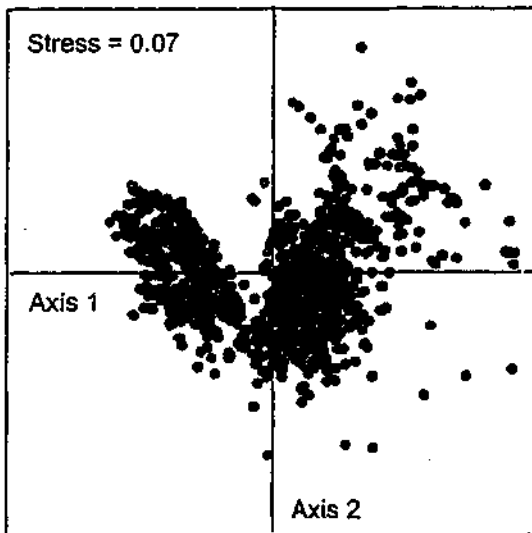
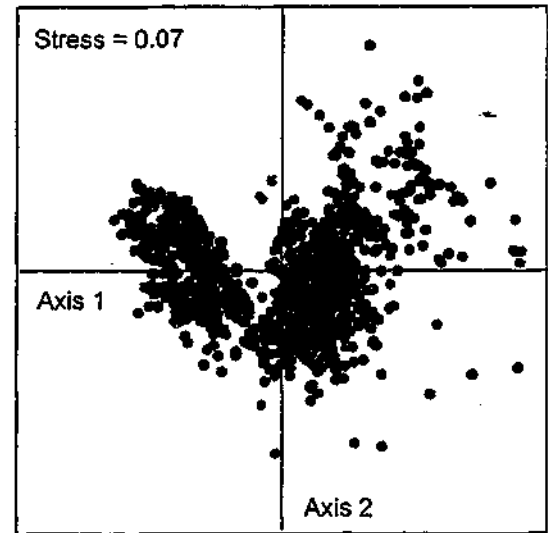
e) *Sloanea woollsii*f) *Heritiera trifoliolata*g) *Castanospermum australe*h) *Alstonia scholaris*

Figure 2.5 e-h Non-metric MDS ordination of the climates of site locations, including all the climate variables. The site locations of individual species are overlaid (black) over all the sites in the ordination.

Temperature variables

Temperature profiles of site locations were significantly different among species (Global $R = 0.61$, $p < 0.01$). However, temperature profiles for sites of *E. lucida* and *N. cunninghamii* were not significantly different (Table 2.11). This was also true of the temperature profiles for sites of *A. smithii* when compared with those of *T. laurina*, *S. woollsii* and *Heritiera trifoliolata* and of the temperature profiles for sites of *T. laurina* when compared with *S. woollsii* (Table 2.11). For the rainforest types, the temperature profiles of site locations tended to be significantly different among rainforest types (Global $R = 0.70$, $p < 0.01$). The warm-temperate and subtropical rainforest types were the only rainforest types not to show significantly different temperature profiles from each other (Table 2.12). The site locations of the climate groups had significantly different temperature profiles (Global $R = 0.30$, $p < 0.01$).

The two-dimensional NMDS plot of the temperature climate of the species locations with the lowest stress is shown in Figure 2.6. The rotational correlations showed that 13 of the 21 temperature variables were highly correlated ($r^2_{corrected} > 0.90$) with the pattern of the two-dimensional plot (Table 2.13). The ten most highly-correlated temperature variables are shown in Figure 2.6. These included annual temperatures (MTA, MinTA and MaxTA), highest monthly temperatures (MTHi and MinTHi), lowest monthly temperatures (MTLo and MaxLo) and temperatures of the wettest month (MTW, MinTW and MaxTW). The pattern of species within the NMDS plot of temperature variables (Figure 2.7) was similar to that within the NMDS plot of all the variables (Figure 2.5). Firstly, the climate profiles of the sites of the cool-temperate species formed a distinct group along the negative arm of axis one (Figures 2.7a & b). Secondly, the climate profiles of the sites of the warm-temperate and subtropical species formed a central group showing a large amount of overlap (Figure 2.7 c-f). The climate profile of the sites of tropical species tended to lie further along the positive arm of axis one than this central group (Figure 2.7 g & h). This shift from cool-temperate to tropical species along axis one was correlated with an increase in the values of the ten most highly-correlated temperature variables.

Table 2.11 *R* values, with unadjusted *p*-values in brackets, for pairwise tests of species derived using ANOSIM on a similarity matrix calculated using only temperature variables for the site locations.

	<i>E. lucida</i>	<i>N. cunninghamii</i>	<i>A. smithii</i>	<i>T. laurina</i>	<i>S. woollsii</i>	<i>H. trifoliolata</i>	<i>C. australe</i>	<i>A. scholaris</i>
<i>E. lucida</i>	-							
<i>N. cunninghamii</i>	-0.07 (1.00)	-						
<i>A. smithii</i>	0.86 (<0.01)	0.90 (<0.01)	-					
<i>T. laurina</i>	0.91 (<0.01)	0.90 (<0.01)	-0.01 (0.66)	-				
<i>S. woollsii</i>	0.98 (<0.01)	0.97 (<0.01)	-0.06 (1.00)	0.05 (<0.01)	-			
<i>H. trifoliolata</i>	0.98 (<0.01)	0.98 (<0.01)	0.04 (0.05)	0.13 (<0.01)	0.25 (<0.01)	-		
<i>C. australe</i>	0.97 (<0.01)	0.99 (<0.01)	0.31 (<0.01)	0.37 (<0.01)	0.47 (<0.01)	0.09 (<0.01)	-	
<i>A. scholaris</i>	1.00 (<0.01)	1.00 (<0.01)	0.65 (<0.01)	0.81 (<0.01)	0.89 (<0.01)	0.56 (<0.01)	0.10 (<0.01)	-

Table 2.12 *R* values, with unadjusted *p*-values in brackets, for pairwise tests of rainforest types derived using ANOSIM on a similarity matrix calculated using only temperature variables for the site locations.

	cool-temperate	warm-temperate	subtropical	tropical
cool-temperate	-			
warm-temperate	0.90 (<0.01)	-		
subtropical	0.97 (<0.01)	-0.02 (0.99)	-	
tropical	0.99 (<0.01)	0.45 (<0.01)	0.40 (<0.01)	-

Table 2.13 Rotational correlation parameters for linear trends surfaces fitting MDS coordinates to the temperature variables. See Table 2.3 for explanations of the variable abbreviations..

Variable	Rotation angle	$r^2_{corrected}$
MTA	83.7	0.991
MTLo	59.5	0.990
MaxTLo	82.4	0.987
MaxTA	-79.0	0.986
MTHi	-76.7	0.977
MinTHi	-87.5	0.977
MTW	-60.7	0.976
MinTA	65.2	0.975
MaxTW	-53.8	0.973
MinTW	-69.7	0.968
MinTLo	37.7	0.949
MaxTHi	-64.3	0.947
MinTR	-14.6	0.909
MTR	1.6	0.871
MTS	53.8	0.854
MaxTS	74.8	0.854
MinTD	13.6	0.832
MTD	18.1	0.758
MaxTR	26.0	0.740
MaxTD	24.8	0.620
MinTS	41.2	0.562

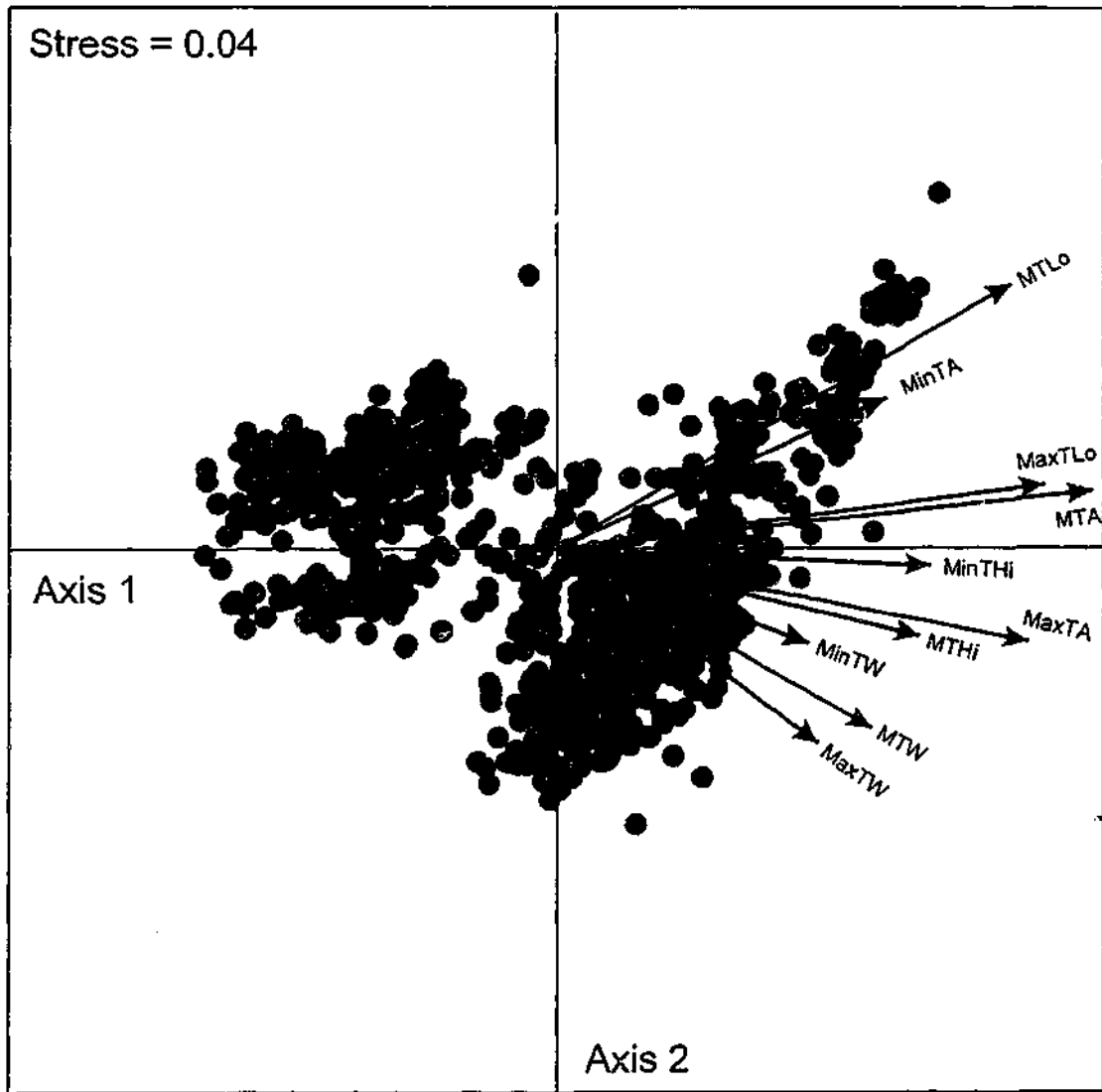


Figure 2.6 Non-metric MDS ordination of the climates of species locations, including only the temperature variables. The rotational positions of the ten temperature variables most highly-correlated with the ordination are shown. For each variable, the value of $r^2_{corrected}$ is represented by the radius length.

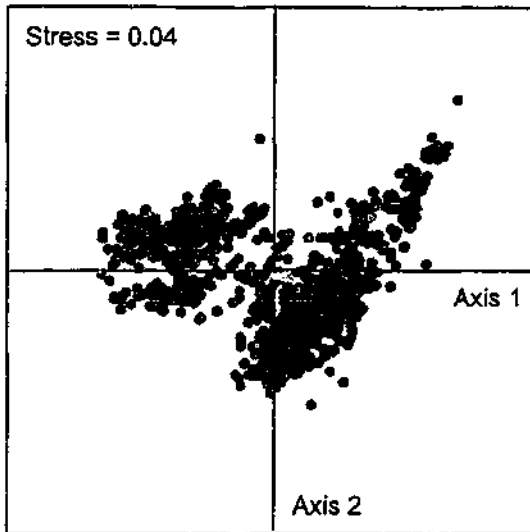
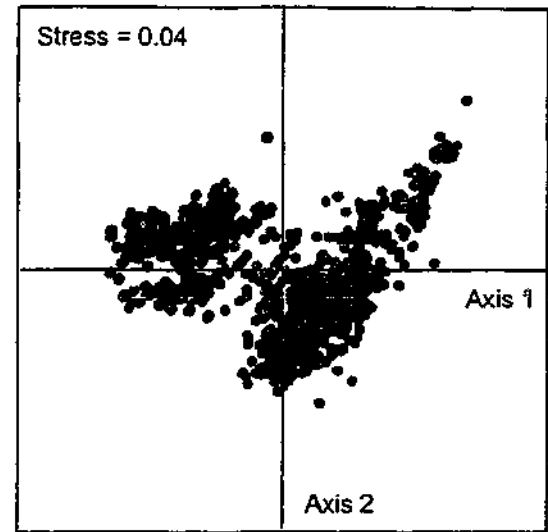
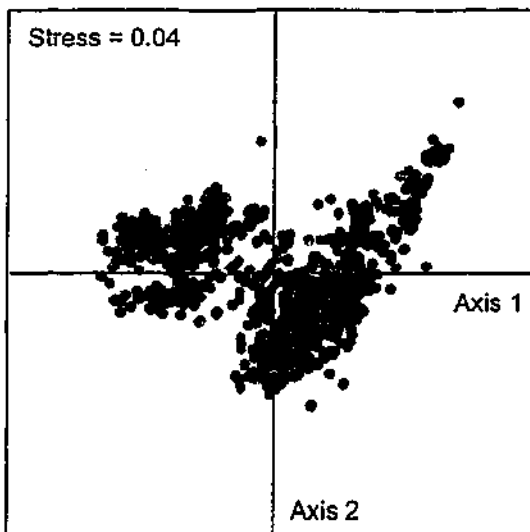
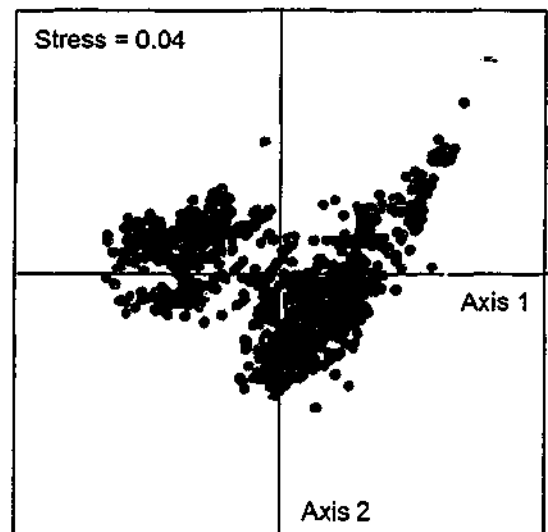
a) *Eucryphia lucida*b) *Nothofagus cunninghamii*c) *Acmena smithii*d) *Tristaniopsis laurina*

Figure 2.7 a-d Non-metric MDS ordination of the climates of site locations, including all the temperature variables. The site locations of individual species are overlaid (black) over all the sites in the ordination.

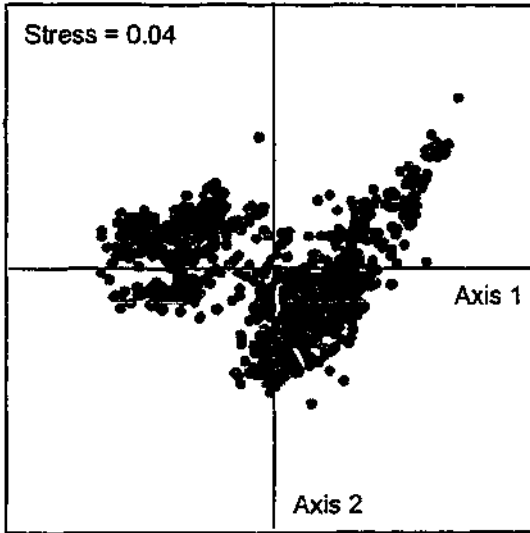
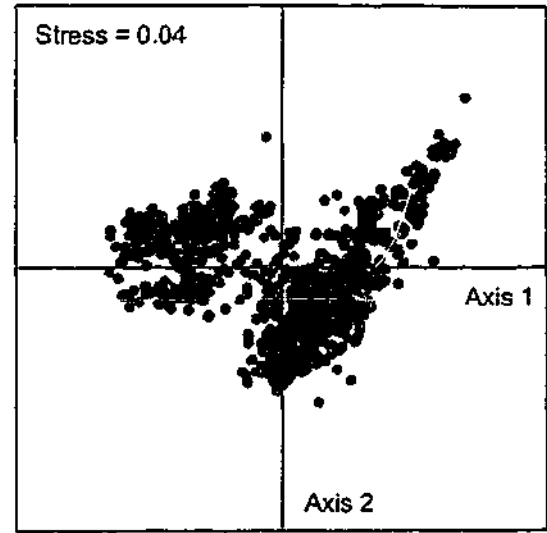
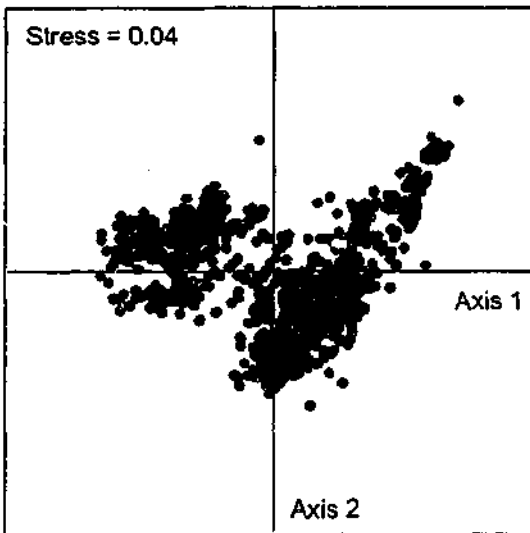
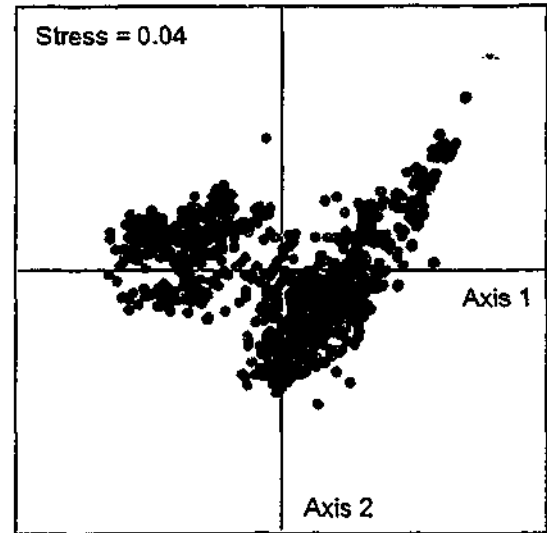
e) *Sloanea woollsii*f) *Heritiera trifoliolata*g) *Castanospermum australe*h) *Alstonia scholaris*

Figure 2.7 e-h Non-metric MDS ordination of the climates of site locations, including all the temperature variables. The site locations of individual species are overlaid (black) over all the sites in the ordination.

Moisture variables

Trends in the moisture profiles of the various taxonomic groups were the same as those shown using all climate variables, reflecting the similarity between the matrices (Table 2.7). The same groups showed similarities in their profiles: *E. lucida* and *N. cunninghamii*, *A. smithii* when compared with that of *T. laurina* and *Sloanea woollsii* (Table 2.14), and the warm-temperate and subtropical rainforest types (Table 2.15). The moisture profiles of site locations were significantly different between climate groups (Global $R = 0.30$, $p < 0.01$).

The two-dimensional NMDS of the site locations using only the moisture variables with the lowest stress is presented in Figure 2.8. The pattern of sites in this NMDS plot is similar to the 'V' formed by the ordination of all the climate variables (compare Figures 2.4 & 2.8). The rotational correlations showed that seven of the 54 moisture variables were highly correlated ($r^2_{corrected} > 0.90$) with the pattern of the two-dimensional NMDS plot (Table 2.16). The ten most highly-correlated moisture variables with the pattern of the NMDS plot included variables of evaporation (ELc, EC, EA and ES), water balance (WBC & WBA), and vapour pressure deficit (MaxVC, MVHi, MVA and MaxVLo). These variables increased in several different directions unlike the NMDS plots of all climate variables and the temperature variables, where they all increased towards the positive direction of axis one (compare Figure 2.8 with Figures 2.4 & 2.6). The pattern shown by these variables was an increase in evaporation and vapour pressure deficit, and a decrease in the water balance of the coldest month (WBC) and the seasonality of evaporation (ES) with decreasing latitude. In addition, annual water balance (WBA) was unrelated to the latitudinal origin of the species.

Table 2.14 *R* values, with unadjusted *p*-values in brackets, for pairwise tests of species derived using ANOSIM on a similarity matrix calculated using only moisture variables for the site locations.

	<i>E. lucida</i>	<i>N. cunninghamii</i>	<i>A. smithii</i>	<i>T. laurina</i>	<i>S. woollsii</i>	<i>H. trifoliolata</i>	<i>C. australe</i>	<i>A. scholaris</i>
<i>E. lucida</i>	-							
<i>N. cunninghamii</i>	0.05 (<0.01)	-						
<i>A. smithii</i>	0.94 (<0.01)	0.81 (<0.01)	-					
<i>T. laurina</i>	0.97 (<0.01)	0.81 (<0.01)	0.04 (0.04)	-				
<i>S. woollsii</i>	0.99 (<0.01)	0.81 (<0.01)	-0.02 (0.76)	0.14 (<0.01)	-			
<i>H. trifoliolata</i>	0.97 (<0.01)	0.89 (<0.01)	0.16 (<0.01)	0.19 (<0.01)	0.21 (<0.01)	-		
<i>C. australe</i>	0.93 (<0.01)	0.93 (<0.01)	0.35 (<0.01)	0.32 (<0.01)	0.38 (<0.01)	0.10 (<0.01)	-	
<i>A. scholaris</i>	0.99 (<0.01)	0.99 (<0.01)	0.75 (<0.01)	0.83 (<0.01)	0.91 (<0.01)	0.57 (<0.01)	0.14 (<0.01)	-

Table 2.16 Rotational correlation parameters for linear trends surfaces fitting MDS coordinates to the moisture variables. See Table 2.3 for explanations of the variable abbreviations.

Variable	Rotation angle	$r^2_{corrected}$	Variable	Rotation angle	$r^2_{corrected}$
ELo	-53.6	0.970	RDSW	-62.7	0.797
EC	-54.9	0.962	PLo	62.2	0.774
EA	-81.5	0.930	WBHi	7.7	0.759
WBC	82.6	0.928	RDHi	30.3	0.746
WBA	32.4	0.926	ER	6.3	0.728
MaxVC	-72.1	0.921	WBLo	68.7	0.704
MVHi	-86.1	0.917	MILo	73.5	0.686
MVA	-79.8	0.906	MVR	61.0	0.674
ES	-53.8	0.904	MIA	58.8	0.665
MaxVLo	-71.6	0.898	MaxVHi	71.3	0.660
RDA	47.5	0.877	MIS	-88.7	0.637
RDTOT	47.5	0.877	MIR	82.6	0.632
MVH	-87.9	0.870	MaxVH	67.7	0.613
PC	63.5	0.863	PH	-20.2	0.568
EH	76.3	0.855	WBR	-6.6	0.560
PR	-13.6	0.854	MaxVS	-68.3	0.555
MaxVA	87.7	0.854	RDS	-39.5	0.551
PHi	-6.0	0.851	MIHQ	19.0	0.539
EHi	65.3	0.847	WBH	1.6	0.507
RDL0	60.9	0.846	PSW	-48.8	0.456
MVC	-60.2	0.844	MICQ	-81.8	0.403
ESW	-59.4	0.843	RDH	-6.2	0.392
PA	12.2	0.827	RDR	8.8	0.379
PTOT	12.2	0.827	MVS	-57.3	0.378
RDC	72.1	0.825	MIHi	22.0	0.201
MVLo	-56.4	0.822	MaxVR	15.6	0.194
PS	-35.1	0.816	WBS	23.2	0.001

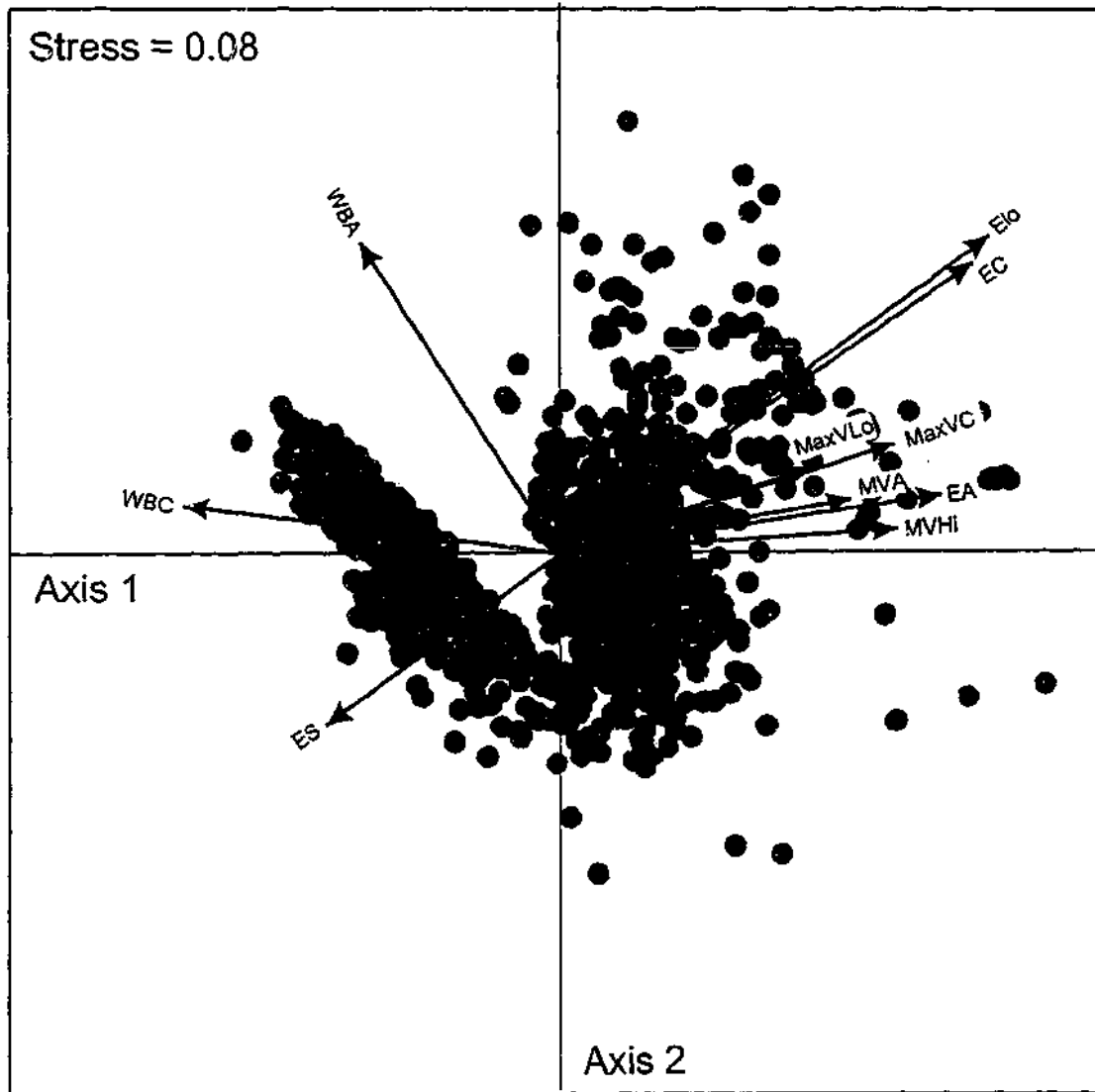


Figure 2.8 Non-metric MDS ordination of the climates of species locations, including all the moisture variables. The rotational positions of the ten moisture variables most highly-correlated with the ordination are shown. For each variable, the value of $r^2_{corrected}$ is represented by the radius length.

The moisture profiles of the site locations of species showed a similar pattern to that showed when all the climate variables were used (compared Figures 2.5 & 2.9). The sites of the cool-temperate species are found along the left arm of the 'V', those of the warm-temperate and subtropical species showed considerable overlap in the central region, and those of the tropical species are found towards the right arm of the 'V'. The region occupied by the cool-temperate species corresponds to sites that have the highest seasonality of evaporation (ES) and water balance during the coldest month (WBC). In contrast, the tropical species are found on sites that have the highest values of evaporation (EA, EC and ELo) and vapour pressure deficit (MVHi, MVA, MaxVC and MaxVLo).

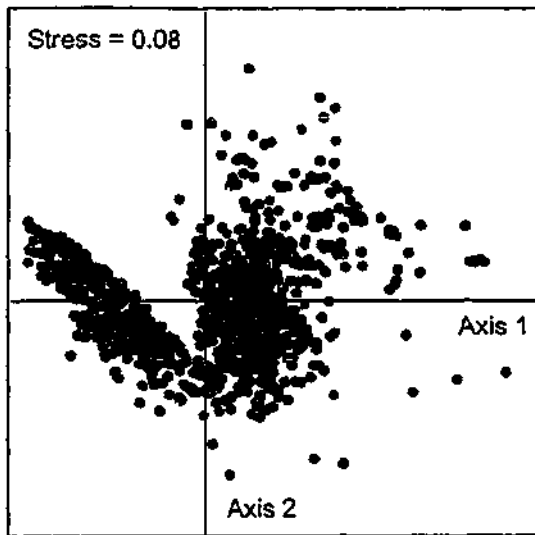
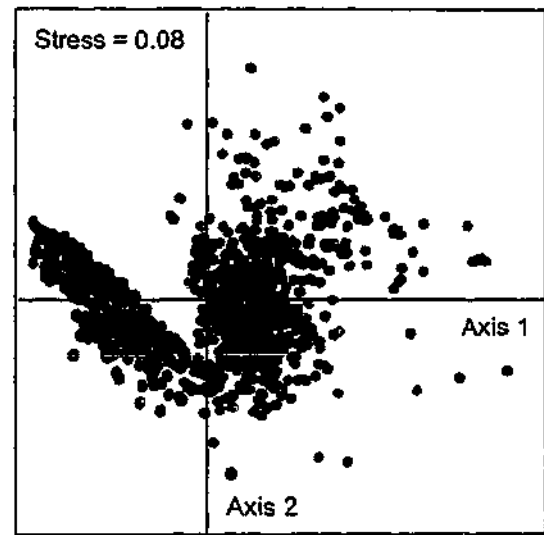
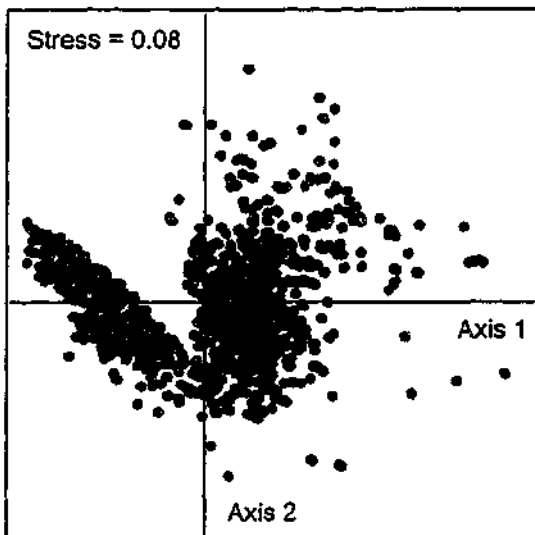
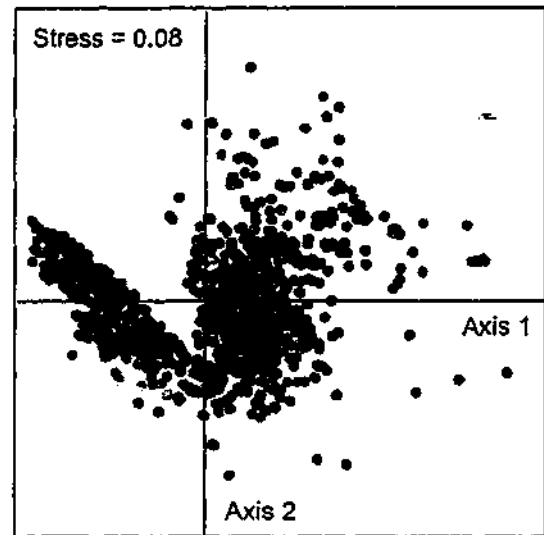
a) *Eucryphia lucida*b) *Nothofagus cunninghamii*c) *Acmena smithii*d) *Tristaniopsis laurina*

Figure 2.9 a-d Non-metric MDS ordination of the climates of site locations, including all the moisture variables. The site locations of individual species are overlaid (black) over all the sites in the ordination.

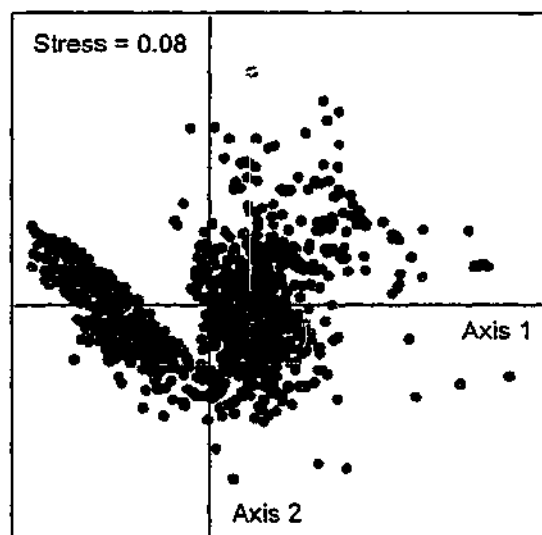
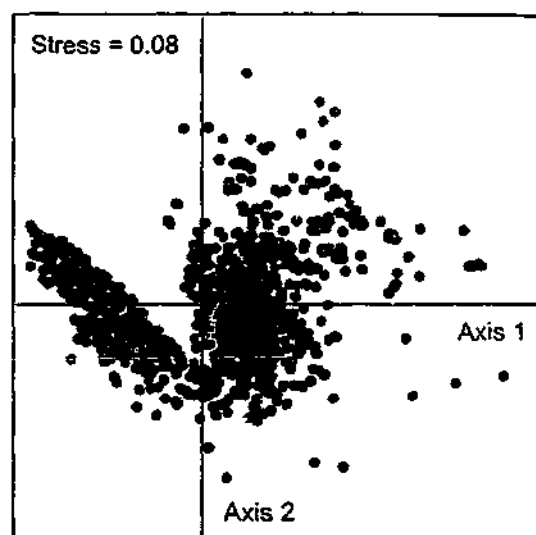
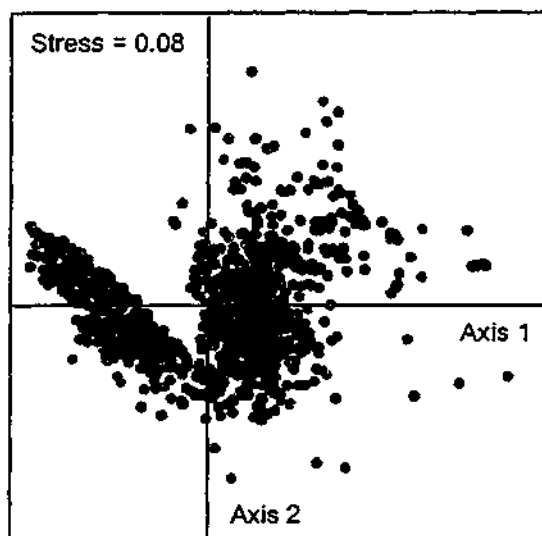
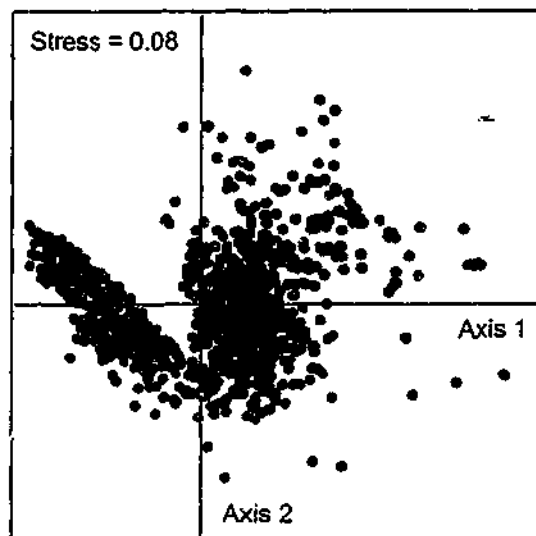
e) *Sloanea woollsii*f) *Heritiera trifoliolata*g) *Castanospermum australe*h) *Alstonia scholaris*

Figure 2.9 e-h Non-metric MDS ordination of the climates of site locations, including all the moisture variables. The site locations of individual species are overlaid (black) over all the sites in the ordination.

Climate variation within a year

There were many differences in the day-to-day variability of climate among the six locations from different latitudes within Australia (Table 2.17). The values for weekly standard deviation (WSD) in maximum temperature range from 3.3°C in Noojee to 1.2°C in Cairns. The remaining locations all had values of WSD in maximum temperature around 2°C. There was little difference in the values of WSD in minimum temperature among the locations except for Cairns, which had a significantly lower value. Values of WSD in precipitation range from 4 mm in Rockhampton to 9 mm in Coffs Harbour. All locations had values of WSD in maximum VPD between 0.3 and 0.4 kPa except for Rockhampton, which had a significantly higher value of 0.6 kPa. The WSD of minimum temperature showed the strongest regression with latitude, with the WSD of maximum temperature and maximum VPD showing weaker regressions with latitude (Table 2.17)

The above latitudinal trends in the WSD of climate variables were quite seasonal (Table 2.18). Both the WSD in maximum and minimum temperature showed significant linear increases with increasing latitude but only during the warmer months of autumn, spring and summer. The values of WSD in precipitation showed contrasting trends in different seasons: values increased with increasing latitude in winter whereas they decreased with increasing latitude in summer. An increase in the WSD of maximum VPD with decreasing latitude was only shown during the cooler months of autumn and winter.

Mean annual diurnal temperature range varied from 8.5 to 11.6°C among the species (Table 2.19). There was a distinct quadratic relationship between diurnal temperature range and the latitudinal origin of the species (Figure 2.10). Species from mid-latitudes showed the greatest diurnal temperature ranges. This trend was true during all seasons except winter when there was no relationship.

Table 2.17 Weekly standard deviations in climate variables for different locations in eastern Australia. Values are means of two years of meteorological data (1995 and 1996) with standard errors in brackets. The results of one-way ANOVAs among locations and linear regressions of latitude against the climate variables are given. Letters denote non-significant groupings of means.

Location		max. temp. (°C)	min. temp. (°C)	precipitation (mm)	max. VPD (kPa)
Strahan (42°S)		2.39 (0.06) ^a	2.49 (0.18) ^a	6.25 (0.62) ^{abc}	0.31 (0.01) ^b
Noojee (38°S)		3.28 (0.03)	2.43 (0.15) ^a	5.50 (0.04) ^{bc}	0.44 (0.02) ^{ab}
Merimbula (37°S)		2.02 (0.02) ^b	2.20 (0.00) ^a	4.66 (0.75) ^c	0.30 (0.01) ^b
Coffs Harbour (30°S)		2.15 (0.05) ^{ab}	2.39 (0.04) ^a	9.19 (0.68) ^a	0.38 (0.01) ^{ab}
Rockhampton (23°S)		2.00 (0.01) ^b	2.10 (0.02) ^a	3.97 (0.37) ^c	0.64 (0.04)
Cairns (17°S)		1.19 (0.06)	1.34 (0.04)	8.06 (0.01) ^{ab}	0.46 (0.03) ^a
ANOVA	<i>F</i>	248	19.8	15.7	32.3
	<i>p</i>	< 0.01	< 0.01	< 0.01	< 0.01
Linear regression	<i>F</i>	12.5	21.6	0.70	7.75
	<i>p</i>	0.01	< 0.01	0.42	0.02
	<i>r</i> ²	0.55	0.68	0.06	0.44

Table 2.18 Seasonal trends in weekly standard deviations of climate variables with increasing latitude. Results presented are linear regressions of mean values for two years of meteorological data (1995 & 1996) from the locations listed in Table 2.4.

		latitudinal trend	<i>F</i>	<i>p</i>	<i>r</i> ²
max. temp.	spring	+	9.58	0.01	0.49
	summer	+	8.63	0.01	0.46
	autumn	+	12.7	0.01	0.56
	winter	0	0.82	0.39	0.08
min. temp.	spring	+	7.85	0.02	0.44
	summer	+	34.0	<0.01	0.77
	autumn	+	47.7	<0.01	0.83
	winter	0	0.27	0.62	0.03
precipitation	spring	0	3.35	0.10	0.25
	summer	-	17.0	<0.01	0.63
	autumn	0	1.97	0.19	0.16
	winter	+	7.22	0.02	0.42
max. VPD	spring	0	4.34	0.06	0.30
	summer	0	2.52	0.14	0.20
	autumn	-	6.11	0.03	0.38
	winter	-	19.4	<0.01	0.66

Table 2.19 Diurnal temperature ranges annually and seasonally for the species. Values are means of the climate profiles for sites locations ($n > 60$) with standard errors in brackets.

Species	annual	spring	summer	autumn	winter
<i>E. lucida</i>	8.5 (0.1)	8.7 (0.1)	10.3 (0.1)	8.3 (0.1)	6.7 (0.1)
<i>N. cunninghamii</i>	8.6 (0.1)	8.9 (0.1)	10.8 (0.1)	8.5 (0.1)	6.4 (0.1)
<i>A. smithii</i>	10.8 (0.1)	11.8 (0.1)	10.5 (0.1)	10.0 (0.1)	10.8 (0.1)
<i>T. laurina</i>	11.2 (0.1)	12.1 (0.1)	10.6 (0.1)	10.6 (0.1)	11.7 (0.2)
<i>S. woollsii</i>	11.6 (0.1)	12.8 (0.1)	10.8 (0.1)	10.8 (0.1)	12.1 (0.1)
<i>H. trifoliolata</i>	10.7 (0.2)	11.9 (0.2)	10.0 (0.1)	10.0 (0.2)	11.2 (0.2)
<i>C. australe</i>	10.4 (0.2)	11.6 (0.2)	9.5 (0.1)	9.3 (0.2)	11.1 (0.2)
<i>A. scholaris</i>	9.2 (0.2)	10.3 (0.3)	10.7 (0.3)	8.3 (0.2)	9.7 (0.3)
Quadratic regression r^2	0.92	0.94	0.08	0.89	0.91

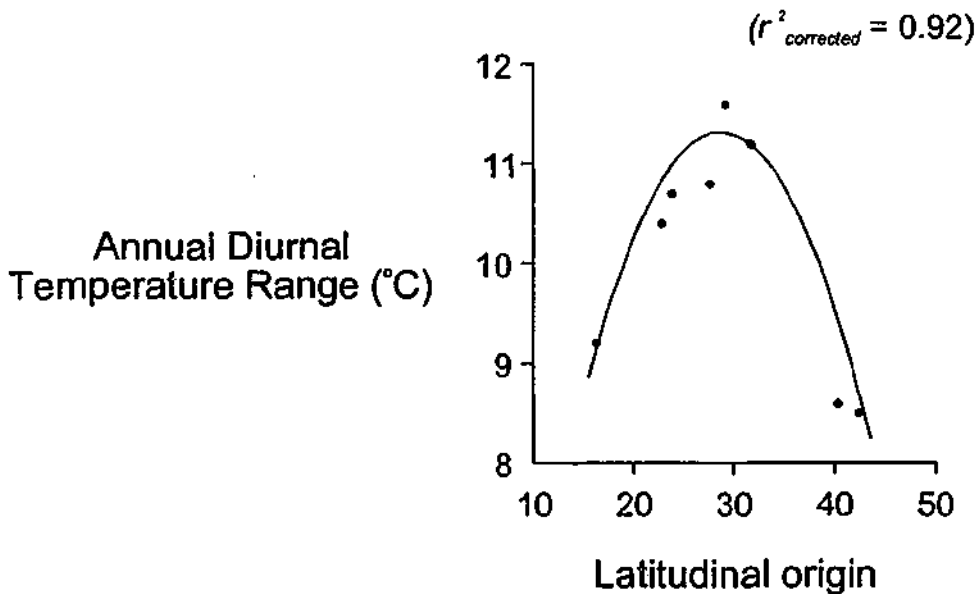


Figure 2.10 Relationship between the annual diurnal temperature range and the mean latitudinal origin of a species. Values of diurnal range are means of climate profiles for site locations ($n > 60$) for individual species.

DISCUSSION

Differences between the climate of tropical and temperate species

The rainforest species studied showed differences in both the magnitude and the temporal variability of climate variables. Some of the differences reflect established differences between temperate and tropical climates of Australia. However, most differences quantified trends that are specific to rainforests of eastern Australia.

The magnitude of temperature variables increased with decreasing latitudinal origin of the species (Table 2.6), which is also shown by the map of mean annual temperature in Australia (Figure 2.1). The seasonality of temperature increased with increasing latitudinal origin of the species, which has been previously noted for the climate of Australia (Nix 1982). In addition, day-to-day variability in temperature is greater in temperate climates than tropical climates of Australia (Table 2.17). These trends in temperature between the temperate and tropical species reflect the global trend of increasing magnitude and stability of temperatures from the poles to the equator (Atwell *et al.* 1999). However, diurnal temperature ranges followed a different pattern with species from mid-latitude rainforests showing slightly greater ranges (Table 2.19).

The climates of all

~~All of the~~ species showed high annual precipitation (> 1000 mm), which is characteristic of most rainforest species of Australia (Table 2.6, Webb & Tracey 1994). There was a trend of lower annual precipitation for species from mid-latitudes (*Acmena smithii*, *Sloanea woollsii* and *Tristanopsis laurina*) relative to those from high and low latitudes. This trend reflects the regions of highest annual precipitation in Australia (> 3000 mm) occurring in the mountainous region of western Tasmania and the northeast coast of Queensland around Cairns (Bureau of Meteorology 1989).

The seasonality of precipitation differed in several ways between the climates of the temperate and tropical species. Firstly, ^{the climates of} the two tropical species showed the lowest and highest monthly precipitation, with ten times as much precipitation falling in the wettest month as in the driest month (Table 2.6). Therefore, the tropical species experience more distinct wet and dry seasons than the temperate species. This is consistent with the greater seasonal variation in precipitation than in temperature in most tropical

climates (Reich 1995). Secondly, there was a shift from winter-dominant precipitation in the temperate species to summer-dominant precipitation in the tropical species, reflecting the known change in the distribution of precipitation in eastern Australia with latitude (Figure 2.2). Consequently, although precipitation is lower during the dry season of the tropical species, the dry season of the temperate species is likely to be more severe because it occurs during summer.

Trends in the variables evaporation, mean VPD and maximum VPD reflect those of temperature (Table 2.6). That is, their magnitude increased with decreasing latitude whereas their seasonality increased with increasing latitude. This is not surprising as both evaporation and vapour pressure deficit increase with increasing temperature (Penman 1948). Furthermore, the rate of evaporation is also related to the vapour pressure deficit and therefore both are measures of atmospheric water deficit. All species showed a higher magnitude of water deficit during the summer than in the winter, reflecting seasonal increases in temperature.

The difference in the seasonality of precipitation between the climates of the temperate and tropical species has important implications for their water budgets (Figure 2.3). During winter, the higher precipitation of the climate of the temperate species resulted in a higher water balance and moisture index than the tropical species. During the potentially more stressful season of summer, the higher precipitation of the tropical species resulted in a higher water balance than the temperate species. In contrast, the higher water deficits (evaporation and VPD) experienced in the tropics meant that the higher precipitation of the tropical species during summer did not produce greater soil moisture. However, the moisture index predicted a wider range of soil moisture among the temperate species than the tropical species during summer, with the warm-temperate species having the driest soils (Table 2.6). The lack of difference in soil moisture compared with water balance during summer between temperate and tropical species suggests that the important difference in water stress is the greater evaporative demand of the temperate summer.

The similarities among climates of several species reflected similarities in their geographical distributions. Firstly, all multivariate analyses showed that the climates of *E. lucida* and *N. cunninghamii* were not significantly different. This is not surprising as

the distribution of *E. lucida*, on a regional scale, is simply a subset of the wider distribution of *N. cunninghamii* (Figures 1.2 a & b). Secondly, the similarities between the climate profiles of *A. smithii* and *T. laurina* are related to the similarity in their overall distributions (Figures 1.2 c & d). Thirdly, the climate profiles of the warm-temperate and subtropical rainforest types, as well as their component species, were similar reflecting the large overlap of their distributions in the subtropics of northern New South Wales and southern Queensland (Figures 1.2c, 1.2d, 1.3a & 1.3b).

The overall differences in climate between the temperate and tropical rainforest species of this study are summarised in Table 2.20. Multivariate analysis showed that the difference between the climates of the temperate and tropical rainforest species was best described by the magnitude of the temperature and evaporation variables. This again shows the strong relationship between temperature and evaporation. In conclusion to the main aims:

1. variables of temperature and evaporation best described the differences among the climate of the species.
2. temperate climates of Australian rainforests showed a higher seasonal and day-to-day variability of temperatures than tropical climates.

Table 2.20 Summary of overall differences between the climates of the tropical and temperate rainforest species.

Climate variable		Temperate	Tropical
temperature	annual	low	high
	seasonality	high	low
	day-to-day variability	high	low
precipitation	annual	high	high
	seasonality	low	high
		winter-dominant	summer-dominant
evaporation	annual	low	high
	seasonality	high	low

Comparisons with other climate studies

Studies of the relationship between climate and rainforest types of Australia have concluded that temperature, presented as mean annual temperature, separates the major rainforest types (Webb 1968; Nix 1991). The amount of precipitation was used to further divide these major rainforest types into structural subformations. The present comparison of temperate and tropical species also found that temperature was an important difference in their climates. In contrast, evaporation instead of precipitation was found to be of equal importance to temperature. However, this reflects differences in the climate variables and scale used in this study compared with previous studies. The present study included more moisture variables than the previous studies, which although correlated with precipitation, fitted the pattern of climates among species better than precipitation. In addition, the previous studies included rainforest types from areas of lower precipitation (down to 500 mm annually) than those of the present study species.

Studies in both the dry and wet tropics of Australia have shown the importance of moisture variables to the distribution of rainforests. In the monsoonal rainforests of northern Australia, changes in floristic composition were best described by the decline in moisture towards the interior (Russell-Smith 1991). A study of rainforests in the wet

tropics of Queensland found that both indices of temperature and the seasonality of precipitation predicted the distribution of rainforest types at a broad scale (Mackey 1993a). However, a catchment hydrology index was a better predictor of structural types at a smaller scale (Mackey 1993b). Therefore, studies restricted to the tropics show a greater variation in moisture than temperature on a geographical scale, which mirrors the differences in the temporal variation of the climate.

A comparison of the climates of temperate rainforest species occurring in southeastern Australia by Hill *et al.* (1988) showed the equal importance of temperature and precipitation to their distribution. The major differences in climate between the southern and northern temperate species were: (i) the higher temperatures of the northern species, (ii) the higher precipitation of the southern species and (iii) the shift from winter-dominant rainfall in the south to a summer-dominant rainfall in the north. Similarly, analyses of the southern temperate species *N. cunninghamii* have found its distribution to be related to the amount of summer precipitation, but this may reflect its sensitivity to fire (Busby 1986; Lindenmayer *et al.* 2000). The higher precipitation in the southern species contrasts with the findings of this study and is a result of not including species from the wet tropics. When the climate analysis is restricted to the southern species found in Tasmania, the main difference between species is temperature, which reflects their altitudinal limits (Read & Busby 1990).

A broad latitudinal study of species of *Nothofagus* in Australia and New Guinea (spanning 44° of latitude) by Read (1990) found that the main differences between the temperate and tropical species were: (i) an increase in mean annual temperature with decreasing latitude and (ii) a greater diurnal and seasonal variation in temperature and precipitation of the temperate species (Read 1990). The present study differs from the above study in finding a greater seasonality of precipitation in the tropical species and a greater diurnal variation in temperature at mid-latitudes. However, this reflects the different origin of the tropical species with those of *Nothofagus* coming from the less seasonal tropics of New Guinea and those in this study coming from the seasonal tropics of Queensland. From the above climate analyses, it is obvious that the scale of the analysis determines which factors best predict the distribution of Australian rainforest species. However, at the continental scale it appears that both temperature and moisture variables are important predictors.

Climate analyses of *Nothofagus* and other common tree species in New Zealand have concluded that temperature is the primary factor determining their latitudinal distribution (Mitchell 1991; Leathwick & Mitchell 1992; Leathwick 1995).

Precipitation is less important to the distribution of tree species within forests of New Zealand as most forests have adequate soil moisture throughout the year (Leathwick 1995). In relation to the other broad-leaved trees of New Zealand, *Nothofagus* species are dominant on the cooler and drier sites (Wardle 1964), and in this respect they are seen as stress tolerators (*sensu* Grime 1979). The absence of *Nothofagus* from the mild and wet climate of central New Zealand has been explained by this restriction to suboptimal sites (Haase 1990) but the greater geological instability of the area has also been implicated (Leathwick 1998). Similarly, temperate rainforest species in Australia, of which *Nothofagus* is a dominant, are believed to be restricted to suboptimal sites by the more competitive subtropical species (Hill *et al.* 1988).

Several models have predicted the distribution of vegetation types in Australia from physiological responses to climate variables. Both Specht (1981) and Nix (1982) proposed similar growth indices based on temperature and moisture that predicted the broad patterns of vegetation types and species composition in Australia. Underlying these models was the assumption that plants fall into broad thermal response types, each showing maximum growth over a different temperature range. In his model, Nix (1982) emphasised the importance of temperature, annual precipitation, and seasonality of precipitation to the distribution of plants in Australia. Recently, a climate model was developed for Australia that predicted broad vegetation types based on the trade-off between light capture and water stress alone but it did not explain changes in composition within types (Haxeltine *et al.* 1996). On a smaller scale, Austin and Gaywood (1984) found that the probabilities of occurrence of species of *Eucalyptus* in southern Australia showed distinct response curves to both annual mean temperature and precipitation, which could then be used to predict their distribution (Austin *et al.* 1990). All these models emphasise the importance of physiological responses to temperature and water availability to the broad patterns of species distribution in Australia.

Global vegetation-climate models tend to include a temperature parameter to delimit forest types, and some estimate of water availability to delimit physiognomic types (see Table 2.21). In this study, minimum and maximum temperatures were also important predictors of the distribution of the rainforest species. Although a moisture index was used in this study, differences in climate among the species were better described by evaporation, water balance and maximum VPD. Many climate models use a temperature sum to estimate the length of the growing season (eg. Woodward 1987; Prentice *et al.* 1992; Box 1995). A temperature sum was not used in this study as the response of plants to temperature is not additive, with the relationship between growth and temperature being nonlinear. Consequently, plants will react differently to climates with the same temperature sum but different lengths of growing season and different temperature extremes (Schenk 1996). At a regional scale, the seasonality of water availability becomes an important predictor of plant distributions (Table 2.21). An important difference between the species in this study was also the seasonality of water availability.

The distribution of a species may be correlated with variables of the present climate but that does not mean the distribution limits are determined by those climate variables (Carey *et al.* 1995). Other factors that could be determining distributional limits include past geological and climatic events, geographical barriers, disturbance, soil type, dispersal, competition, predators and pathogens. However, these factors do not act independently of climate, for example, fire increases with reduced precipitation and increased temperatures (Stephenson 1998; Kirschbaum 2000). Furthermore, these other factors may only become important when the climate is marginal (Mitchell 1991).

Possible strategies of trees to compete under different climates

Several climate models have proposed physiological explanations for how the predicted climate variables could control the distribution of plant species (eg. Box 1981; Woodward 1987; Prentice *et al.* 1992). These have included freezing tolerance, chilling requirements, length of warm growing season requirements and drought tolerance. Woodward (1987) also suggested that the cost of a greater tolerance of extreme conditions was a reduced competitive ability under more favourable conditions. In general, climate models explain the distributional limits of species by an intolerance of

Table 2.21 Climate variables found to best predict the distribution of vegetation in previous studies.

Type/source	Scale	Predictive variables
<u>Global vegetation patterns</u>		
Box (1981)		temperature, precipitation & moisture index.
Woodward (1987)		min. temperature & water balance.
Prentice <i>et al.</i> (1992)		min. temperature, temperature sum & actual/equilibrium evapotranspiration.
Box (1995)		min. and max. temperatures, temperature sum & moisture index.
<u>Regional vegetation types</u>		
Fang and Yoda (1989)	China	temperature sum
Looman (1983)	Canada	summer/spring precipitation.
Neilson (1995)	U. S. A.	water balance.
Sowell (1985)	North America	temperature, precipitation & seasonality.
Stephenson (1990)	North America	water balance.
<u>Regional forest types</u>		
Brzeziecki <i>et al.</i> (1995)	Switzerland	mean annual temperature.
Fang and Yoda (1990a; 1990b; 1991)	China	temperature sum, min. temperature & moisture index.
Gavilán and Fernández-González (1997)	Spain	temperature, annual and seasonal water availability.
Stephenson (1998)	California	evapotranspiration & water deficit.
<u>Species distributions</u>		
Cao <i>et al.</i> (1995)	China	high temperatures & water deficit.
Franklin (1998)	California	min. and max. temperature & annual precipitation.
Huntley <i>et al.</i> (1995)	Europe	min. temperature, temperature sum & actual/equilibrium evapotranspiration.
Leniham (1993)	North America	temperature sum, min. temperature, moisture index & summer evapotranspiration.
Parker (1994)	California	annual precipitation, summer temperature and summer precipitation.
Shao and Halpin (1995)	Eastern U.S.A.	evapotranspiration and temperature sum.
Sykes <i>et al.</i> (1996)	Europe	temperature sum, min. temperature & growing season moisture.

extremes at high latitudes and competitive exclusion at low latitudes. This concept is no different to the earlier proposals of Dobzhansky (1950) and MacArthur (1972) that biotic factors will limit distributions at low latitudes whereas abiotic factors will be more important at high latitudes. However, competition is likely to determine both the low and high latitude limits of species well before they reach their tolerance limits.

The present study has shown that the magnitudes of temperature and evaporation, and the seasonality of temperature and precipitation are the most important differences among the climates of rainforest species of eastern Australia. However, whether the climate variables that show the greatest variation with latitude will be the most biologically significant is uncertain. With respect to temperature, possible physiological factors explaining the distribution of rainforest trees include different responses of growth and photosynthesis to temperature. There are likely to be differences in the growth temperatures for maximum net photosynthesis between temperate and tropical rainforest species and these will be investigated in Chapter 4. As predicted by Nix (1991), the rainforest species may have maximum growth at temperatures representative of their native climates. However, higher growth rates of tropical species at high temperatures or broader tolerances of temperature in the temperate species might also be important differences. These different possibilities will be investigated in Chapter 5. The greater seasonal variability in temperature experienced by temperate species may reflect a greater ability to maintain maximum net photosynthesis during changes in growth temperature than tropical species, which is the focus of Chapter 6. With respect to water stress, the difference between temperate and tropical species may be in their strategies to tolerate the evaporative demands of summer. The species may differ in the response of net photosynthesis and growth to vapour pressure deficit. These differences will be investigated in Chapters 7 and 8.

CHAPTER 3

Responses of net photosynthesis to growth irradiance

Rainforest tree species differ in the range of light environments in which they can regenerate. Tree species that form the canopy of rainforests range from shade-intolerant species that can only regenerate in full sunlight, to shade-tolerant species which are most competitive in heavy shade. The shade tolerance of a tree species can be characterised by the response of net photosynthesis to different growth irradiances.

The response of net photosynthesis to increasing irradiance has several characteristic points (see Figure 3.1). The *light compensation point*, where photosynthesis and respiration are equal, occurs at very low irradiances. Beyond this point, at low irradiances, net photosynthesis increases linearly with irradiance. This initial rate of increase in net photosynthesis is known as the *quantum yield*. Then at intermediate irradiances, the increase in net photosynthesis becomes less linear with increasing irradiance. Ultimately, an irradiance level, known as the *light-saturation point*, is reached, above which further increases do not increase the net photosynthetic rate (Larcher 1980; Björkman 1981b).

The form of the photosynthetic light-response curve of a leaf is dependent on the irradiance level of its growth environment (see Figure 3.1). Leaves grown in full sunlight tend to have higher light-saturated net photosynthetic rates, light saturation points, light compensation points and dark respiration rates than leaves grown in the shade (Boardman 1977; Björkman 1981b). Leaves developed in sunlight also tend to have lower area per unit mass (specific leaf area, Evans 1996). Consequently, differences in light-saturated net photosynthesis between sun and shade leaves apparent on an area basis often disappear when expressed on a per unit mass basis (Kitajima 1994).

Shade-tolerant species are characterised by an inability to increase the light-saturated rate of net photosynthesis with increases in growth irradiance. In some species, growth at high irradiances results in a reduction in the light-saturated rate of net photosynthesis due to photoinhibition (Björkman 1981b). Shade-tolerant species tend to have lower light-saturated net photosynthetic rates, light saturation points, light compensation points and dark respiration rates than shade-intolerant species (Patterson 1980; Strauss-Debenedetti & Bazzaz 1996).

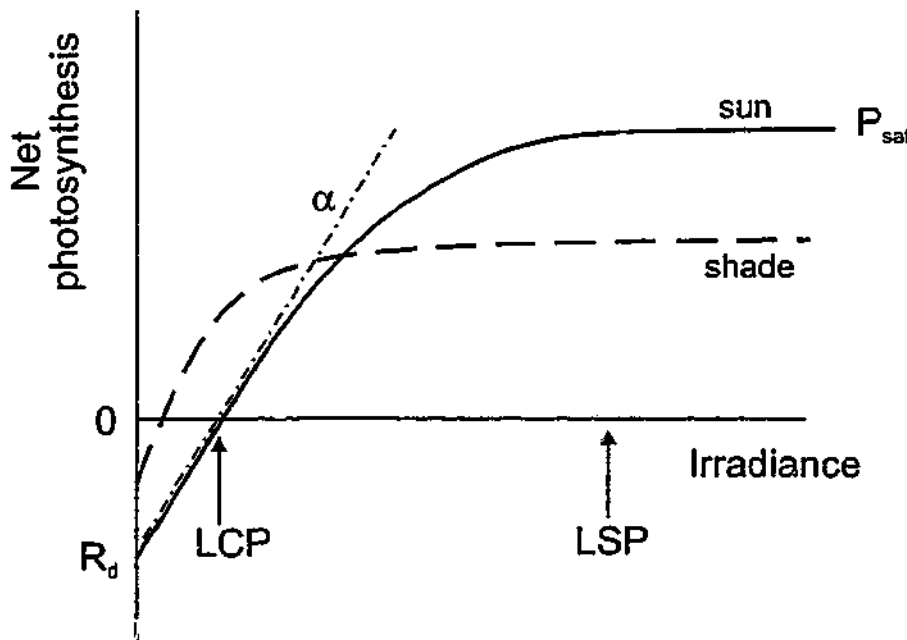


Figure 3.1 Typical photosynthetic light-response curves for sun (solid line) and shade (dashed line) grown leaves. The derivation of several parameters is indicated on the curve for the sun leaf. These parameters include the light-saturated net photosynthetic rate (P_{sat}), the light saturation point (LSP), the light compensation point (LCP), the quantum yield (α) and the dark respiration rate (R_d)

Rainforest species can be broadly classified into those that can establish in large gaps following disturbance (early successional) and those which establish under a mature canopy (late successional). There is of course a spectrum of species ranging between these extremes. Initially, early successional species were predicted to show greater acclimation of photosynthesis to changing irradiance than late successional species because of greater variability in their environments (Bazzaz 1979). However, late successional species are exposed to various light environments as they grow from the

shaded understorey, with short-term sunflecks, through different canopy layers to the upper canopy (Bazzaz & Pickett 1980). Therefore, Pearcy (1987) proposed that late successional species should also show photosynthetic acclimation to changes in irradiance levels. The hypothesis that early successional species have a greater acclimation ability than late successional species is supported by some studies (Oberbauer & Strain 1984; Kwesiga *et al.* 1986; Strauss-Dedenedetti & Bazzaz 1991), but not by others (Langenheim *et al.* 1984; Ramos & Grace 1990; Turnbull 1991). Recent work in the rainforests of Panama has shown that shade-tolerant species grow in lower but more variable irradiance environments and show a similar acclimation ability to shade-intolerant species (Ellis *et al.* 2000). Therefore, the photosynthetic response to growth irradiance of a canopy species can not be simply determined from its regeneration niche.

Studies of Australian rainforest species found that species that are rarely present in the upper canopy showed a reduced photosynthetic plasticity to irradiance compared with upper canopy species (Read 1985; Read & Hill 1985). These species also showed narrower photosynthetic responses to temperature than would be predicted from their climatic distributions (Hill *et al.* 1988; Read & Busby 1990). Therefore, it was desirable for this thesis to select upper canopy species, which are more likely to show adaptations to the macroclimate. In addition, an attempt was made to select species that can only establish in large canopy gaps to ensure an ability to acclimate to high irradiance. For many species, particularly those of tropical rainforests, it was not possible to obtain information on their gap tolerance. However, as already stated, the ability to acclimate to changing irradiance can not be predicted from its ability to establish under shade. The aim of this chapter, therefore, was to investigate the photosynthetic shade-tolerance of the study species using a shading experiment. The specific aims were:

1. to determine the photosynthetic shade-tolerance of the selected species, which indicates the potential flexibility of the photosynthetic apparatus to temperature.
2. to determine the light saturation points of each species in full sunlight, so that a saturating level of irradiance levels could be used in the main experiments.

METHODS

Seedling collection and raising

For most of the species, small seedlings (< 10 cm tall) were collected in the field. However, this was not possible for the tropical species (*Alstonia scholaris* and *Castanospermum australe*), so seed was obtained for these species. Seedlings collected from the field were bare-rooted and planted into seedling trays containing vermiculite. Seed of the two tropical species was germinated in trays of DEBCO potting mixture (DEBCO, Australia). The seedlings were raised in a propagating house, fitted with a misting system, until all seedlings had produced two pairs of new leaves. At this stage, the seedlings were potted into 75 ml plastic bag pots using a sterilised organic/sand soil mix and moved into two glasshouses.

Seedlings of each species were randomly positioned throughout the two glasshouses. The glasshouses were heated during the cooler months so that the night temperature did not fall below 10°C. The glasshouses were whitewashed during summer to reduce temperatures, which can reach over 50°C during summer. The irradiance within these whitewashed glasshouses was $330 \pm 32 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ at midday on a sunny day. On days above 30°C, 90% shade cloth was used to cover the top half of the glasshouses to further reduce the temperature. This procedure resulted in air temperatures within the glasshouse being closed to external air temperatures. However, the combination of whitewashing and shade cloth reduced the light levels to $102 \pm 11 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$.

Pots were watered regularly to ensure that soil never dried out. Fertiliser was added to the soil every four weeks in the form AQUASOL (Hortico (Aust.) Pty Ltd) at seedling strength (4g/5L). Seedlings of many species began dying after six months and the problem appeared to be a combination of soil toxicity and poor drainage. All seedlings were replanted into DEBCO potting mixture, which has a lower organic content. After replanting in the new soil, seedlings of all species showed healthy growth. Fertiliser was added in the form of FOGG-IT fish emulsion fertilizer (FOGG-IT Nozzle Company, San Francisco) diluted 1/500 with water to provide 98 mg L⁻¹ of nitrogen, 20 mg L⁻¹ of potassium, and 31 mg L⁻¹ of phosphorus.

Irradiance treatments

Seedlings of each species were grown in two contrasting light regimes to determine their shade tolerances. These irradiances were recorded at midday on a clear day during the experiment. The experiment was set up as a split plot design within a single glasshouse. There were eight plots in total with four plots per irradiance treatment. Two seedlings of each species were placed randomly within each plot. The shade treatment was achieved by enclosing the plot in a frame of 70% shade cloth. Plots were spaced far enough apart that the shade boxes did not shade adjacent sunlight plots for at least nine hours of the day. Seedlings were spaced within plots such that adjacent seedlings did not shade them during this period. The crowns of all seedlings were raised to the same height so that all new leaves developed at a similar irradiance level. Irradiance levels at crown height, measured at midday on a cloudless day were 150 ± 17 and $1021 \pm 43 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ for the shade and sunlight treatments respectively. Seedlings were watered at least every three days, and more frequently during hot weather. Fertiliser was added, in the form of diluted FOGG-IT fish emulsion, every two weeks to ensure that nutrients were not limiting.

Seedlings were tagged at the beginning of the experiment and the development of leaves was recorded every week to determine when enough new leaves were fully expanded for photosynthetic measurements. Photosynthetic measurements were begun after eight weeks when enough leaves had expanded. Seedlings were selected randomly for measurement and watered the night before measurement to ensure they were fully hydrated during measurement.

Photosynthetic measurements

Photosynthesis was measured using an LCA4 Infrared gas analyser (ADC, United Kingdom), which is an open gas system. Using this system, it was possible to control the air temperature ($\pm 0.5^\circ\text{C}$), the vapour pressure deficit ($\pm 0.05 \text{ kPa}$) and the CO_2 concentration ($\pm 5 \text{ ppm}$) within the leaf chamber. During photosynthetic measurements, the vapour pressure deficit was kept at a constant 0.7 kPa , the temperature at 22°C and the CO_2 concentration at 350 ppm . The irradiance source was from a slide projector containing a Phillips Projection Lamp globe Type 7748S 250W. Photographic film

was exposed for different lengths of time to produce filters for altering the irradiance level.

Photosynthetic measurements were taken from the leaves of eight seedlings per species per treatment. A single leaf (or leaves in the case of *Nothofagus cunninghamii*) was placed in the chamber to equilibrate at an irradiance of $770 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. After fifteen minutes, five readings of net photosynthetic rate were taken every five minutes, until the leaf was equilibrated to the environment within the leaf chamber. The leaf was determined as equilibrated when there was less than 3% difference in the means of three consecutive sets of rates. The irradiance level was then raised and the assimilation rate measured after five minutes. The time interval of five minutes was decided upon after it was found that there was less than 3% difference in measurements after three minutes at a new irradiance level. The irradiance was changed in the sequence 770, 990, 1500, 770, 560, 165, 120, 80, 35, 15 and $0 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. After the measurement at $1500 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, the leaf was kept at $770 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ until the net photosynthetic rate was within 3% of the original rate. Darkness ($0 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$) was achieved by placing a reflective aluminium cover over the leaf chamber window and placing a black plastic bag over the whole plant and the leaf chamber.

The portion of leaf or leaves within the leaf chamber during measurement was dissected and the area determined using image analysis (BIOSCANTM Image Analyser). The leaf sections were also dried in an oven at 75°C for four days (to constant weight) to determine dry weights. In the case of *N. cunninghamii*, a portion of stem was inside the leaf chamber during measurements. The respiration rate of the stems was measured, at an irradiance of $770 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, a week after the leaves had been removed.

Data analysis

The net photosynthesis versus irradiance data were regressed using the Bannister (1979) equation. This equation was chosen over the more widely used rectangular hyperbola (Baly 1935) and non-rectangular hyperbola (Prioul & Chartier 1977) as they tend to over estimate the values of light-saturated net photosynthesis for data with sharp transitions from light-limited to light-saturated net photosynthesis (Henley 1993). The Bannister equation has the following form:

$$P = P_{\text{sat}} \{(\alpha I) / [P_{\text{sat}}^c + (\alpha I)^c]^{1/c}\} + R_d \quad (\text{equation 3.1})$$

where P_{sat} is the light-saturated net photosynthetic rate, α is the quantum yield, I is the irradiance level, c is the curvature parameter and R_d is the dark respiration rate.

The regression equations were used to determine several other parameters besides P_{sat} , α and c . The light-saturation point of net photosynthesis (LSP) was determined as the irradiance at which an increase in irradiance of $1000 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ would only increase the photosynthetic rate by $0.5 \mu\text{mol quanta}^{-1} \text{ m}^{-2} \text{ s}^{-1}$. The light compensation point of net photosynthesis (LCP) was determined as the irradiance at which the net photosynthesis was zero. The net photosynthetic rate at the low irradiance of $50 \mu\text{mol quanta}^{-1} \text{ m}^{-2} \text{ s}^{-1}$ (P_{50}) was also determined using the regression equations. The dark respiration rates determined directly were used instead of those derived from the Bannister equation. The parameters P_{sat} , P_{50} and R_d were expressed per unit area and per unit mass.

These data were analyzed as a split-plot design with irradiance as the between plot effect and species as the within plot effect. For each species, the mean values of the two subreplicate plants within each plot were used. For parameters that showed a significant effect of growth irradiance or interaction between irradiance and species, comparisons of irradiance treatments within a species were analyzed as a one-way ANOVA. Comparisons of species within an irradiance treatment were analyzed as a randomized complete block design with plot as the blocking variable.

RESULTS

All the species, except for *Castanospermum australe*, showed distinct differences between the net photosynthetic response to instantaneous irradiances of leaves grown in shade and sunlight (Figure 3.2). Most parameters were significantly affected by irradiance or showed a significant irradiance by species interaction (Table 3.1). The two parameters unaffected by irradiance were the quantum yield (α) and the curvature (c).

The magnitude of light-saturated net photosynthesis in sun-grown leaves varied, with the species falling into three groups: 4-5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (*C. australe*, *Sloanea woollsii* and *Eucryphia lucida*), 7-8 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (*Alstonia scholaris*, *Acmena smithii*, *Heritiera trifoliolata* and *Nothofagus cunninghamii*) and 10 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (*Tristaniaopsis laurina*; Table 3.2). The light-saturated net photosynthetic rate per unit area of all species, except for *C. australe*, was significantly higher in leaves grown in sunlight compared with those grown in shade (Table 3.3). In contrast, light-saturated net photosynthetic rates per unit mass were not significantly different between growth irradiances for most species (Table 3.3). However, *H. trifoliolata* showed a significantly higher light-saturated net photosynthetic rate per unit mass when grown in sunlight compared with shade.

Dark respiration rates ranged from $0.23 \pm 0.09 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ to $0.83 \pm 0.03 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Table 3.3). There was a trend of decreased dark respiration per unit area in shade-grown leaves compared with sunlight-grown leaves (Table 3.3). However, this difference was only significant for *A. scholaris*. By comparison, the difference in dark respiration per unit mass was significant for *A. smithii*, *A. scholaris*, *S. woollsii* and *T. laurina* (Table 3.3).

Few species showed differences in net photosynthesis at low irradiance ($50 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) between leaves grown in shade and sunlight (Table 3.3). The species *A. smithii*, *S. woollsii* and *C. australe* showed significant increases in net photosynthesis at low irradiance on an area basis when grown in shade compared with sunlight.

Castanospermum australe was the only species to showed a significant increase in net

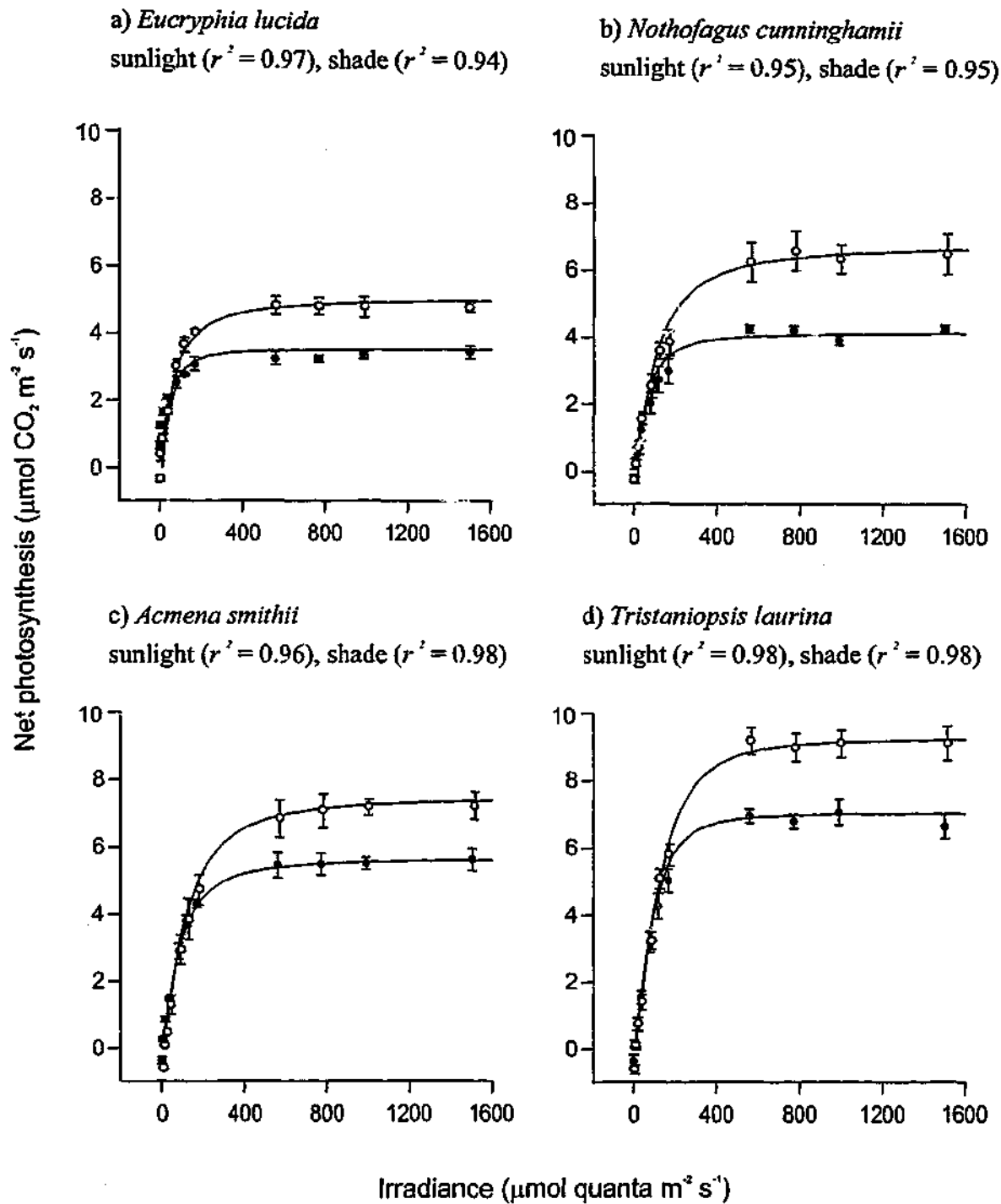


Figure 3.2 a-d Relationship between net photosynthesis and irradiance for different species. The sunlight treatment is represented by open squares (\square) and the shade treatment is represented by closed circles (\bullet). Values of net photosynthesis are means of four plots with standard errors represented by bars.

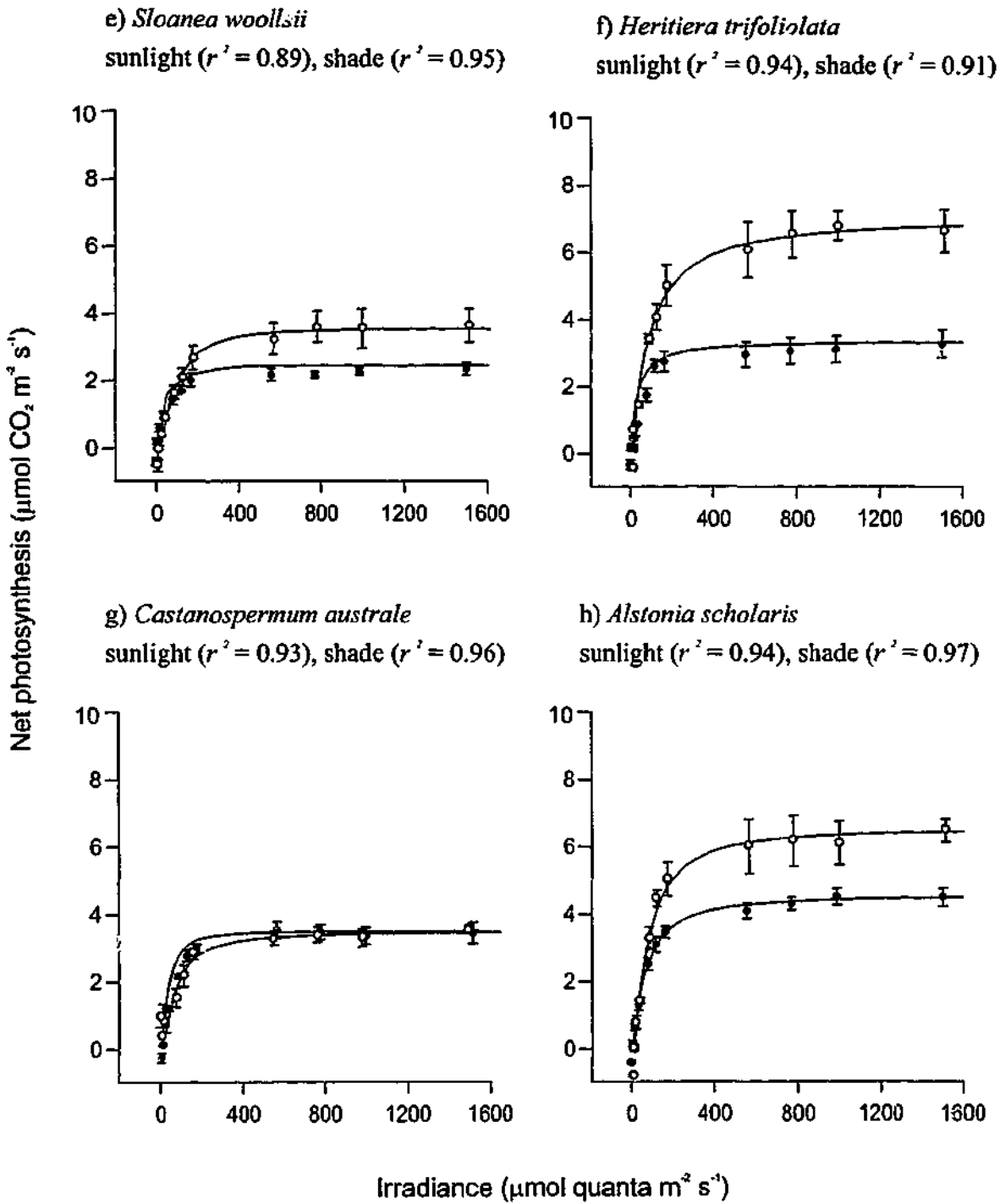


Figure 3.2 e-h Relationship between net photosynthesis and irradiance for different species.

Table 3.1 Results of split-plot ANOVAs for the various parameters describing the photosynthetic response to irradiance.

Parameter	Hypothesis test	<i>F</i>	<i>p</i>
P_{sat} (area)	irradiance	184	<0.01
	species	72.6	<0.01
	irradiance \times species	13.0	<0.01
P_{sat} (mass)	irradiance	0.08	0.79
	species	12.7	<0.01
	irradiance \times species	5.04	<0.01
R_d (area)	irradiance	11.6	0.01
	species	2.63	0.02
	irradiance \times species	1.38	0.24
R_d (mass)	irradiance	53.6	<0.01
	species	6.61	<0.01
	irradiance \times species	2.78	0.02
P_{50} (area)	irradiance	1.48	0.27
	species	12.1	<0.01
	irradiance \times species	6.46	<0.01
P_{50} (mass)	irradiance	29.1	<0.01
	species	6.79	<0.01
	irradiance \times species	2.53	0.03
LSP	irradiance	138	<0.01
	species	3.96	<0.01
	irradiance \times species	0.67	0.69
LCP	irradiance	7.70	0.03
	species	1.03	0.42
	irradiance \times species	2.13	0.06
α	irradiance	0.96	0.37
	species	0.99	0.45
	irradiance \times species	0.81	0.58
<i>c</i>	irradiance	0.19	0.68
	species	3.74	<0.01
	irradiance \times species	0.32	0.94

Table 3.2 Light-saturated net photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of leaves grown in sunlight. Values are means of four blocks and standard errors are given in brackets. Letters denote non-significant groupings of means.

Species		
<i>Eucryphia lucida</i>		4.97 (0.29) ^b
<i>Nothofagus cunninghamii</i>		7.27 (0.51) ^a
<i>Acmena smithii</i>		7.85 (0.33) ^a
<i>Tristaniopsis laurina</i>		9.68 (0.27)
<i>Sloanea woollsii</i>		4.14 (0.22) ^b
<i>Heritiera trifoliolata</i>		7.45 (0.38) ^a
<i>Castanospermum australe</i>		3.63 (0.17) ^b
<i>Alstonia scholaris</i>		7.09 (0.36) ^a
<hr/>		
Species	<i>F</i>	37.0
	<i>p</i>	< 0.01
Block	<i>F</i>	0.64
	<i>p</i>	0.60

Table 3.3 Photosynthetic parameters of leaves grown in sun and shade. Parameters included are light-saturated net photosynthetic rate (P_{sat}), dark respiration (R_d) and net photosynthetic rate at low irradiance (P_{50}) expressed both per area and per mass. Values are means of four blocks and standard errors are given in brackets. Asterisks indicate significant differences in a parameter between growth irradiances within a species.

Species	Growth Irradiance	P_{sat} (area) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	P_{sat} (mass) ($\mu\text{mol g}^{-1} \text{ s}^{-1}$)	R_d (area) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	R_d (mass) ($\mu\text{mol g}^{-1} \text{ s}^{-1}$)	P_{50} (area) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	P_{50} (mass) ($\mu\text{mol g}^{-1} \text{ s}^{-1}$)
<i>E. lucida</i>	sun	4.97 (0.29) *	88.3 (5.4)	0.39 (0.08)	12.9 (2.5)	2.19 (0.08) *	38.5 (3.0)
	shade	3.98 (0.24)	123.2 (15.4)	0.51 (0.09)	9.2 (2.1)	1.75 (0.15)	61.4 (11.2)
<i>N. cunninghamii</i>	sun	7.27 (0.51) *	101.7 (7.7)	0.32 (0.08)	5.9 (1.4)	1.80 (0.17)	25.4 (2.6)
	shade	4.29 (0.29)	76.5 (8.3)	0.23 (0.09)	3.2 (1.2)	1.54 (0.27)	29.1 (5.3)
<i>A. smithii</i>	sun	7.85 (0.33) *	112.0 (9.4)	0.57 (0.08)	12.3 (2.1) *	1.87 (0.25)	29.1 (3.7) *
	shade	5.83 (0.29)	121.2 (6.7)	0.39 (0.08)	6.2 (1.5)	2.08 (0.09)	44.6 (1.3)
<i>T. laurina</i>	sun	9.68 (0.27) *	145.5 (9.2)	0.79 (0.14)	19.6 (4.0) *	2.05 (0.17)	31.3 (3.5)
	shade	7.21 (0.31)	172.7 (13.7)	0.39 (0.16)	5.6 (2.1)	2.07 (0.19)	51.6 (7.4)
<i>S. woollsii</i>	sun	4.14 (0.22) *	91.6 (7.2)	0.57 (0.14)	22.1 (4.6) *	1.16 (0.13)	25.2 (2.9) *
	shade	2.82 (0.11)	120.4 (22.0)	0.42 (0.09)	9.2 (2.2)	1.22 (0.08)	48.9 (8.8)
<i>H. trifoliolata</i>	sun	7.45 (0.38) *	129.2 (17.9) *	0.45 (0.09)	8.0 (1.8)	2.16 (0.06) *	32.6 (1.8) *
	shade	3.65 (0.18)	64.9 (2.5)	0.35 (0.12)	5.4 (1.9)	1.26 (0.05)	22.0 (1.9)
<i>C. australe</i>	sun	3.63 (0.17)	75.2 (10.3)	0.40 (0.12)	9.7 (3.3)	0.77 (0.18) *	14.2 (3.0) *
	shade	3.70 (0.21)	87.8 (7.8)	0.30 (0.12)	5.4 (2.0)	1.62 (0.05)	38.5 (0.9)
<i>A. scholaris</i>	sun	7.09 (0.36) *	144.5 (12.2)	0.83 (0.03) *	25.4 (1.0) *	2.23 (0.12)	46.2 (7.3)
	shade	4.87 (0.21)	139.7 (8.8)	0.43 (0.04)	8.9 (1.3)	1.83 (0.14)	56.9 (7.6)

photosynthesis at low irradiance on a mass basis when grown in shade compared with sunlight. In contrast, *H. trifoliolata* and *E. lucida* showed significant decreases in net photosynthesis at low irradiance on a area basis, and also on a mass basis for *H. trifoliolata*, when grown in shade compared with sunlight.

Light saturation points for net photosynthesis of leaves grown in sunlight ranged from $567 \pm 62 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ for *C. australe*, to $867 \pm 97 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ for *T. laurina* (Table 3.4). However, there were no significant differences between the light saturation points of the species when grown in sunlight ($F = 1.39, p = 0.26$). All species showed a trend of lower light saturation points for net photosynthesis in leaves grown in shade than in leaves grown in sunlight, but this was only significant for five of the species.

Light compensation points ranged from 2.9 ± 0.5 to $12.9 \pm 6.3 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ among species (Table 3.4). *Acmena smithii* and *A. scholaris* were the only species to show a significantly higher light compensation point for net photosynthesis in leaves grown in sunlight compared with leaves grown in the shade.

Five of the eight species showed a significant increase in the specific leaf area (SLA) of leaves grown in shade compared with leaves grown in sunlight (Table 3.5). Both *H. trifoliolata* and *C. australe* showed no significant difference between the SLA of leaves grown in shade and sunlight. In contrast, *T. laurina* was the only species to show a significant decrease in the SLA of leaves grown in shade compared with leaves grown in sunlight.

Table 3.4 Photosynthetic parameters of leaves grown in sun and shade. Parameters included are light-saturation point (LSP), light compensation point (LCP), quantum yield (α) and curvature of the response (c). Values are means of four blocks and standard errors are given in brackets. Asterisks indicate significant differences in a parameter between growth irradiances within a species.

Species	Growth Irradiance	LSP ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$)	LCP ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$)	α ($\text{mol CO}_2 \text{ mol quanta}^{-1}$)	c
<i>E. lucida</i>	sun	645 (68) *	3.48 (1.36)	0.06 (0.01)	1.31 (0.02)
	shade	334 (11)	8.28 (1.55)	0.07 (0.01)	1.73 (0.21)
<i>N. cunninghamii</i>	sun	732 (132)	2.86 (0.45)	0.06 (0.01)	1.33 (0.34)
	shade	453 (64)	3.64 (1.32)	0.05 (0.02)	1.58 (0.32)
<i>A. smithii</i>	sun	805 (110)	7.64 (1.03) *	0.05 (0.01)	1.60 (0.20)
	shade	655 (55)	3.30 (1.01)	0.05 (0.00)	1.60 (0.05)
<i>T. laurina</i>	sun	867 (97) *	8.33 (2.14)	0.05 (0.00)	2.14 (0.27)
	shade	556 (77)	4.02 (2.19)	0.05 (0.00)	2.24 (0.45)
<i>S. woollsii</i>	sun	664 (44) *	7.87 (1.08)	0.07 (0.03)	1.38 (0.38)
	shade	327 (38)	4.41 (1.42)	0.20 (0.10)	1.22 (0.11)
<i>H. trifoliolata</i>	sun	839 (93) *	5.41 (1.29)	0.08 (0.01)	1.09 (0.16)
	shade	437 (61)	4.11 (1.14)	0.11 (0.07)	1.06 (0.18)
<i>C. australe</i>	sun	567 (62)	12.93 (6.26)	0.11 (0.09)	1.66 (0.43)
	shade	394 (41)	3.37 (0.82)	0.06 (0.03)	1.84 (0.34)
<i>A. scholaris</i>	sun	793 (32) *	8.68 (0.71) *	0.07 (0.01)	1.39 (0.11)
	shade	557 (15)	5.39 (0.90)	0.06 (0.01)	1.27 (0.07)

Table 3.5 Values of specific leaf area ($\text{m}^2 \text{kg}^{-1}$) for leaves initiated in different irradiance levels. Values are means of four blocks and standard errors are given in brackets.

Species	Growth Irradiance		<i>F</i>	<i>P</i>
	sun	shade		
<i>Eucryphia lucida</i>	18.0 (1.4)	31.1 (3.9)	10.3	0.02
<i>Nothofagus cunninghamii</i>	14.0 (0.4)	17.7 (0.9)	14.1	0.01
<i>Acmena smithii</i>	14.2 (0.6)	20.8 (0.7)	49.8	< 0.01
<i>Tristaniopsis laurina</i>	15.0 (0.9)	24.0 (1.9)	18.8	< 0.01
<i>Sloanea woollsii</i>	22.0 (0.8)	43.5 (9.0)	5.70	0.05
<i>Heritiera trifoliolata</i>	17.3 (2.0)	17.8 (0.3)	0.08	0.79
<i>Castanospermum australe</i>	20.8 (2.9)	23.7 (1.2)	0.84	0.39
<i>Alstonia scholaris</i>	20.3 (0.8)	28.8 (2.0)	16.3	0.01

DISCUSSION

The eight study species showed distinct differences between the photosynthetic response to instantaneous irradiance of leaves grown in shade and sunlight (Figure 3.2). The species varied in the parameters that differed between shade-grown and sun-grown leaves (Tables 3.3 & 3.4). Some photosynthetic parameters did not change with growth irradiance, however this may reflect more the accuracy of the gas analyser used than an actual lack of response.

All species, except *Castanospermum australe*, showed significant reductions in the light-saturated rates of net photosynthesis in shade-grown leaves compared with sun-grown leaves (Table 3.3). Previous studies including some of these species, have also shown reductions in light-saturated net photosynthesis in shade-grown leaves compared with sun-grown leaves (Table 3.6). The difference in the magnitude of these reductions between the present and previous studies is likely to be a reflection of the different irradiances under which plants were grown in the experiments. For example, Thompson *et al.* (1992a) found less of a reduction in the light-saturated net photosynthetic rate of *Heritiera trifoliolata* when grown at low irradiance than in this study however the high irradiance they used was only $535 \mu\text{mol m}^{-2} \text{s}^{-1}$. The differences in the magnitude of light-saturated net photosynthesis in sun-grown leaves among studies (Table 3.7) are also likely to be a result of the different levels of irradiance used in the highest treatment.

The lack of a significant change in light-saturated rate of net photosynthesis with growth irradiance in leaves of *C. australe* is the characteristic response of a shade-tolerant species (Read 1985; Read & Hill 1985; Riddoch *et al.* 1991). The response of *C. australe* is similar to that of the Australian rainforest tree *Atherosperma moschatum* (Read 1985) in showing no difference between sun-grown and shade-grown leaves. However, *C. australe* is not as shade-tolerant as some other Australian rainforest trees, such as *Ceratopetalum apetalum* and *Dorophora sassafras*, which show a higher light-saturated net photosynthetic rate in shade-grown compared with sun-grown leaves (Read & Hill 1985).

Table 3.6 Percentage of light-saturated net photosynthesis (P_{sat}) of leaves grown in sunlight shown by leaves grown in shade. Values recorded in other studies are included for comparison. Values of irradiance are $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ unless otherwise stated.

Species	% P_{sat} in shade	<u>Previous studies</u>			
		% P_{sat} in shade	shade irradiance	sunlight irradiance	source
<i>Eucryphia lucida</i>	80	43	30-80	sunlight	Read (1985)
<i>Nothofagus cunninghamii</i>	59	57	30-80	sunlight	Read (1985)
<i>Acmena smithii</i>	74	77	5% sunlight	sunlight	Melick (1990a)
<i>Tristanopsis laurina</i>	74	58	5% sunlight	sunlight	Melick (1990a)
<i>Sloanea woollsii</i>	68	NA			
<i>Heritiera trifoliolata</i>	49	69	30	535	Thompson <i>et al.</i> (1992a)
<i>Castanospermum australe</i>	99	NA			
<i>Alstonia scholaris</i>	69	NA			

Table 3.7 Parameter derived from net photosynthesis-irradiance curves of some of the study species from previous studies.

Species	Growth irradiance	P_{sat} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	R_d ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	LCP ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$)	LSP ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$)	source
<i>Eucryphia lucida</i>	sun	6.82	2.03	30	1000	Read (1985)
	shade	2.66	0.83	15	300	
<i>Nothofagus cunninghamii</i>	sun	6.18	1.73	27	800	Read (1985)
	shade	3.33	1.05	17	300	
<i>Acmena smithii</i>	sun	7.15	1.49	16	800	Melick (1990a)
	shade	5.49	0.63	7	800	
<i>Tristaniopsis laurina</i>	sun	13.07	0.33	39	1100	Melick (1990a)
	shade	7.55	0.22	20	800	
<i>Heritiera trifoliolata</i>	sun	5.8	0.7	18	650	Thompson <i>et al.</i> (1992a)
	shade	4.0	0.5	16	320	

Castanospermum australe showed the lowest light-saturated net photosynthetic rate in sun-grown leaves which is consistent with it being a shade-tolerant species. Previous studies have found lower net photosynthetic rates in shade-tolerant species than those of shade-intolerant species (Boardman 1977). This has been shown to be true of rainforest trees in Australia (Read 1985; Read & Hill 1985; Thompson *et al.* 1992a). However, the relatively shade-tolerant species *Nothofagus alpina* from the temperate rainforests of Chile was shown to have a similar maximum net photosynthetic rate as shade-intolerant species from Australia and Chile (Read & Hill 1985). Shade-intolerant species are expected to have high light-saturated net photosynthetic rates, as this would confer a competitive advantage in the early successional environments, which they dominate. In contrast, shade-tolerant species, which survive in the understorey, are likely to depend more on defence against herbivores and pathogens than on maintaining a high net photosynthetic rate for their survival (Strauss-Debenedetti & Bazzaz 1996).

Most species showed thinner leaves with an increased SLA when grown in shade, which is common in other species (Table 3.5, Boardman 1977). Pearcy (1994) proposed that increase in SLA was the major factor contributing to the decrease in net photosynthesis on an area basis in shade grown leaves. For this reason, they proposed that net photosynthetic rate per unit mass gives a better estimate of the photosynthetic return of a given investment than net photosynthesis per unit area. In this study, the species that showed significant increases in SLA in shade-grown compared with sun-grown leaves also showed a significant decrease in light-saturated net photosynthesis per unit area but not per unit mass (Tables 3.3 & 3.5). Therefore, in these species it is not the intrinsic rate of net photosynthesis which is reduced in the shade but the investment in photosynthetic apparatus per area.

The consequences of changing investment in photosynthetic apparatus with irradiance are shown by the species *Castanospermum australe* and *Heritiera trifoliolata* in this study. The inability of *H. trifoliolata* to increase SLA in shade resulted in a reduced gain from its photosynthetic investment. In contrast, the inability of *C. australe* to decrease SLA in sunlight resulted in loss of potential photosynthesis.

Another way to maintain rates of net photosynthesis in shade is to lower dark respiration rates. Shade-grown leaves tend to show a reduced dark respiration rate compared with

sun-grown leaves (Boardman 1977; Björkman 1971). In contrast, few of the study species showed significantly lower dark respiration in shade-grown compared with sun-grown leaves (Table 3.3). Pearcy (1994) suggested the higher respiration rates of sun-grown leaves, shown by many species, may simply be a result of a higher net photosynthetic rate and therefore higher protein turnover. However, in this study no species showed a significant correlation between the rates of net photosynthesis and dark respiration on a mass basis (Table 3.8).

Dark respiration rates were found to be of a similar magnitude among the study species. Dark respiration rates are expected to be lower in shade-tolerant than shade-intolerant species as they influence net carbon gain at low irradiances (Kitajima 1994). Many studies have found that shade-tolerant species have lower dark respiration rates than shade-intolerant species (Loach 1967; Boardman 1977; Björkman 1981b; Reich *et al.* 1998; Davies 1998). However, *Castanospermum australe*, which showed a shade-tolerant photosynthetic response in other respects, did not show a lower dark respiration than the other species.

The lack of significant difference in dark respiration with growth irradiances is likely to be a reflection of the accuracy of the gas analyser. The average standard error for five consecutive measurements of net photosynthesis was $0.21 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is the same magnitude as the respiration readings. Previous work using an earlier model of the same infrared gas analyzer (ADC LCA-2, United Kingdom) also found that differences in dark respiration with irradiance were beyond the resolution of the machine (Ramos & Grace 1990; Newell *et al.* 1993).

The survival of plants in shade is likely to be dependent on the rate of photosynthesis at low irradiance and the light compensation point. An improved rate of net photosynthesis at low irradiances in shade-grown leaves compared with sun-grown leaves is commonly found in plants (Loach 1967; Boardman 1977). Few of the species showed such an adjustment to growth in shade. *Heritiera trifoliolata* again showed an inability to adjust to growth in shade, showing a significant decrease in the net photosynthetic rate at low irradiances in shade-grown leaves compared with sun-grown leaves. The species that did show increase net photosynthesis at low irradiance when

grown in shade included those known to grow in shade (*A. smithii*, *C. australe* and *Heritiera trifoliolata*) as well as *S. woollsii*. In contrast, all species showed light compensation points at less than 2% of sunlight ($\sim 40 \mu\text{mol m}^{-2} \text{s}^{-1}$) which makes them shade-tolerant species according to Jarvis (1964). Most species showed a trend of a lower light compensation point in shade-grown leaves compared with sun-grown leaves, which is consistent with other species (Bazzaz & Carlson 1982; Langenheim *et al.* 1984; Read 1985; Melick 1990a; Thompson *et al.* 1992a).

Most species showed a higher light saturation point in sun-grown leaves compared with shade-grown leaves (Table 3.4). Species that show higher light-saturated net photosynthetic rates when grown in higher irradiances also tend to show increases in the light saturation point (Langenheim *et al.* 1984; Thompson *et al.* 1988; Thompson *et al.* 1992a; Newell *et al.* 1993). *Castanospermum australe* showed the lowest light saturation point for net photosynthesis in sun-grown leaves of all the species which is characteristic of shade-tolerant plants (Boardman 1977). The range of light-saturation points in sun-grown leaves among the species suggests an irradiance of $800 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ would ensure that all species were light-saturated in the main experiments.

Table 3.8 Results of linear regressions between rates of light-saturated net photosynthesis and dark respiration per unit mass.

Species	$r^2_{\text{corrected}}$	F	P
<i>Eucryphia lucida</i>	< 0.01	0.04	0.85
<i>Nothofagus cunninghamii</i>	0.10	1.79	0.23
<i>Acmena smithii</i>	< 0.01	0.01	0.92
<i>Tristaniaopsis laurina</i>	0.22	2.97	0.14
<i>Sloanea woollsii</i>	0.18	2.56	0.16
<i>Heritiera trifoliolata</i>	< 0.01	0.29	0.61
<i>Castanospermum australe</i>	< 0.01	0.03	0.87
<i>Alstonia scholaris</i>	< 0.01	0.03	0.87

There was no difference in either the quantum yield or curvature of the photosynthesis-irradiance response (Table 3.4). Reported patterns of the response of quantum yield to growth irradiance are not consistent, with shade-grown leaves showing higher (Boardman 1977; Langenheim *et al.* 1984; Oberbauer & Strain 1985; Davies 1998), lower (Kwesiga *et al.* 1986; Riddoch *et al.* 1991) or not significantly different (Read 1985; Thompson *et al.* 1988) quantum yields from sun-grown leaves. In other studies, shade-grown leaves showed a more sharply curved photosynthetic response to irradiance than sun-grown leaves (Kwesiga *et al.* 1986; Ramos & Grace 1990; Riddoch *et al.* 1991). The greater curvature of the response in shade-grown leaves has been correlated with higher concentrations of chlorophyll compared with sun-grown leaves (Leverenz 1987).

Several parameters indicate that *C. australe* should be considered photosynthetically shade-tolerant. The shade-grown leaves of this species showed no significant difference in light-saturated net photosynthesis and a significantly increased rate at low irradiance compared with sun-grown leaves. In addition, this species showed the lowest light-saturated net photosynthetic rate and light saturation point in sun-grown leaves among the species.

In conclusion to the specified aims:

1. The species *Castanospermum australe* is consider shade-tolerant with respect to photosynthesis.
2. Net photosynthesis of sun-grown leaves of all species was saturated at $800 \mu\text{mol m}^{-2} \text{s}^{-1}$. Therefore, irradiances close to this will be used in the main experiments.

Part B

Temperature

CHAPTER 4

Responses of Net Photosynthesis to Growth Temperature

The response of net photosynthesis to instantaneous temperature in plants is curvilinear with a distinct optimum temperature for maximum net photosynthesis. Net photosynthesis is limited by the rates of enzymes at low temperatures (Berry & Björkman 1980) whereas it is limited by an increasing rate of respiration and a decreased affinity of the carboxylating enzyme Rubisco for CO₂ at high temperatures (Larcher 1969; Björkman 1973). The shape of the photosynthetic response of leaves to instantaneous temperature is altered by both short-term (daily) and long-term (seasonal) temperature changes. Growth temperature can change the magnitude, the optimum temperature and the span of instantaneous temperatures over which maximum net photosynthesis is shown.

In the past, photosynthetic responses of plants grown at different temperatures have been loosely termed *photosynthetic acclimation* (eg. Berry & Björkman 1980; Öquist 1983). However, it is important to separate these responses according to the developmental stage of the leaves used, as developing leaves are able to make greater adjustments in response to temperature changes than mature, fully-expanded leaves (Krol & Huner 1985; Rütten & Santarius 1992). I will use the term *plasticity* to refer to differences between leaves initiated and developed under different growth temperatures and the term *acclimation* to refer only to changes in mature leaves induced by altered growth temperatures.

Our present understanding of plasticity has come from comparisons of species from the climatic extremes of alpine, arctic and desert environments (Mooney *et al.* 1964; Billings *et al.* 1971; Slatyer 1977b; Björkman 1981a). There is a trend for species from colder environments to show maximum net photosynthesis at lower growth temperatures than species from hotter environments (Björkman *et al.* 1975). This trend has also been shown among desert species with different growing seasons (Monson *et al.* 1983) and altitudinal populations of single species (Slatyer 1977a; Baruch 1979).

In contrast, studies of taxa from different latitudes have not shown consistent trends in the growth temperature for maximum net photosynthesis. The few studies of tropical and temperate species have shown differences in the growth temperature for maximum net photosynthesis, which were not always consistent with their climatic origins (Scott 1970; Paul *et al.* 1990). Comparisons of latitudinal populations of single species have shown that the growth temperature for maximum net photosynthesis is either higher in low latitude populations compared with high latitude populations (Billings *et al.* 1971; Mooney & Billing 1961; Treharne & Eagles 1970) or similar between latitudinal populations (McNaughton 1973).

In addition to the growth temperature for maximum net photosynthesis, the plasticity of species from contrasting environments differs in several ways. Species from environments that have large temperature fluctuations, such as deserts or mountains, usually show maximum photosynthesis over a greater range of growth temperatures (Billings *et al.* 1971; Pearcy 1977; Mooney *et al.* 1978a). Species with larger distributions or from climates that are more variable show greater shifts in the optimum temperature for net photosynthesis than species that are restricted to constant environments, such as the tropics (Mooney & West 1964). The difference in plasticity of species or populations of species can simply be the altered rate of net photosynthesis at extreme temperatures (Milner & Hiesey 1964; Regehr & Bazzaz 1976; Vallejos & Pearcy 1987). Some species show little adjustment in photosynthetic capacity with growth temperature as they are able to maintain a broad temperature response over a wide range of growth temperature (Kemp *et al.* 1977; Forseth & Ehleringer 1982; Williams & Black 1993).

So far, direct comparisons of plasticity between tropical and temperate species have been restricted to herbaceous species (Scott 1970; Paul *et al.* 1990). Furthermore, there appear to be no studies of plasticity to temperature in tropical trees. Studies of the acclimation potential of net photosynthesis in Australian rainforest trees have shown different trends concerning species from different latitudes. Firstly, within the temperate species of Australian rainforests, the lower latitude species tend to have higher optimum temperatures (20-25°C) for maximum net photosynthesis than the higher latitude species (18-21°C, Hill *et al.* 1988). In contrast, temperate and tropical

species of *Nothofagus*, from a 44° latitudinal range, showed the same range of optima (18-23°C, Read 1990). Instead, the difference in the response of *Nothofagus* species was in the ability of the temperate species to maintain close to maximum net photosynthesis over a greater range of acclimation temperatures than the tropical species.

The climate analysis of Chapter 2 showed there are important differences between the climates of temperate and tropical rainforest species. Firstly, tropical species occur in climates with higher mean temperatures than temperate species. Secondly, the climates of temperate species showed a greater day-to-day and seasonal variability in temperature than those of tropical species. Previous trends between climate and plasticity of the photosynthetic response to temperature lead to the following predictions about rainforest canopy trees in Australia:

1. Temperate species will show maximum net photosynthesis at lower growth temperatures than the tropical species.
2. Temperate species will have a more plastic photosynthetic response with respect to growth temperature than tropical species. In particular:
 - a) Temperate species will show close to maximum net photosynthesis over a broader range of growth temperatures than tropical species.
 - b) Temperate species will show greater shifts in the optimum temperature for net photosynthesis with growth temperature than the tropical species.

The photosynthetic capacity of leaves of the species developed under five growth temperature regimes was used to test these hypotheses. Measurements of the maximum rate of net photosynthesis of these leaves were used to test hypotheses 1 and 2a. The optimum instantaneous temperatures for net photosynthesis of leaves from the five growth temperatures were measured to test hypothesis 2b. In addition, measurements of net photosynthesis were taken over a range of instantaneous temperatures in leaves from three of the growth temperatures.

METHODS

Seedlings of the eight species were grown in controlled environment cabinets under five different temperature regimes. These seedlings were grown to determine photosynthetic responses to temperature, which are discussed in this chapter, and growth responses to temperature, which are discussed in Chapter 5.

The following day/night temperature regimes were chosen: 14°C/6°C, 19°C/11°C, 22°C/14°C, 25°C/17°C, and 30°C/22°C. The two extreme temperature regimes were chosen to cover the widest range of sublethal temperatures. A minimum night temperature of 6°C was used, as temperatures below 5°C are known to be lethal for many tropical species (Bauer *et al.* 1975). The mean diurnal temperature range for the eight species in their native environment ranges from 8°C to 12°C (see Chapter 2). Consequently, the lowest day temperature used was 14°C to maintain a realistic diurnal range of 8°C and a sublethal night temperature of 6°C. A day temperature above 30°C was not used as in previous experiment a week under constant 32°C had killed all *Eucryphia lucida* seedlings (Read & Busby 1990). The intermediate temperatures were chosen to cover the range (18-26°C) in which the majority of optimum temperatures for net photosynthesis and growth were believed to occur.

The experiment was performed in two separate runs between May and November 1997. This was done to resolve the problem of pseudo-replication in growth cabinet experiments. That is, replicate plants within a growth cabinet are not considered independent samples as they are growing under the same conditions. The theoretical solution to this problem is to put one replicate plant in each cabinet and repeat the experiment many times. However, the number of experiments required to get an appropriate level of replication is not practical. A practical design was chosen which consisted of two replicate runs. Each consisted of five subreplicate plants per species per cabinet to reduce the variation in photosynthetic and growth rates.

The seedlings used in this experiment were taken from the stock of plants raised under the glasshouse conditions described in Chapter 3. The seedlings were twelve months old at the beginning of the experiment. However, twelve-month-old seedlings of *Castanospermum australe* were too tall and would have quickly outgrown the growth

cabinets. Consequently, one-month-old *C. australe* seedlings were grown in the second run only with six plants per cabinet.

For each run of the experiment, the temperature regimes were randomised among five growth cabinets. Five seedlings of each species were moved into each of the five growth cabinets and arranged randomly. The growth cabinets were custom built (TRENT Refrigeration, Melbourne) with internal dimensions of 1.5 x 1.0 x 0.5 m. Temperature was thermostatically controlled to within one degree of the set temperature and air was fan forced through the chamber. However, there was a 3°C temperature difference between the top and bottom of the cabinets due to the heat produced by the overhead lights. Four 1000W metal halide globes supplied light within the growth cabinets. The irradiance in each cabinet ranged from 600-800 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ at the tops of the seedlings. This irradiance was known to be saturating for all species from the shading experiment (Chapter 3). Temperature and irradiance followed a daylength of 16 hours. It was not possible to maintain the same vapour pressure deficit (vpd) in the cabinets due their refrigerated cooling systems. The mean values of vpd for each temperature treatment are given in Table 4.1.

Seedlings were watered every two days to ensure that the soil never dried out. Fertiliser was added, in the form of diluted FOGG-IT fish emulsion (FOGG-IT Nozzle Company, San Francisco), every 14 days to ensure that nutrients were not limiting. The fertilizer was diluted 1/500 with water to provide 98 mg l^{-1} of nitrogen, 20 mg l^{-1} of potassium, and 31 mg l^{-1} .

Net photosynthesis was measured in the last four weeks of each run of the experiment. Seedlings were tagged at the beginning of each run and the development of leaves was recorded every week to determine when enough new leaves were fully-expanded for photosynthetic measurements. The new leaves were developed under an irradiance of 600-800 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ for 16 hours a day and one of the above day/night temperature regimes. To ensure leaves developed under the same conditions within a cabinet, seedlings were raised on stands so that the new leaves of all seedlings were at the same height. Periodically during each run, stands were replaced by shorter stands to ensure the new leaves stayed at the same height. This also prevented shading of the new leaves of a seedling by adjacent faster-growing seedlings.

Table 4.1 Vapour pressure deficit (kPa) of the different temperature regimes. Means are of two cabinets with standard errors in brackets. Values for each cabinet were averaged from daily means measured on four separate days.

Temperature regime	Day	Night
14°C/6°C	1.06 (0.03)	0.27 (0.01)
19°C/11°C	1.20 (0.04)	0.30 (0.02)
22°C/14°C	1.22 (0.05)	0.42 (0.04)
25°C/17°C	1.44 (0.07)	0.43 (0.03)
30°C/22°C	2.12 (0.08)	0.82 (0.01)

Photosynthetic measurements were recorded from the most recently fully-expanded leaf or leaves in the case of *Nothofagus cunninghamii*. For each species, three seedlings were measured from each growth temperature regime during both runs of the experiment making a total of six plants per treatment. However, for *C. australe*, seedlings were only grown in the second run of the growth temperature experiment so all measurements were taken from these seedlings. The order in which seedlings were measured was randomised across growth temperature regimes and species.

Photosynthetic measurements were taken from an hour after the start of the day cycle to an hour before the end of the day cycle of the growth cabinets. Seedlings were brought into the laboratory no more than two hours before measurement to minimise acclimation to the temperature of the laboratory.

The rate of maximum net photosynthesis (P_{\max}) and the temperature at which it was shown (T_{opt}) were determined from plants grown under the five temperature regimes. In addition, instantaneous temperature dependence curves were measured for seedlings from the 14°C/6°C, 22°C/14°C and 30°C/22°C growth temperature regimes to determine the shape of the photosynthetic response and the performance at extreme temperatures.

Net photosynthesis was measured using the same setup as described for the shading experiment (Chapter 3). For all measurements, the leaves were equilibrated at an air temperature of 22.0 °C, a CO₂ concentration of 350 ppm, a vapour pressure deficit (VPD) of 1.05 kPa and an irradiance of $800 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$. A leaf was determined as equilibrated to the environment within the leaf chamber when there was less than 5% difference in the mean of three consecutive sets of net photosynthetic rates. The time taken for leaves to equilibrate varied from 25 to 60 minutes depending mainly on the species being measured.

For the ITD curves, photosynthetic measurements were taken at 10°C, 14°C, 18°C, 20°C, 22°C, 24°C, 26°C, and 30°C. The VPD was maintained at a constant 1.05 kPa at all air temperatures and the leaf was allowed to equilibrate for five minutes at each new temperature before measurement. This time interval was chosen because the photosynthetic rate was found to stabilise within three minutes of the air temperature being changed. After the initial measurement at 22°C, the air temperature was then raised to 24.0°C followed by 26.0°C. The air temperature was then returned to 22.0°C and the net photosynthetic rate was allowed to recover to its initial level at 22.0°C, which took between 15 and 30 minutes. Then the air temperature was lowered in the sequence 20°C, 18°C, 14°C, and 10°C.

Accurate measurements of net photosynthesis at 30°C were not possible at room temperature (~22°C) due to the loss of water vapour from the returning air producing erroneous measurements. Water vapour would condense in the outlet line due to the temperature differential between the chamber and the room. Raising the room temperature to around 30°C solved this problem. Once all the replicate seedlings had been measured at room temperature, measurements were repeated on the same leaves at a room temperature of 30°C. To ensure that seedlings did not close their stomata under the drier conditions of the 30°C room they were enclosed in a plastic bag, which was humidified using a spray bottle. Leaves were equilibrated at 22°C and then measurements were taken at the instantaneous temperatures of 22°C, 26°C, and 30°C. Leaves were in the leaf chamber for up to 120 minutes during the room temperature measurements and up to 60 minutes during the 30°C room measurements.

For the seedlings from the 19°C/11°C and 25°C/17°C growth temperature regimes, only the maximum photosynthetic rate was determined. After the initial measurement at an air temperature of 22°C, the net photosynthetic rate was measured at 1.0°C increments every 5 minutes. The air temperature was first lowered until the net photosynthetic rate dropped more than 5% of the highest value and then raised until the rate dropped more than 5% of the highest value. The maximum photosynthetic rate was determined as the highest rate recorded.

A portion of stem was inside the leaf chamber during photosynthetic measurements of *N. cunninghamii* leaves. To measure the stem respiration the leaves were removed and after a week the respiration of the stem section was measured under the same conditions as the leaves at 22°C. The amount of stem respiration was small ranging from 0.3 to 0.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. This measure of respiration was then added to the net photosynthetic measurements, with the assumption that the loss was of a similar magnitude at all temperatures.

The leaves used for the photosynthetic measurements were also part of the growth experiment and so were not harvested immediately. Instead the area of leaf surface placed within the leaf chamber was traced on to paper and measured using image analysis (BIOSCANTM Image Analyser). The accuracy of this method was determined by a comparison trial. Leaves from ten different seedlings of each species were traced onto paper and then the section (or leaves) within the leaf chamber was cut out. The areas of these leaf traces and sections (or leaves) were measured using image analysis. These area data were analysed as paired *t*-tests, the results of which are given in Table 4.2. For all species, there was no significant difference ($p > 0.10$) between the measured area of leaf sections and leaf traces.

Table 4.2 Results of paired *t* tests comparing the leaf area estimated from leaf traces with the area estimated from the actual leaf section for each of the species.

Species	Trace area/Leaf area	<i>t</i>	<i>P</i>
<i>E. lucida</i>	1.003	-0.64	0.54
<i>N. cunninghamii</i>	0.993	-0.58	0.58
<i>A. smithii</i>	0.996	0.43	0.68
<i>T. laurina</i>	0.995	0.95	0.37
<i>S. woollsii</i>	0.988	-1.07	0.31
<i>H. trifoliolata</i>	1.011	-0.16	0.87
<i>C. australe</i>	0.995	-0.52	0.62
<i>A. scholaris</i>	1.021	1.45	0.18

Data analysis

The data used for the ITD curves consisted of the net photosynthetic rates at 10°C, 14°C, 18°C, 20°C, 22°C, and 24°C measured at room temperature and the rates at 26°C and 30°C measured at a room temperature of 30°C. A split-plot, repeated measures ANOVA of the rate of net photosynthesis at 22°C measured at the different room temperatures determined there was no significant effect of room temperature on the measured net photosynthetic rate (Table 4.3). The ITD curve data for each replicate leaf were regressed using several models. The data tended to produce asymmetrical curves, with the rate dropping off more rapidly at higher temperatures. Therefore, a quadratic equation did not provide an accurate fit as assumed by other researchers (eg. Sall & Pettersson 1994). Cubic equations were tried but they produced curves in which net photosynthesis increased again after a minimum at extreme temperatures. An appropriate regression curve was found to be the following relationship previously used to fit the photosynthetic response to temperature (Li 1985) and formulated by Ratkowsky *et al.* (1983):

$$P = \{b(T-T_{\min}) \times [1 - \exp(c(T-T_{\max}))]\}^2 \quad (\text{equation 4.1})$$

where *P* is the net photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), *T* is the air temperature (°K), *T*_{min} and *T*_{max} are the minimum and maximum temperatures (°K) at which the net

photosynthetic rate is zero, and b and c are fitting parameters. T_{\min} and T_{\max} were simply parameters estimated to fit the curve and their values were believed to have no physiological significance.

These regression curves were used to estimate P_{\max} , T_{opt} , and the temperature span over which at least 80% of P_{\max} was maintained (T_{span}). The relationships of these parameters to an ITD curve are shown in Figure 4.1a. T_{opt} was determined from the following differential of equation 4.1:

$$\begin{aligned} \delta P / \delta T = \{ 2b^2 (T - T_{\min}) \times [1 - \exp(c(T - T_{\max}))]^2 \} \\ - \{ 2b^2 (T - T_{\min})^2 \times [1 - \exp(c(T - T_{\max}))] \times c[\exp(c(T - T_{\max}))] \} \end{aligned} \quad (\text{equation 4.2})$$

by solving $\delta A / \delta T = 0$ for T . P_{\max} was then determined as the net photosynthetic rate at this temperature. The upper and lower temperatures at which 80% of P_{\max} occurred were determined using the Solver function of Microsoft® Excel 97 which uses a generalized reduced gradient nonlinear optimization algorithm. T_{span} was determined from the difference of these two temperatures.

For each species, the mean values of P_{\max} for each growth temperature regime were regressed against growth temperature separately for each run using equation 4.1. Several parameters were determined from these regression equations and their relationships to the curve are shown in Figure 4.1b. The maximum rates of P_{\max} (P_{GTmax}) and the optimum growth temperature for P_{\max} (GT_{opt}) were determined in the same way as P_{\max} and T_{opt} respectively using equation 4.2. The span of temperatures over which at least 80% of P_{GTmax} was shown (GT_{span}) was determined in the same way as the temperature span of P_{\max} .

Table 4.3 Results of split-plot repeated measures ANOVA comparing net photosynthesis measured at an instantaneous temperature of 22°C between a heated (~30°C) and unheated room (~22°C).

source	<i>F</i>	<i>P</i>
<u>between subjects</u>		
growth temperature	116	< 0.01
cabinet(growth temperature)	155	< 0.01
species	12.0	< 0.01
species × growth temperature	0.29	0.84
species × cabinet(growth temperature)	1.04	0.42
<u>within subjects</u>		
room	0.01	0.93
room × growth temperature	1.01	0.43
room × cabinet(growth temperature)	0.40	0.67
room × species	0.12	0.12
room × species × growth temperature	0.41	0.41
room × species × cabinet(growth temperature)	0.21	1.00

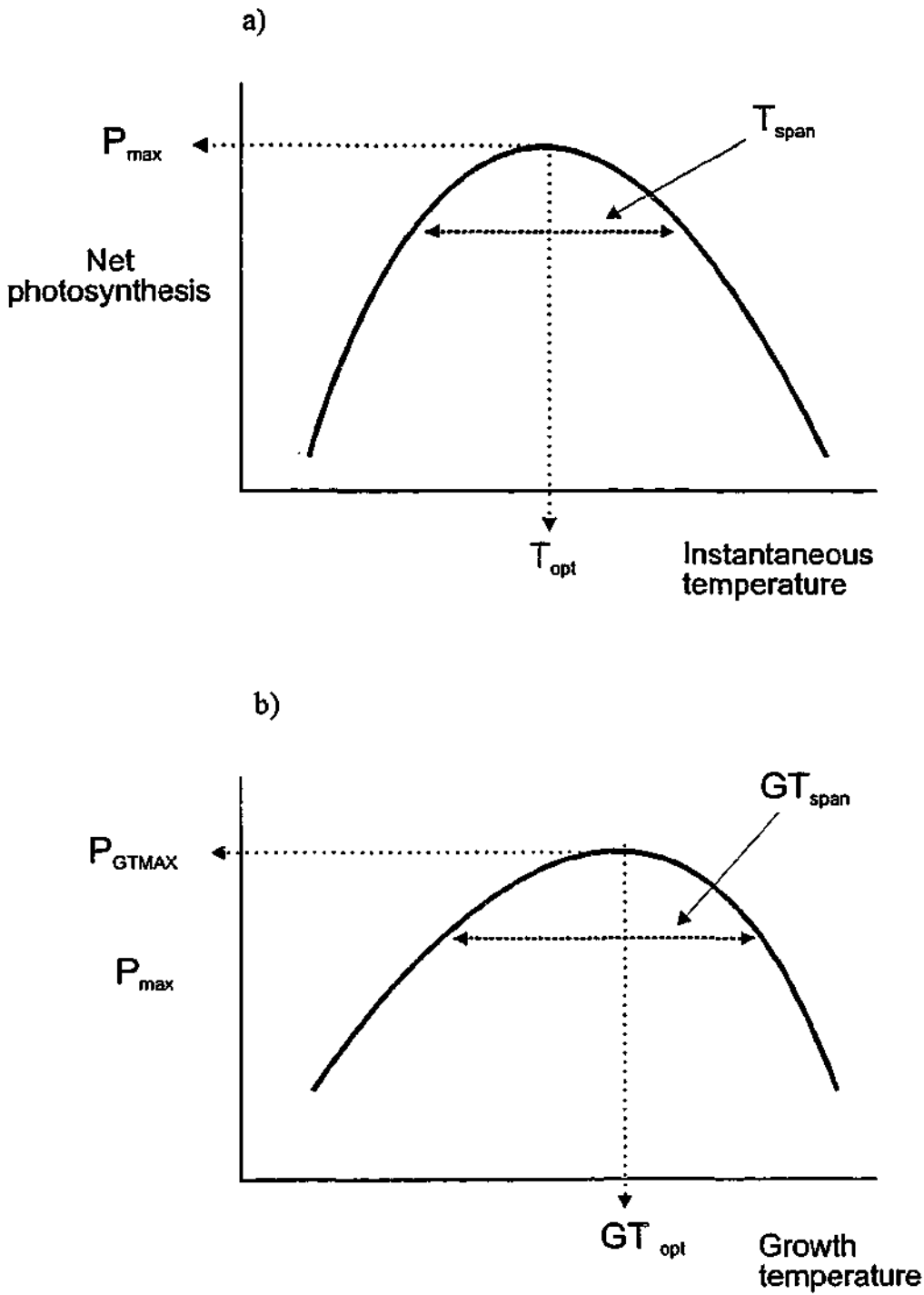


Figure 4.1 The derivation of parameters estimated from a) regressions of net photosynthesis against instantaneous temperature and b) regressions of mean P_{\max} against growth temperature.

The photosynthetic rate at specific instantaneous temperatures was analysed for seedlings grown under the 14°C/6°C, 22°C/14°C and 30°C/22°C growth temperature regimes. To determine the relative performance of the species at extreme temperatures the net photosynthetic rates measured at 10°C and 30°C were analysed as percentages of P_{GTmax} . These two standardised parameters were arcsine-transformed for statistical analysis as they were both positively-skewed.

Parameters directly measured or derived from ITD curves were analysed as a split plot design with the five growth cabinets from the two runs treated as ten separate plots, growth temperature as the effect between cabinets and group as the effect within cabinets. Data were first analysed grouped by species using the averaged values of the three subreplicate plants of a species in each cabinet. Then the data were analyzed grouped as rainforest types and climate groups (see Table 2.4). Species were the replicates for the rainforest types and climate groups. However, using the same two species in both runs meant that the species within cabinets of the same temperature were pseudoreplicates. Therefore, the mean values of the groups within a cabinet were used for analysis. For significant effects, pairwise comparisons of means were performed within each level of the other effect and a Bonferroni adjustment was used for probability values. Comparisons of growth temperature within a group were analyzed as a one-way ANOVA. Comparisons of groups within a growth temperature were analyzed as a random complete block design with cabinet as the blocking variable.

Parameters derived from regressions of maximum net photosynthesis against growth temperature were analysed different^{ly} depending on the group. Species were analyzed as a random complete block design, with run as the blocking variable and using cabinets' means. In contrast, rainforest types and climatic groups were analysed as one-way ANOVAs using the mean values for each species across the cabinets.

RESULTS

Effect of growth temperature on maximum net photosynthesis

The highest values of maximum net photosynthesis (P_{GTmax}) shown by a species ranged from $3.26 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Castanospermum australe* to $10.78 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Tristaniopsis laurina* (Table 4.4). There was no relationship between the magnitude of P_{GTmax} and the latitudinal origin of the species ($F = 0.06$, $p = 0.82$). P_{GTmax} of the two tropical species, *C. australe* and *Alstonia scholaris*, included the lowest ($3.26 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and one of the highest ($9.39 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) rates of net photosynthesis respectively. The remaining species showed values of P_{GTmax} of around $6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. For all species, the highest value of P_{max} was not significantly different ($p > 0.05$) from values of P_{max} for several other growth temperatures. Specific leaf area did not change significantly with growth temperature, so the same trends were shown on a mass basis for maximum net photosynthesis (Table 4.5).

The optimum growth temperatures for P_{max} (GT_{opt}) ranged from 18.7°C to 27.3°C among the species (Table 4.4). The magnitude of GT_{opt} increased with the latitudinal origin of the species except for the warm-temperate species (Figure 4.2). The warm-temperate species *Acmena smithii* had a low GT_{opt} of 19.5°C , which placed it between the two cool-temperate species, considering it extends well into tropical latitudes. In contrast, the warm-temperate species *T. laurina* had a GT_{opt} of 25.4°C that was within the range of the tropical species (24.2 - 27.3°C). The strongest correlation between GT_{opt} and various temperature parameters from the species climate profiles was the maximum temperature of the hottest month for the species' collection sites (Table 4.6). This is a result of the GT_{opt} of *A. smithii* (19.5°C) being closer to the maximum temperature of the hottest month at the collection site (21.7°C) than of its climate profile (26.5°C , Figure 4.3).

Table 4.4 Parameters obtained from the P_{\max} versus growth temperature regressions for individual species (see Figure 2). Parameters are means of regressions for the two runs with standard errors in brackets. Shared letters represent non-significant ($p < 0.05$) groupings of species. *Castanospermum australe* was only measured during the second run of the run and therefore only one regression curve was produced and parameters do not have standard errors

Species	$P_{GT\max}$		Temperature span ($^{\circ}\text{C}$) for $\gg 80\%$ of $P_{GT\max}$	
	($\mu\text{mol m}^{-2} \text{s}^{-1}$)	GT_{opt} ($^{\circ}\text{C}$)		
<i>E. lucida</i>	5.40 (0.09) ^b	18.7 (0.1) ^c	11.8 (0.3) ^{ab}	
<i>N. cunninghamii</i>	6.87 (0.17) ^a	21.5 (0.1)	15.7 (1.2) ^a	
<i>A. smithii</i>	6.07 (0.13) ^{ab}	19.5 (0.1) ^c	13.6 (1.6) ^{ab}	
<i>T. laurina</i>	10.78 (0.14)	25.4 (0.1) ^{bc}	15.2 (0.9) ^{ab}	
<i>S. woollsii</i>	6.76 (0.32) ^a	24.2 (0.2) ^d	10.5 (1.1) ^{ab}	
<i>H. trifoliolata</i>	6.24 (0.04) ^{ab}	24.5 (0.2) ^{cd}	9.7 (0.3) ^{ab}	
<i>C. australe</i>	3.26	26.3 ^{ab}	9.4 ^{ab}	
<i>A. scholaris</i>	9.39 (0.19)	27.3 (0.2) ^a	8.6 (0.4) ^b	
Species	<i>F</i>	143	579	8.25
	<i>p</i>	< 0.01	< 0.01	0.01
Cabinet	<i>F</i>	1.02	2.04	1.55
	<i>p</i>	0.35	0.20	0.26

Table 4.5 Results of a split-plot ANOVA comparing values of specific leaf area (SLA).

Hypothesis test	<i>F</i>	<i>p</i>
growth temperature	3.44	0.10
species	25.1	< 0.01
growth temperature \times species	0.54	0.95

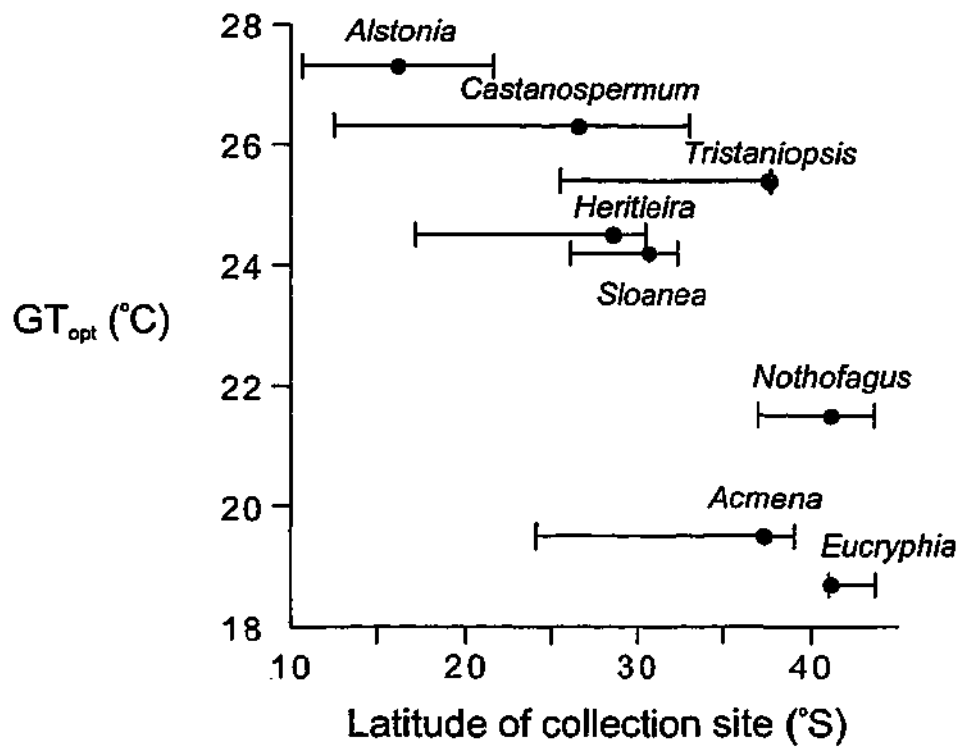


Figure 4.2 The relationship between the day growth temperature for maximum net photosynthesis (GT_{opt}) and the latitude of the collection site for the species. For each species the dot marks the collection site and the bars represent the distributional range.

Table 4.6 Results of Pearson correlations between growth temperature for maximum net photosynthesis and various temperature parameters from climate profiles of species. For derivation of parameters see Table 2.3

Temperature parameter	Pearson's correlation coefficient	<i>p</i>
<u>Mean temperature</u>		
annual	0.78	0.02
hottest month	0.78	0.02
<u>Maximum temperature</u>		
annual	0.78	0.02
hottest month	0.78	0.02
annual ¹ for collection site	0.80	0.02
hottest month for collection site	0.82	0.01

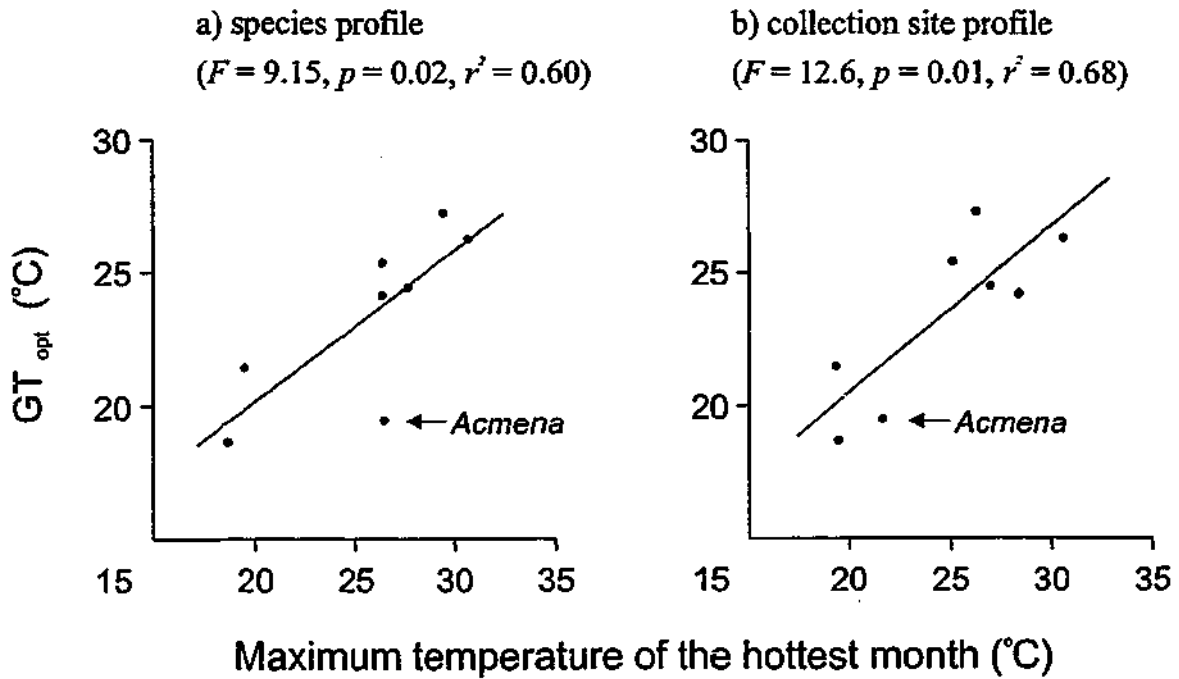


Figure 4.3 Relationship between the growth temperature for maximum net photosynthesis and the maximum temperature of the hottest month of the climate profile for the a) species and b) their collection sites. The point representing *Acmena smithii* is labelled to show its significance to the fit of the linear regressions.

The rainforest types showed distinct responses of maximum net photosynthesis to growth temperature (Figure 4.4). The GT_{opt} values of the rainforest types increased with decreasing latitudinal origin of the group but they were not significantly different (Table 4.7). However, when analysed as climate groups the GT_{opt} of the tropical climatic group at 25.6°C was significantly higher than the GT_{opt} of the temperate group at 21.3°C ($F = 6.85, p = 0.04$).

The tropical species showed larger spans of growth temperature over which at least 80% of P_{GTmax} was shown (12–16°C) than in the temperate species (9–11°C, Table 4.4). However, the only significant difference was the larger span of *Nothofagus cunninghamii* compared with the span of *A. scholaris*. When the temperature spans of the rainforest types were compared there was nearly a significant difference ($p = 0.06$, Table 4.7) between the spans of the warm-temperate and tropical rainforest types. When climate groups were compared, there was a significant difference ($F = 21.8, p < 0.01$) between the temperature span of the temperate group (14.1°C) and the tropical group (9.5°C). Regressions of the temperature span for maximum net photosynthesis

shown by the species against climate variables showed strong relationships between the temperature span and the seasonality of temperature and the annual range of maximum temperatures (Table 4.8).

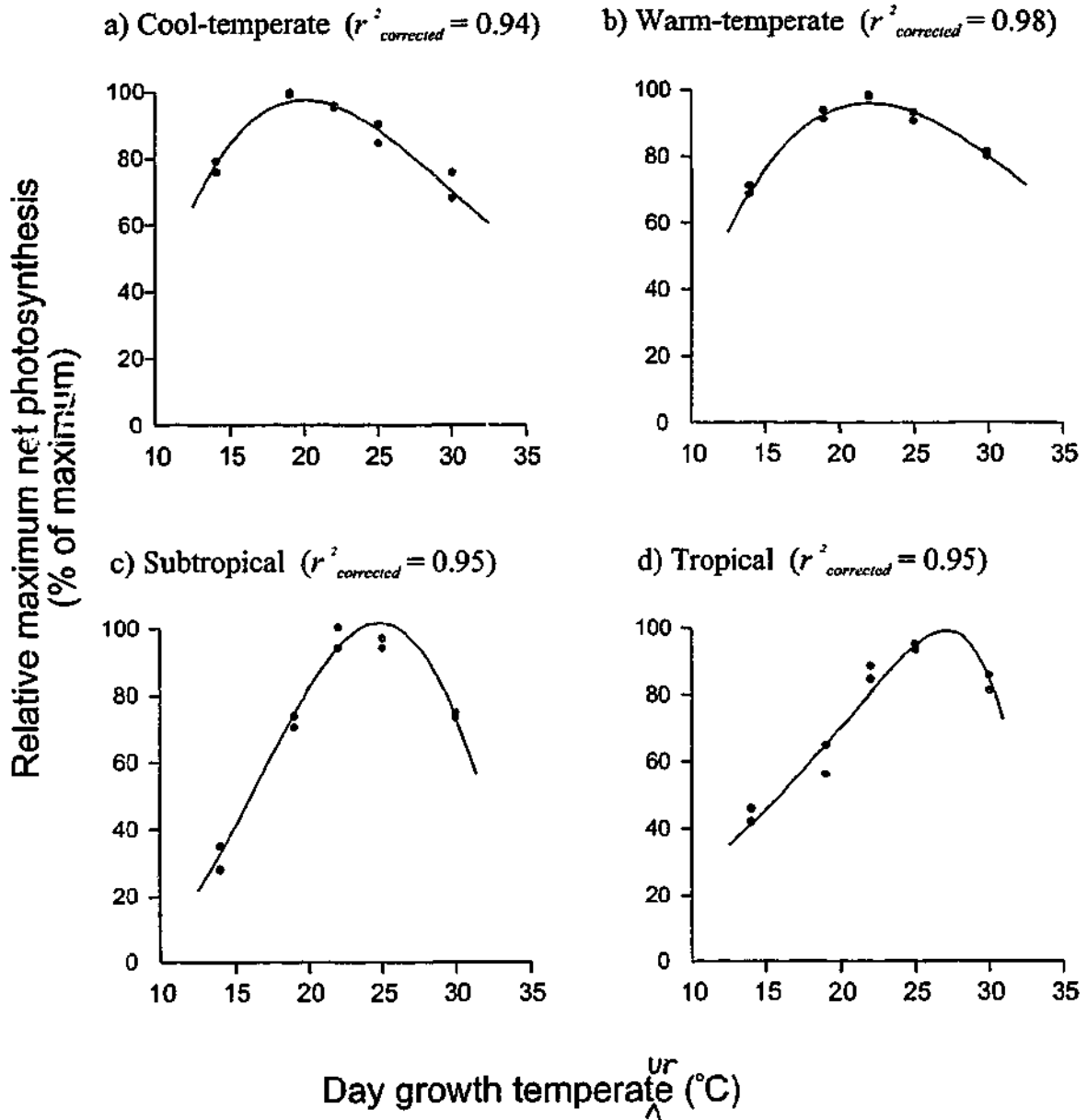


Figure 4.4 Relationship between maximum net photosynthesis (P_{max}) and day growth temperature for rainforest types. Values of maximum net photosynthesis are presented as a percentage of the maximum rate of P_{max} . Points are the mean values for each run.

Table 4.7 Growth temperature for maximum net photosynthesis (GT_{opt}) and the span of growth temperature over which $\gg 80\%$ of maximum net photosynthesis was shown for the rainforest types. Parameters are means of the two species from each rainforest type with standard errors in brackets.

Rainforest type	GT_{opt} ($^{\circ}C$)	GT_{span} ($^{\circ}C$)
Cool-temperate	20.1 (0.8)	13.8 (1.2)
Warm-temperate	22.4 (1.7)	14.4 (0.9)
Subtropical	24.4 (0.1)	10.1 (0.4)
Tropical	27.0 (0.4)	8.8 (0.4)
<i>F</i>	3.08	5.92
<i>p</i>	0.15	0.06

Table 4.8 Results of Pearson correlations between the span of growth temperature over which 80% of maximum net photosynthesis was shown and various temperature parameters from climate profiles of species. For derivation of parameters see Table 2.3

Temperature parameter	Pearson's correlation coefficient	<i>p</i>
<u>Mean temperature</u>		
seasonality of profile (MTS)	0.73	0.04
annual range of profile (MTR)	0.42	0.30
range of annual values among sites	0.12	0.79
range of values for highest month among sites	0.64	0.09
<u>Maximum temperature</u>		
seasonality of profile (MaxTS)	0.70	0.05
annual range of profile (MaxTR)	0.78	0.02
range of annual values among sites	0.60	0.11
range of values for highest month among sites	0.71	0.05
seasonality of collection site	0.83	0.01
annual range of collection site	0.54	0.17

Effect of growth temperature on the optimum temperature for net photosynthesis

The optimum temperature for net photosynthesis (T_{opt}) of the species varied with the growth temperature under which the leaf had been grown, with a significant linear relationship shown by all species except *E. lucida* (Table 4.9). The increase in T_{opt} with increasing growth temperature varied among species with *Heritiera trifoliolata*, *N. cunninghamii* and *T. laurina* making small increases and the tropical species *A. scholaris* and *C. australe* making the largest increases. Furthermore, the tropical rainforest type made greater increases in T_{opt} ($0.4^{\circ}\text{C}/^{\circ}\text{C}$) than the subtropical and warm-temperate rainforest types ($0.2^{\circ}\text{C}/^{\circ}\text{C}$) and the cool-temperate rainforest type ($0.1^{\circ}\text{C}/^{\circ}\text{C}$; Figure 4.5). Both climate groups showed significant increases in T_{opt} with growth temperature ($F = 116.9, p < 0.01$). The temperate group showed a larger increase in T_{opt} from 21°C to 26°C between the day growth temperatures of 14°C and 30°C than the tropical group, which only increased from 20°C to 23°C .

Table 4.9 Results of linear regressions of T_{opt} against day growth temperature for species.

Species	equation	<i>F</i>	<i>p</i>	r^2
<i>E. lucida</i>		1.00	0.35	0.11
<i>N. cunninghamii</i>	$T_{\text{opt}} = 0.17\text{GT} + 16.02$	22.0	< 0.01	0.73
<i>A. smithii</i>	$T_{\text{opt}} = 0.35\text{GT} + 14.06$	35.5	< 0.01	0.82
<i>T. laurina</i>	$T_{\text{opt}} = 0.10\text{GT} + 22.27$	24.0	< 0.01	0.75
<i>S. woollsii</i>	$T_{\text{opt}} = 0.25\text{GT} + 18.43$	37.9	< 0.01	0.83
<i>H. trifoliolata</i>	$T_{\text{opt}} = 0.16\text{GT} + 21.00$	16.4	< 0.01	0.67
<i>C. australe</i>	$T_{\text{opt}} = 0.40\text{GT} + 15.51$	14.0	0.01	0.64
<i>A. scholaris</i>	$T_{\text{opt}} = 0.48\text{GT} + 12.18$	36.1	0.01	0.92

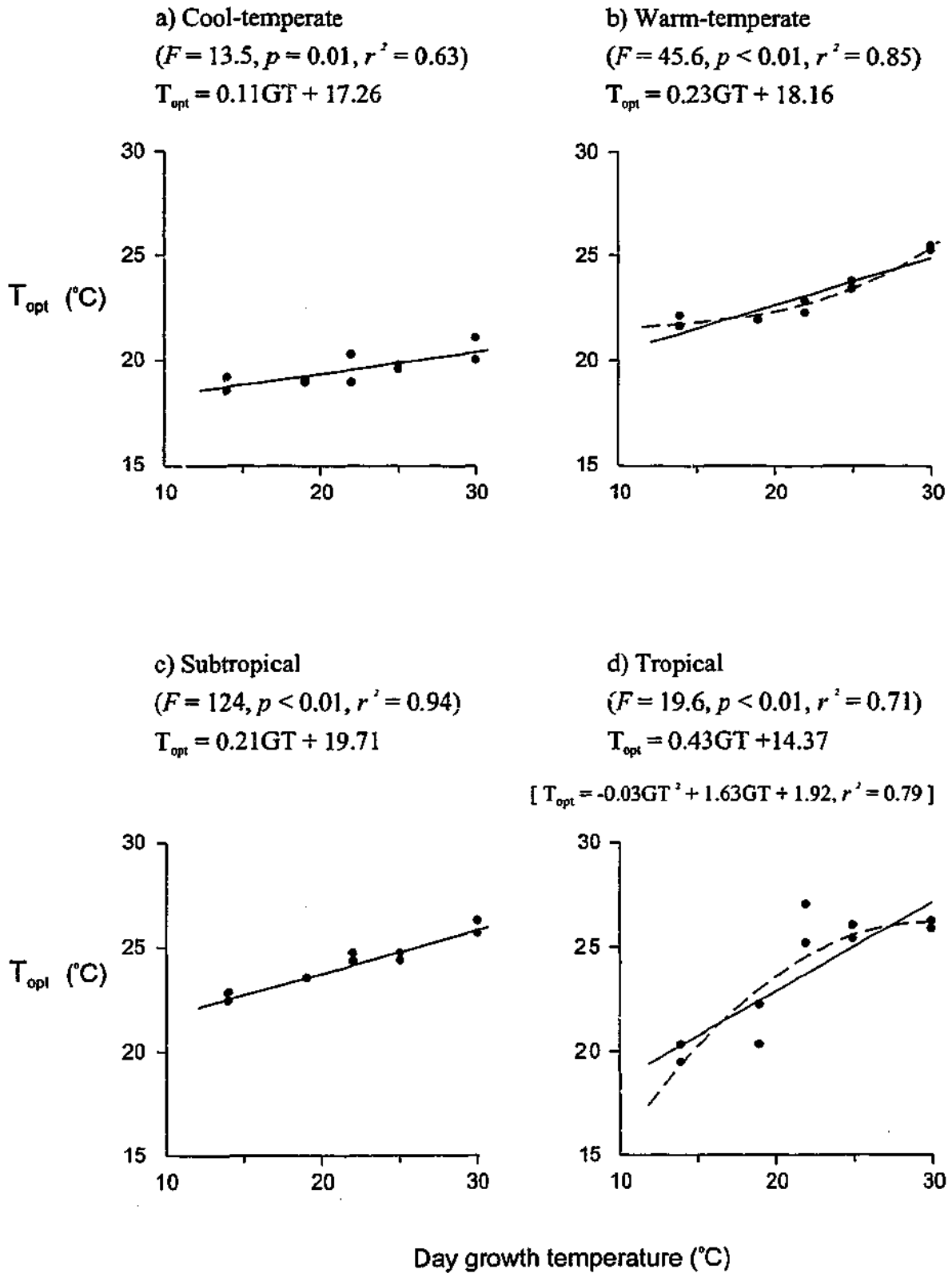


Figure 4.5 Relationship between T_{opt} and growth temperature for the different rainforest types. Values of T_{opt} are means for the two runs.

The relationship of T_{opt} among the rainforest types changed with growth temperature (Table 4.10). This was a result of the minor changes in T_{opt} of the cool-temperate rainforest type compared with the other rainforest types. At the lower growth temperatures, there was little differences in T_{opt} among the rainforest types whereas when grown at 25°C and 30°C the cool-temperate rainforest type had a significantly lower T_{opt} than all the other rainforest types. The T_{opt} of the temperate group (26.0 ± 0.1) was only significantly higher than the tropical group (23.0 ± 0.2) when grown at a day temperature of 30°C ($F = 387, p = 0.03$).

Table 4.10 The optimum temperatures of net photosynthesis (T_{opt}) for the rainforest types grown under different temperature regimes. Values of T_{opt} are means of two runs with standard errors in brackets. Shared letters denote non-significant groupings ($p > 0.05$) of rainforest types within a growth temperature.

Rainforest type	Growth Temperature Regime (day °C/night °C)				
	14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C
Cool-temperate	18.9 (0.3) ^b	19.1 (0.1) ^b	19.7 (0.7) ^b	19.8 (0.1) ^c	20.6 (0.5)
Warm-temperate	22.0 (0.3) ^a	22.0 (1.2) ^{ab}	22.6 (0.3) ^{ab}	23.7 (0.2) ^b	25.5 (0.1) ^a
Subtropical	22.6 (0.2) ^a	23.5 (0.0) ^a	24.5 (0.2) ^{ab}	24.5 (0.2) ^{ab}	26.0 (0.3) ^a
Tropical	19.9 (0.4) ^{ab}	21.3 (1.0) ^{ab}	26.1 (0.9) ^a	25.7 (0.3) ^a	26.0 (0.2) ^a
Rainforest type <i>F</i>	24.9	14.2	16.0	210	61.5
<i>p</i>	0.01	0.03	0.02	< 0.01	< 0.01
Cabinet <i>F</i>	0.26	0.80	0.02	2.63	0.69
<i>p</i>	0.65	0.44	0.91	0.20	0.47

Effect of growth temperature on the span of the photosynthetic response to instantaneous temperature

For each species the temperature span over which at least 80% of P_{\max} was achieved did not change significantly with growth temperature ($F = 1.04$, $p = 0.37$). The tropical species *Castanospermum australe* did show a reduced temperature span when grown at 30°C/22°C. However, this could not be statistically tested as this species was only grown in one run of the experiment. Temperature spans of species ranged from 16°C to 20°C, however, no significant differences were shown between them under the three temperature regimes (Table 4.11). The temperature spans of P_{\max} for the rainforest types also did not change with growth temperature ($F = 0.24$, $p = 0.80$) whereas the relationship among the rainforest types within temperature regimes did show some significant differences ($F = 10.74$, $p < 0.01$). This difference in temperature span among the rainforest types was only shown in the 14°C/6°C regime and although the same trend was shown the magnitude of spans was significantly different between cabinets. However, the cool-temperate rainforest type maintained 80% of P_{\max} over the largest span of instantaneous temperatures at all three growth temperatures (Table 4.12). The temperature span for 80% of P_{\max} of the climate groups did not change significantly with growth temperature ($F = 0.24$, $p = 0.80$). However, under the growth regimes of 14°C/6°C and 22°C/14°C the temperate group maintained a slightly larger temperature span for 80% of P_{\max} of 18.1-18.2°C than the tropical group at 16.7-17.5°C ($F = 14.03$, $p = 0.03$).

Table 4.11 The span of temperatures over which at least 80% of maximum net photosynthesis (P_{\max}) was maintained for individual species. Values are means of the two runs with standard errors in brackets except for *C. australe* for which the means are of six subreplicate plants from the second run.

Species		Growth Temperature Regime (Day °C/Night °C)		
		14°C/6°C	22°C/14°C	30°C/22°C
<i>E. lucida</i>		20.0 (0.7)	19.4 (0.9)	18.6 (0.7)
<i>N. cunninghamii</i>		19.9 (0.7)	19.1 (0.6)	18.8 (0.8)
<i>A. smithii</i>		15.6 (0.8)	15.9 (1.0)	16.0 (1.0)
<i>T. laurina</i>		17.1 (1.0)	18.5 (0.7)	19.1 (0.7)
<i>S. woollsii</i>		17.6 (0.4)	19.7 (0.6)	17.8 (1.3)
<i>H. trifoliolata</i>		18.2 (1.0)	17.0 (0.8)	16.9 (1.0)
<i>C. australe</i>		16.1	16.0	13.9
<i>A. scholaris</i>		15.9 (1.1)	17.4 (1.2)	16.6 (1.2)
species	<i>F</i>	5.73	1.41	3.08
	<i>p</i>	0.02	0.34	0.10
cabinet	<i>F</i>	7.77	0.19	0.77
	<i>p</i>	0.03	0.67	0.41

Table 4.12 The span of temperatures over which at least 80% of P_{\max} was maintained by rainforest types. Values are means of the two runs with standard errors in brackets. Shared letters represent non-significant groupings ($p > 0.05$) of rainforest types within a growth temperature.

Rainforest type		Growth Temperature Regime (day °C/night °C)		
		14°C/6°C	22°C/14°C	30°C/22°C
Cool-temperate		19.9 (0.7) ^a	19.3 (0.6)	18.7 (0.7)
Warm-temperate		16.4 (0.8) ^{ab}	17.2 (1.0)	17.6 (0.6)
Subtropical		18.0 (0.3) ^{ab}	18.4 (0.6)	17.4 (0.5)
Tropical		16.0 (0.7) ^b	16.8 (0.9)	15.3 (0.2)
Rainforest type	<i>F</i>	22.5	1.7	2.06
	<i>p</i>	0.01	0.34	0.28
Cabinet	<i>F</i>	14.5	0.19	1.24
	<i>p</i>	0.03	0.69	0.35

Effect of growth temperature on net photosynthesis at extreme temperatures

Most species showed significant changes in the percentage of P_{GTmax} shown at the instantaneous temperatures of 10°C and 30°C with growth temperature (Tables 4.13 & 4.14). The trends in the percentage of P_{GTmax} at 10°C and 30°C varied among species from the cool-temperate species *E. lucida*, which showed its highest percentages at the day growth temperatures of 14°C and 22°C, to the tropical species *A. scholaris*, which showed its highest percentages at the day growth temperatures of 22°C and 30°C. The only significant changes in the percentage of P_{GTmax} shown at 10°C with day growth temperature for the rainforest types were a reduced percentage when grown at 30°C for the cool-temperate rainforest type and a reduced percentage when grown at 14°C for the subtropical rainforest type (Figure 4.6 a & c). In contrast, all rainforest types showed a significant reduction in the percentage of P_{GTmax} shown at 30°C when grown at a day temperature of 14°C (Figure 4.6). The climate groups had their highest percentages of P_{GTmax} at the instantaneous temperatures of 10°C and 30°C when grown at a day temperature of 22°C (Figure 4.7). Both climate groups had a significant reduction in the percentage of P_{GTmax} shown at 10°C and 30°C when grown at a day temperature of 14°C. The temperate group also showed a reduction in the percentage of P_{GTmax} shown at 10°C when grown at a day temperature of 30°C.

Table 4.13 The percentage of P_{GTmax} shown at the instantaneous temperatures of 10°C by leaves of the individual species grown under different growth temperature regimes. Values are means of two runs with standard errors in brackets except for *C. australe*, which was only measured, in the second run. Shared letters represent no significant difference ($p < 0.05$) between those growth temperatures.

Species	Growth Temperature Regime			<i>F</i>	<i>p</i>
	14°C/6°C	22°C/14°C	30°C/22°C		
<i>E. lucida</i>	68.9 (1.5) ^a	72.6 (0.7) ^a	47.0 (1.3)	120	< 0.01
<i>N. cunninghamii</i>	56.0 (5.5)	77.3 (2.0)	56.4 (4.4)	9.71	0.05
<i>T. laurina</i>	30.0 (2.0)	58.2 (1.7)	45.2 (0.2)	84.6	< 0.01
<i>A. smithii</i>	51.3 (0.7)	59.3 (1.1)	35.4 (3.6)	2.90	0.20
<i>S. woollsii</i>	17.0 (2.4) ^b	60.1 (6.2) ^a	39.7 (0.2) ^{ab}	25.5	0.01
<i>H. trifoliolata</i>	21.4 (4.7)	45.4 (3.8)	36.7 (5.9)	6.13	0.09
<i>C. australe</i>	20.0	42.1	23.4		
<i>A. scholaris</i>	24.5 (1.7)	37.5 (2.1) ^a	37.9 (1.5) ^a	78.3	0.02

Table 4.14 The percentage of P_{GTmax} shown at the instantaneous temperatures of 30°C by leaves of the individual species grown under different growth temperature regimes. Values are means of two runs with standard errors in brackets except for *C. australe*, which was only measured, in the second run. Shared letters represent no significant difference ($p < 0.05$) between those growth temperatures.

Species	Growth Temperature Regime			<i>F</i>	<i>p</i>
	14°C/6°C	22°C/14°C	30°C/22°C		
<i>E. lucida</i>	60.2 (3.0) ^a	69.6 (1.1) ^a	44.8 (1.7)	36.0	0.01
<i>N. cunninghamii</i>	54.6 (0.4) ^b	72.6 (3.7) ^a	68.0 (1.7) ^{ab}	12.9	0.03
<i>T. laurina</i>	46.5 (3.4)	88.5 (0.4) ^a	87.3 (1.4) ^a	140	< 0.01
<i>A. smithii</i>	58.2 (1.7) ^b	71.7 (0.8) ^a	64.5 (0.2) ^{ab}	39.2	0.01
<i>S. woollsii</i>	22.6 (0.5) ^b	93.5 (6.5) ^a	69.5 (1.3) ^{ab}	13.2	0.03
<i>H. trifoliolata</i>	28.0 (6.3) ^b	89.3 (5.7) ^a	66.6 (7.6) ^{ab}	16.4	0.02
<i>C. australe</i>	17.5	63.8	63.7		
<i>A. scholaris</i>	30.4 (0.1)	82.7 (2.1) ^a	78.9 (0.8) ^a	251	< 0.01

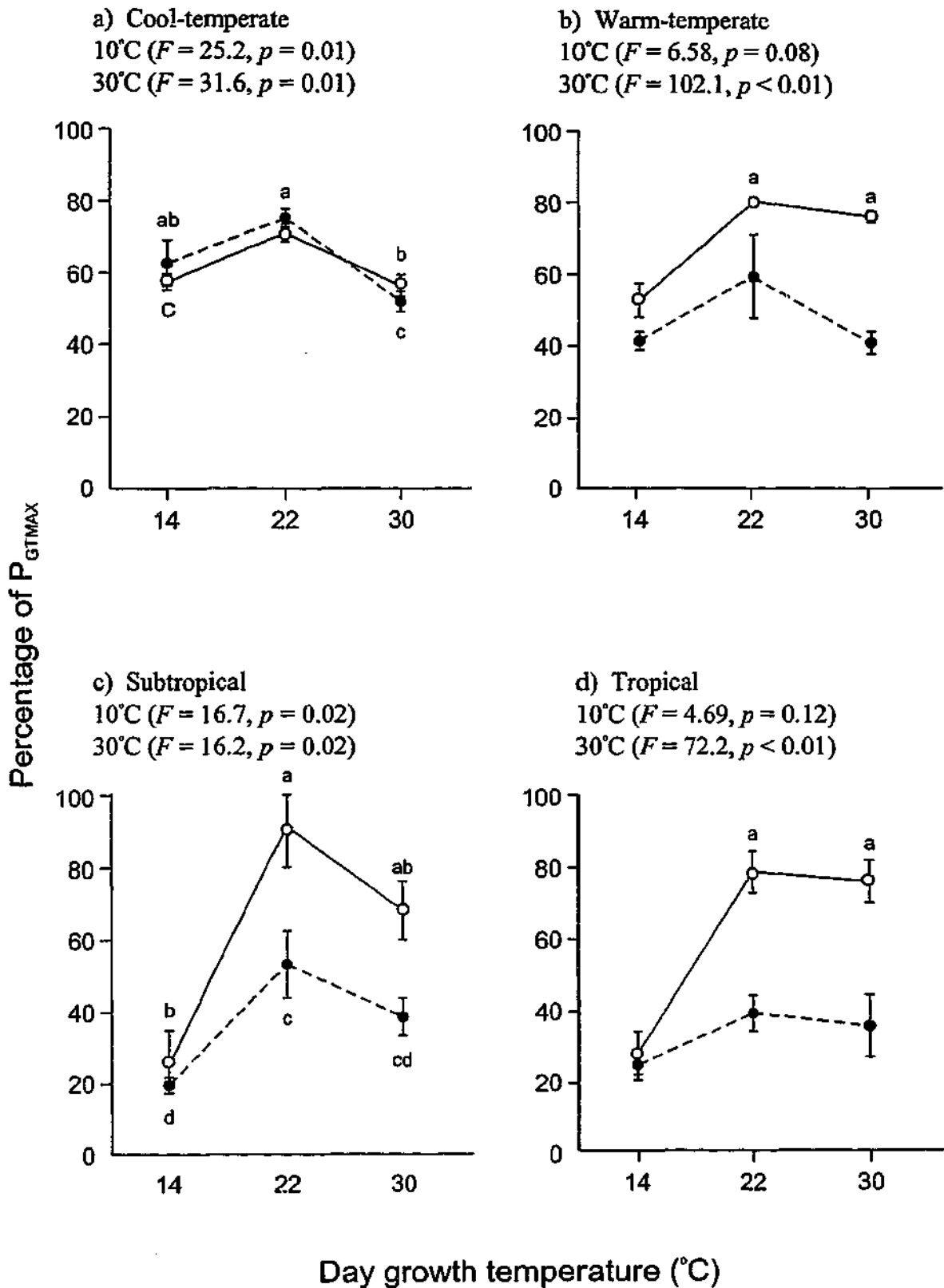


Figure 4.6 Percentage of P_{GTMAX} shown at the instantaneous temperatures of 10°C (●) and 30°C (○) by leaves of the rainforest types grown under the $14^{\circ}\text{C}/6^{\circ}\text{C}$, $22^{\circ}\text{C}/14^{\circ}\text{C}$ and $30^{\circ}\text{C}/22^{\circ}\text{C}$ regimes. Values are means of two runs with standard errors. Letters denote non-significant groupings of means. The data were arcsine transformed for analysis.

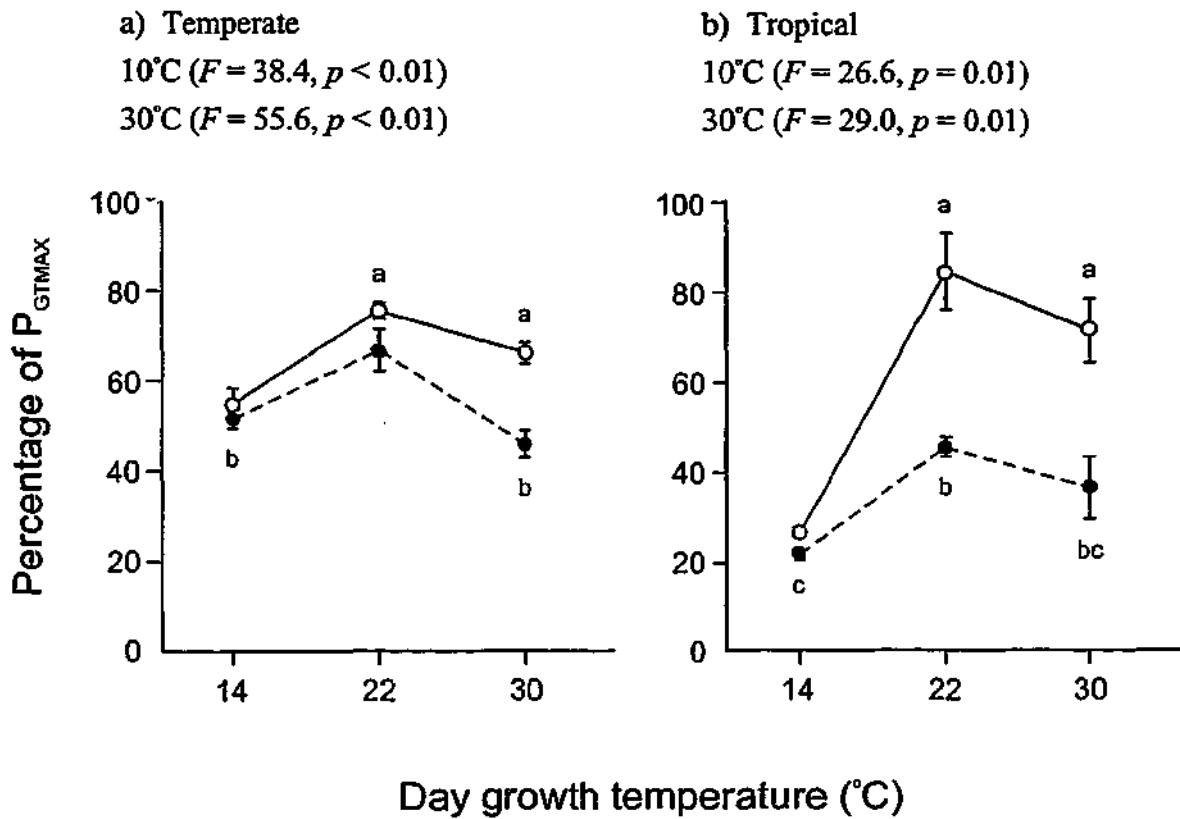


Figure 4.7 Percentage of P_{GTMAX} shown at the instantaneous temperatures of 10°C (●) and 30°C (○) by leaves of the climate types grown under the $14^{\circ}\text{C}/6^{\circ}\text{C}$, $22^{\circ}\text{C}/14^{\circ}\text{C}$ and $30^{\circ}\text{C}/22^{\circ}\text{C}$ regimes. Values are means of two runs with standard errors. Letters denote non-significant groupings of means. The data were arcsine transformed for analysis.

DISCUSSION

Effect of growth temperature on maximum net photosynthesis

The growth temperature for maximum net photosynthesis increased with the decreasing latitudinal origin of the rainforest types (Table 4.6). That is, the growth temperature for maximum net photosynthesis was lowest in the cool-temperate rainforest type and highest in the tropical rainforest type. This is consistent with previous research on species from climatic extremes, which showed species from cool climates tend to have maximum net photosynthesis at lower growth temperatures than species from hot climates (Berry & Björkman 1980). Alpine studies have found that species and populations of species from low altitudes have maximum net photosynthesis at higher growth temperatures than those from high altitudes (Mooney *et al.* 1964; Slatyer 1977b). Comparisons of desert and coastal species have shown that desert species have maximum net photosynthesis at higher growth temperatures than coastal species (Björkman 1981a). Furthermore, summer and winter desert annuals have maximum net photosynthesis at temperatures representative of their different growth seasons (Williams 1974; Toft & Percy 1982; Monson *et al.* 1983).

Comparisons of tropical and temperate species are few and general trends are not clear. In the limited studies of herbaceous species, tropical species tend to show maximum net photosynthesis at higher growth temperatures than temperate species (Scott 1970; Paul *et al.* 1990). However, in the study of Scott (1970) a tropical and temperate alpine grass both showed maximum net photosynthesis when grown at 30°C, whilst another temperate species showed maximum net photosynthesis when grown at 20°C. Latitudinal populations of species are more consistent in showing maximum net photosynthesis at higher growth temperatures in low latitude populations compared with high latitude populations (Mooney & Billings 1961; Billings *et al.* 1971; Treharne & Eagles 1970). However, *Typha latifolia* showed no difference between populations separated by 18° of latitude (McNaughton 1973).

There have been few comparisons of the response of net photosynthesis to temperature in species from different latitudes in Australia. Previous studies have been of the acclimation potential and not the plasticity of different species. Hill *et al.* (1988) found

that among temperate rainforest species the lower latitude species had higher acclimation temperatures for maximum net photosynthesis than higher latitude species. This is consistent with the present finding that tropical species have maximum net photosynthesis at higher growth temperatures compared with temperate species. In contrast, a study of *Nothofagus* species, covering a latitudinal range of 44°, showed a similar range of acclimation temperatures for maximum net photosynthesis among low and high latitude species (Read 1990). However, this lack of difference in optima is likely to be a reflection of the similarities in their climates. That is, the low latitude species of *Nothofagus* were from higher altitudes than the high latitude species and both have similar maximum temperatures in summer. A study of *Eucalyptus* species from different latitudes showed all species had maximum net photosynthesis at the same low acclimation temperature (Ferrar *et al.* 1989). However, the lack of differentiation among the species was due to only two extreme acclimation temperatures being used. This is potentially a problem with any studies that only use a few growth temperatures.

The two warm-temperate species showed almost as much variation in the growth temperature for maximum net photosynthesis (20-25°C) as the rainforest types (20-27°C, Tables 4.4 & 4.6). Both these species show substantial overlap in distribution and climate with the subtropical species (see Figures 1.3, 1.4 & 2.5). Therefore, it is not surprising that *Tristanopsis laurina* showed maximum net photosynthesis at a similar growth temperature to the subtropical species. In contrast, *Acmena smithii* showed maximum net photosynthesis at a similar growth temperature to that of the two cool-temperate species. The seedlings of both species used in this study were collected from sites at the temperate end of their distributions. Therefore, the low growth temperature for maximum net photosynthesis of *Acmena smithii* suggests an adaptation of the population used to the local climate and the existence of different ecotypes across its latitudinal range. The species *A. smithii* does contain three races, however the typical form used in this study covers the same latitudinal distribution as the whole species. Alternatively, the relatively low growth temperature for maximum net photosynthesis shown by *A. smithii* may suggest that net photosynthesis is maximised towards the temperatures of spring when seasonal growth is at a maximum (Ashton & Frankenberg 1976).

Photosynthesis involves a series of reactions that are rate-limited at low temperatures (Berry & Raison 1981). This is reflected by the reduced rates of net photosynthesis in leaves exposed to or developed under low temperatures (Falk *et al.* 1996). Therefore, the growth temperature for maximum net photosynthesis is likely to be optimised towards the temperature of the warmer months of the year. This was supported by a strong correlation between the growth temperature for maximum net photosynthesis and the maximum temperature of the hottest month (Table 4.7). However, the strongest correlation was with the maximum temperature of the hottest month for the species' collection sites and not of their climate profiles. This was a result of GT_{opt} for *A. smithii* being closer to the maximum temperature of the hottest month of its collection site than its climate profile (Figure 4.3).

The temperate rainforest types showed at least 80% of maximum net photosynthesis over a greater span of growth temperatures than the tropical rainforest types (Table 4.6). That is, the tropical rainforest types showed greater reductions in maximum net photosynthesis at suboptimal growth temperatures. The ability of the temperate rainforest types to adjust maximum net photosynthesis to a greater range of growth temperatures than the tropical rainforest types reflects the greater variability in temperature in temperate climates. In particular, the temperate species are exposed to a greater range of maximum temperature throughout the year than the tropical species (Table 2.6). Janzen (1967) argued that the greater stability of temperature regimes in the tropics might have allowed plants to become more narrowly adapted to the conditions. Similarly, desert evergreen species, which are exposed to a highly seasonal climate, show close to maximum net photosynthesis over a broader range of growth temperatures than desert annuals or coastal species (Björkman *et al.* 1980). The greater spans shown by the temperate species are likely to be an adaptation to maximise net photosynthesis during the changing temperatures of the temperate growing season.

Effect of growth temperature on the optimum temperature for net photosynthesis

In many species the optimum temperature for net photosynthesis increases with increasing growth temperature (Berry & Björkman 1980). The rate of change in the optimum temperature for net photosynthesis with growth temperature among species ranges from $1.0^{\circ}\text{C}/^{\circ}\text{C}$ suggesting complete adjustment (eg. Downton & Slatyer 1972) to

0°C/°C showing no adjustment to growth temperature (eg. Williams & Black 1993). A literature search revealed the average rate of change to be 0.4°C/°C (Table 4.15). Therefore, on average, plants increase their optimum temperature 2°C for every 5°C increase in growth temperature. In this study, all species except *Eucryphia lucida* showed significant increases in the temperature optimum for net photosynthesis with increasing growth temperature (Table 4.9). The tropical rainforest type showed the largest shifts (0.4 °C/°C) in the optimum temperature for net photosynthesis. In contrast, the cool-temperate species showed no shifts or small shifts of 0.1°C/°C in the optimum temperature for net photosynthesis.

Previous studies have found that widespread species or species from variable climates show greater shifts in temperature optima (Strain *et al.* 1976; Björkman *et al.* 1978). In addition, within a region evergreen species show greater shifts in temperature optima than seasonal species (Forseth & Ehleringer 1982; Toft & Pearcy 1982; Monson *et al.* 1983). Furthermore, populations of species from more variable climates show greater shifts in the optimum temperature for net photosynthesis (McNaughton 1973; Smith & Hadley 1974). Therefore, there is a trend for species from variable climates to show greater shifts in the optimum temperature for net photosynthesis.

The results for the rainforest species contrast with previous findings in that the tropical species, from the less seasonal climate, showed greater shifts in the temperature optimum for net photosynthesis than the temperate species. However, other species that have shown no shifts in temperature optima with growth temperature include *Betula pubescens* an alpine species with a seasonally variable climate and *Pennisetum setaceum* a widespread invasive grass (Hallgren *et al.* 1982; Williams & Black 1993). It is important to note these two species showed at least 80% of maximum net photosynthesis over a wide range (~23°C) of instantaneous temperatures thus reducing the need for an adjustment. Therefore, species that show no adjustment in their optimum temperature for net photosynthesis with growth temperature are not necessarily from climates that have low seasonal variation in temperature.

Table 4.15 The rate of change in the optimum for net photosynthesis (T_{opt}) with increase in growth temperature (α) from previous studies.

Species	α ($^{\circ}\text{C}/^{\circ}\text{C}$)	Source
<u>Trees</u>		
<i>Betula pubescens</i>	0	Hallgren <i>et al.</i> (1982)
<i>Betula tortuosa</i>	0.33	Hallgren <i>et al.</i> (1982)
<i>Eucalyptus pauciflora</i>	0.34	Slatyer (1977b)
<i>Picea sitchensis</i>	0.37	Neilson <i>et al.</i> (1972)
<i>Pinus taeda</i>	0.67	Strain <i>et al.</i> (1976)
<u>Shrubs</u>		
<i>Atriplex lentiformis</i>	0.50	Pearcy (1976)
<i>Gossypium hirsutum</i>	1.00	Downton and Slatyer (1972)
<i>Larrea divaricata</i>	0.28	Mooney <i>et al.</i> (1978a)
<i>Ledum groenlandicum</i>	0.33	Smith and Hadley (1974)
<i>Nerium oleander</i>	0.33	Björkman <i>et al.</i> (1978)
<i>Oxyria digyna</i>	0 - 0.63	Billings <i>et al.</i> (1971)
<i>Petrophytum cinerascens</i>	0.50	Moore <i>et al.</i> (1998)
<i>Tidestromia oblongifolia</i>	0.63	Björkman <i>et al.</i> (1975)
<u>Herbs</u>		
<i>Brassica napus</i>	0.59	Paul <i>et al.</i> (1990)
<i>Dicoria canescens</i>	0.20	Toft and Percy (1982)
<i>Geraea canescens</i>	0.33	Toft and Percy (1982)
<i>Helianthus annuus</i>	0.59	Paul <i>et al.</i> (1990)
<i>Heliotropium curassavicum</i>	0.60	Mooney (1980)
<i>Lupinus arizonicus</i>	0.23	Forseth and Ehleringer (1982)
<i>Machaeranthera gracilis</i>	0	Monson and Szarek (1979)
<i>Malvastrum rotundifolium</i>	0.27	Forseth and Ehleringer (1982)
<i>Typha latifolia</i>		
- medium latitude	0.22	McNaughton (1973)
- high latitude	0.06	
<u>Grasses</u>		
<i>Agropyron smithii</i>	0.33	Monson <i>et al.</i> (1983)
<i>Asrebla lappacea</i>	0.50	Doley and Yates (1976)
<i>Bouteloua eriopoda</i>	0.33	Bowman and Turner (1993)
<i>Bouteloua gracilis</i>	0.33	Bowman and Turner (1993)
<i>Buchloe dactyloides</i>	0.33	Monson <i>et al.</i> (1983)
<i>Carex eleocharis</i>	0.8	Monson <i>et al.</i> (1983)
<i>Pennisetum setaceum</i>	0	Williams and Black (1993)
mean	0.38 ± 0.04	

The greater shifts in the optimum temperature for net photosynthesis towards the growth temperature shown by the tropical rainforest type than the cool-temperate rainforest type do not represent a greater plasticity. At low growth temperatures, the tropical rainforest type showed large reductions in both the optimum temperature for net photosynthesis and the maximum photosynthetic rate, resulting in an overall inferior performance. Species often show similar shifts in temperature optima with growth temperature but show large reductions in maximum net photosynthesis at temperatures outside their native temperature regime (Vallejos & Pearcy 1987; Paul *et al.* 1990; Bowman & Turner 1993). Shifts in the optimum temperature that are associated with significant reductions in the maximum rate of net photosynthesis can not be taken as photosynthetic plasticity but indicate the plant has suffered some sort of injury or strain (Mooney *et al.* 1978a).

Species from colder environments tend to have maximum net photosynthesis at lower instantaneous temperatures than species from hotter environments. Larcher (1980) records that optimum temperatures for net photosynthesis of tropical trees are 25°C to 30°C, whereas optimum temperatures for temperate evergreen trees are 10°C to 25°C. Similarly, high altitude species show maximum net photosynthesis at lower instantaneous temperatures than low altitude species (Mooney *et al.* 1964; Körner & Diemer 1987). However, in many species the optimum temperature for net photosynthesis has been shown to change with growth temperature (eg. Strain *et al.* 1976; Slatyer 1977b). In this study, the tropical rainforest type showed a higher optimum temperature for net photosynthesis to the cool-temperate rainforest type when grown at the higher temperatures (Table 4.10). However, when grown at the low temperatures the tropical rainforest type showed a similar optimum temperature for net photosynthesis to the cool-temperate rainforest type. Therefore, the differences in temperature optima for net photosynthesis quoted between tropical and temperate species may only be true when measured under conditions representative of their native environments.

Effect of growth temperature on the span of the photosynthetic response to instantaneous temperature

The span of the photosynthetic responses to instantaneous temperature of the species did not change significantly with growth temperature (Table 4.11). However, the tropical species *Castanospermum australe* showed a narrower photosynthetic response to instantaneous temperature when grown at 30°C. A recent field study of *C. australe* showed no difference in the breadth of the photosynthetic response to temperature between a high and low altitude site (Swanborough *et al.* 1998). However, the lack of difference may be due to the mean temperatures at the time of measurement being well below 30°C. Scott (1970) also found that the tropical grass *Zea mays* maintained a narrower photosynthetic response to temperature when grown at high temperatures. In both these cases, the broader photosynthetic response at lower growth temperatures was the result of a large reduction in the overall photosynthetic capacity. However, this study showed that such a response is not found in all tropical species. In addition, temperate species also show a broadening of their photosynthetic response to temperature when grown at low temperatures (Vallejos & Pearcy 1987).

The cool-temperate rainforest type maintained close to maximum net photosynthesis over a larger span of instantaneous temperatures than the tropical rainforest type (Table 4.12). Similarly, Read (1990) found that, within the genus *Nothofagus*, temperate species showed close to maximum net photosynthesis over a larger span of instantaneous temperatures than tropical species. The span of the photosynthetic response to instantaneous temperature is often related to the seasonal and diurnal changes of a species climate (Read 1990; Battaglia *et al.* 1996). Shrubs from mediterranean-type ecosystems, which are characterized by large seasonal changes, show the broadest photosynthetic responses to temperature, with at least 80% of maximum net photosynthesis shown over 20 to 30°C (Oechel *et al.* 1981; Mooney *et al.* 1983). Populations of species from areas with longer growing season, which expose the plant to greater temperature variation, also have broader photosynthetic responses to instantaneous temperatures than populations from more constant climates (Milner & Hiesey 1964; McNaughton 1973). Furthermore, weed species with wide climatic distributions also maintain maximum photosynthetic rates over a wide range of temperatures (Patterson & Mortensen 1985; Williams & Black 1993).

The differences in the breadth of the photosynthetic response to instantaneous temperature between the tropical and temperate species were small (around 3°C) in both Read's (1990) and this study. This small difference between tropical and temperate rainforest species reflects the similar diurnal temperature ranges of the species in this study (Table 2.19), whereas the tropical species of *Nothofagus* from New Guinea experience relatively little diurnal temperature variation compared with the Australian species (Read 1990). In this study, an important difference between the climates of the species is the greater seasonal variation in temperatures experienced by the temperate compared with the tropical species (Table 2.6a). The ability of the cool-temperate rainforest type to maintain maximum net photosynthesis over the largest span of instantaneous temperatures would allow them to tolerate the greater seasonal variation in temperature of their climate. This greater short-term acclimation to instantaneous temperatures in the cool-temperate rainforest type may be associated with a greater ability to acclimate to seasonal changes in growth temperature.

Effect of growth temperature on net photosynthesis at extreme temperatures

Growing plants at hot or cold temperatures often improves their photosynthetic performance at that temperature (eg. Forseth & Ehleringer 1982; Vallejos & Pearcy 1987). However, growing many species at temperatures outside their native range results in an overall reduction in their photosynthetic response (Berry & Björkman 1980). Desert evergreen species, which experience large temperature fluctuations during their growing season, show a high net photosynthetic rate at the growth temperature over a wide range of growth temperatures (Percy 1977; Björkman *et al.* 1978). Growth temperature had a significant effect on the percentage of P_{GTmax} shown at the extreme temperatures of 10°C and 30°C (Table 4.13 & 4.14). All rainforest types showed their highest percentage of P_{GTmax} at the day growth temperature when grown at 22°C (Figure 4.6). Out of the three growth temperatures measured, 22°C/14°C is closest to the optimum growth temperature for maximum net photosynthesis (20 – 27°C) and the optimum instantaneous temperature for maximum net photosynthesis (19 – 26°C) for the majority of species. Therefore, photosynthetic responses at extreme temperatures appear to simply reflect the response of maximum net photosynthesis to growth temperature. However, the differences among the rainforest types in their

photosynthetic response to extreme temperatures also reflected their climatic origins. For example, the cool-temperate rainforest type showed the highest percentage of P_{GTmax} at 10°C when grown at all temperatures and one of the lowest percentages of P_{GTmax} at 30°C when grown at warm temperatures.

Overall, the response of net photosynthesis to growth temperature differed among the rainforest types. The largest differences were between the cool-temperate and tropical rainforest types, which also have the largest differences between their climates. The tropical rainforest type showed maximum net photosynthesis at high instantaneous temperatures and growth temperatures and a limited ability to adjust to low growth temperatures. In contrast, the cool-temperate rainforest type showed maximum net photosynthesis at moderate instantaneous temperatures and growth temperatures, maintained maximum net photosynthesis over a wider range of instantaneous and growth temperatures and therefore showed a greater photosynthetic plasticity.

In conclusion to the stated hypotheses:

1. The temperate species showed maximum net photosynthesis at lower growth temperatures than the tropical species.
2. The temperate species showed close to maximum net photosynthesis over a broader range of growth temperatures than tropical species.
3. The temperate species did not show greater shifts in the optimum temperature for net photosynthesis with growth temperature than the tropical species.

CHAPTER 5

Growth under different temperature regimes

Rainforests grow over a wide range of climates in Australia. The most comprehensive floristic classification of Australian rainforests groups species into eight structural types, which are found under distinct climatic conditions (Webb *et al.* 1984, Table 2.1). The distribution of these structural types has been correlated with temperature (Nix 1991). However, many rainforest species are successively cultivated outside of their natural distribution and show a wide tolerance of temperature conditions. Therefore, the present distributions of species within rainforests are likely to be the result of competitive exclusion.

An obvious explanation for the competitive exclusion of species under different climates is that species have different growth responses to temperature. Numerous models have been proposed to explain the distribution of plants according to climate (eg. Shugart 1984; Landsberg 1986; Woodward 1987; Botkin 1993; Prentice *et al.* 1993). Many of these models are based on theoretical growth responses to temperature. However, these growth responses are often based on direct relationships with photosynthetic responses to temperature and distribution, which are not supported by physiological research (Schenk 1996).

Many models assume that the growth response to temperature takes the same form as the net photosynthetic response to instantaneous temperature. However, there is often not a strong correlation between the response of growth and net photosynthetic to temperature in a plant (Körner 1991; Pereira 1994). Furthermore, variation in relative growth rates among species are not explained by differences in the rate of net photosynthesis (Lambers 1987; Poorter 1990). Growth is the result of many metabolic processes, such as respiration in leaves, stems and roots, photosynthesis and stomatal conductance, each with a different optimum temperature. The effect of temperature on growth is largely a result of how new photoassimilates are partitioned between "productive" (photosynthetic tissues) and "support" (roots and shoots) biomass (Pereira

1994). Therefore, maximum growth may occur when allocation to photosynthetic tissues is maximized and not when the rate of net photosynthesis is at a maximum.

The second major assumption of some climatic models is that the present distribution of a species represents its physiological limits (eg. Shugart 1984; Botkin 1993). These models predict a species will have maximum growth in the middle of their range with growth rates being reduced towards their limits, which is not true of most species (Schenk 1996). Most tree species grow best at their warm limit and are capable of growing beyond this limit when transplanted (Hellmers & Rook 1973; Jacobs 1981; Roberds *et al.* 1990; Bonan & Sirois 1992). However, Loehle (1998) showed for tree species of the United States that as conditions become warmer low latitude species have faster growth rates than high latitude species, therefore predicting their competitive exclusion.

The above climatic models suffer from not including the concept of the fundamental versus the realised niche of a species (*sensu* Hutchinson 1957). Primarily, the distribution of a species is restricted by its tolerance of climate extremes and this range is known as its fundamental niche. The actual distribution of a species is reduced to the range of conditions under which a species is competitive, which is known as its realised niche. Even Woodward's (1987) climatic model is not clear on this point, invoking physiological tolerances to explain high latitude limits and competition to explain low latitude limits.

The current model used to predict the distribution of species according to climate in Australia is the GROWEST model first proposed by Fitzpatrick (1970), and later expanded by Specht (1981) and Nix (1982). This model includes bell-shaped thermal response functions for growth of species (see Figure 5.1). It is proposed that species fall into five broad thermal groups that have different cardinal temperatures for growth (Table 5.1). The GROWEST model proposes that each thermal group will dominate areas where the annual mean temperature is close to their optimum temperature for growth. Nix (1991) went on to propose that these thermal groups dominate different rainforest types in Australia (Table 2.1). The overall prediction being that rainforest species from low latitudes will have maximum growth at higher temperatures than high latitude species.

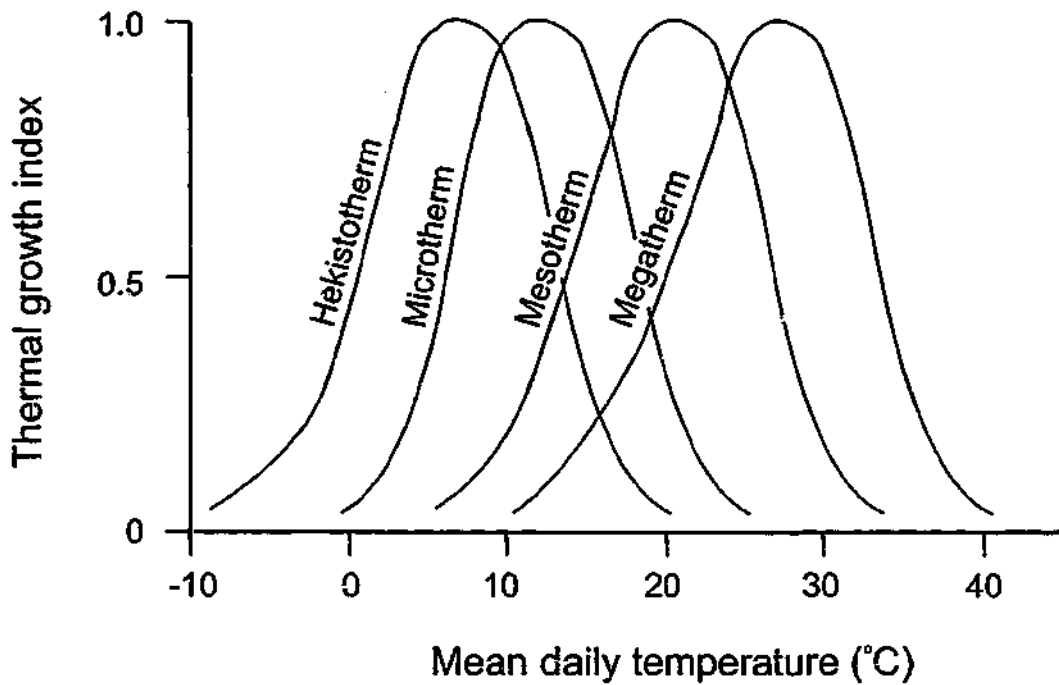


Figure 5.1 The thermal response curves of the GROWEST model adapted from Nix (1982). See Table 5.1 for cardinal temperatures of response curves.

Table 5.1 Cardinal temperatures (°C) for the thermal groups of Nix's GROWEST model following Nix (1991). The relationship between the thermal groups and the rainforest types of Australia proposed by Nix (1991) is shown.

Thermal group	Mean daily temperature		Rainforest types
	optimum	range	
Hekistotherm	6 - 8	-10 - 20	
Microtherm	10 - 14	0 - 25	Cool-temperate & Warm-temperate
Mesotherm	19 - 22	5 - 33	Subtropical
Megatherm (C ₃)	26 - 28	10 - 38	Tropical
Megatherm (C ₄)	30 - 33	10 - 46	

Tree species from temperate latitudes tend to have maximum growth at day temperatures over the range of 15°C to 25°C (Brix 1971; Hellmers & Rook 1973; Paton 1980; Schaffer & Andersen 1994a). In contrast, tropical and subtropical trees tend to have higher optimum growing temperatures between 25°C and 35°C (Opeke 1982; Schaffer & Andersen 1994b). These ranges have been supported by studies of *Banksia* and *Eucalyptus* species from different latitudes along the east coast of Australia (Scurfield 1961; Specht & Brouwer 1975; Groves 1978; Paton 1980; Sa-ardavut *et al.* 1984).

The current distribution of tree species within rainforests of Australia may be a result of differences in growth responses to temperature. Species may have maximum growth at a temperature representative of its native environment as predicted by Nix (1982). However, as stated above, many species show maximum growth at the warm limit of their distribution. Therefore, such species are being outcompeted at temperatures below their temperature for maximum growth. Thus, the species that dominate a climatic region may have the fastest growth rate, but not necessarily maximum growth, at temperatures representative of that climate. This leads to the following hypotheses:

1. Tropical species will have maximum growth at higher temperatures than temperate species.
2. Tropical species will have higher growth rates than the temperate species at high temperatures.
3. Maximum growth will occur at a temperature that maximises allocation to photosynthetic tissues.

These hypotheses were tested by growing seedlings of the eight species under optimal conditions in controlled environment cabinets under the five different temperature regimes described in Chapter 4.

METHODS

Seedlings of each species were grown in controlled environment cabinets for 16 weeks under the following day/night temperature regimes: 14°C/6°C, 19°C/11°C, 22°C/14°C, 25°C/17°C, and 30°C/22°C. The experiment was conducted in two runs, with five seedlings of each species being grown in each treatment within each run. The exception was *Castanospermum australe*, which had seedlings too large to use at the time of the first run, so six one-month-old seedlings were grown in the second run only. A subset of the seedlings grown in this experiment were used for the photosynthetic measurements described in Chapter 4. For a detailed description of the growing conditions within the controlled environment cabinets refer to the previous chapter.

At the start of each run, five seedlings of each species were randomly selected for harvest to determine initial masses. Each plant was separated into leaf laminas, petioles, stems and roots. The stem was cut off at soil level with any material below this being considered roots. Soil was washed off the roots and through a 2 mm sieve to collect any broken roots. Roots were then stored at 2°C for up to 20 days until material still attached to the roots was removed. The petioles of *Nothofagus cunninghamii* and *Tristaniopsis laurina* were considered too small proportionally, to be worth separating from the laminas. The total leaf area of each plant was measured using image analysis (BIOSCANTM Image Analyzer). Then the roots, stems, petioles and laminas were dried at 75°C for 96 hours and weighed. At the end of the 16-week growth period, seedlings were harvested in the same way as the initial harvest. A random order of harvesting was used as it took 10 days to complete the main harvest and further 10 days to process the roots.

Data analysis

The biomass and leaf area data were used to calculate relative growth rates (RGR), root/shoot ratio (RSR), specific leaf area (SLA), leaf weight ratio (LWR), leaf area ratio (LAR) and net assimilation rate (NAR). These parameters were calculated as follows:

$$\text{RGR} = (\ln M_2 - \ln M_1) / t \quad (\text{equation 5.1})$$

$$\text{NAR} = [(M_2 - M_1) \ln (A_2/A_1)] / [(A_2 - A_1) * t] \quad (\text{equation 5.2})$$

$$\text{LAR} = A_2 / M_2 \quad (\text{equation 5.3})$$

$$\text{LWR} = \text{leaf mass} / M_2 \quad (\text{equation 5.4})$$

$$\text{SLA} = A_2 / \text{lamina mass} \quad (\text{equation 5.5})$$

$$\text{RSR} = \text{root mass} / (\text{leaf mass} + \text{stem mass}) \quad (\text{equation 5.6})$$

where M_1 is the mean initial total mass for the species, M_2 is the final total mass, A_1 is mean initial total leaf area for the species, A_2 is the final total leaf area and t the growth interval.

These parameters were analysed as a split plot design as described in Chapter 4. The data were analyzed separately as species, rainforest types and latitudinal groups as previously described.

Growth parameters were analysed as a split plot design with the five growth cabinets from the two runs treated as ten separate plots, growth temperature as the effect between cabinets and taxonomic group as the effect within cabinets. Data were first analysed grouped by species using the averaged values of the subreplicate plants of a species in each cabinet. Then the data were analyzed grouped as rainforest types and climate groups using the mean values of the groups within a cabinet (see Table 2.4). For significant effects, pairwise comparisons of means were performed within each level of the other effect and a Bonferroni adjustment was used for probability values. Comparisons of growth temperature within a taxonomic group were analyzed as a one-way ANOVA. Comparisons of groups within a growth temperature were analyzed as a random complete block design with cabinet as the blocking variable.

The relative growth rate (RGR) of species was regressed against the day growth temperature using the exponential equation:

$$\text{RGR} = \exp (aGT^2 + bGT + c) \quad (\text{equation 5.7})$$

where GT is the day growth temperature, and a , b and c are fitting parameters. This equation was chosen for its ability to fit both the Gaussian response curves predicted by the GROWEST model of Fitzpatrick (1970) as well as a simple exponential curve. The

growth response of trees to temperature in the field has also been found to follow a Gaussian curve (Roberds *et al.* 1990). The differential of equation 6.7 was used to determine the day growth temperature for maximum growth (GT_{opt}) and the rate of change in RGR with day growth temperature at a day growth temperature of 30°C (G_{R30}). These parameters were analysed ^{ly}different depending on the taxonomic group. Species were analyzed as a random complete block design, with run as the blocking variable and using cabinets means. In contrast, rainforest types and climatic groups were analysed as one-way ANOVAs using the mean values for each species across the cabinets.

RESULTS

Effect of temperature on relative growth rate

The relative growth rate (RGR) of all species increased with growth temperature (Figure 5.2). The highest RGRs recorded for the species ranged from 17 mg g⁻¹ day⁻¹ for *Eucryphia lucida* to 30 mg g⁻¹ day⁻¹ for *Tristaniopsis laurina*. When grown at 14°C/6°C, the majority of species maintained 60-80% of their highest RGR whereas *Alstonia scholaris* and *Castanospermum australe* maintained 50% and *E. lucida* maintained a low 36%. The regressions of RGR against day growth temperature for *Nothofagus cunninghamii*, *E. lucida* and *T. laurina* were the only ones to produce maxima within the experimental temperature range (Figure 5.2a, b & d). The temperatures for maximum growth of these three high latitude species range from 25.7°C for *N. cunninghamii* to 29.6°C for *E. lucida* (Table 5.2). In contrast, all the low latitude species have maximum growth at day temperatures above 30°C.

In the absence of maxima for most species, the rate of increase in RGR with day growth temperature at 30°C (G_{R30}) was determined to give an indication of how close the species were to reaching their maxima. The tropical species showed the highest rates of increase in RGR at 30°C among the species that did not show maxima (Table 5.2). This suggests the tropical species are the furthest from reaching their maximum temperature growth. The rate of increase in RGR at 30°C of the rainforest types increased with decreasing latitudinal origin of the type (Table 5.3). However, there ^{are} no significant differences among the rainforest types due to the large variation in responses of their component species. Similarly, the tropical and temperate groups did not show significantly different rates of change in RGR at 30°C ($F = 86.2, p = 0.7$).

At the highest growth temperature of 30°C/22°C, the cool-temperate and subtropical rainforest types showed significantly lower values of RGR than the tropical rainforest type, with the warm-temperate rainforest type showing an intermediate RGR (Table 5.4). In contrast, at the lowest temperature of 14°C/6°C, the warm-temperate rainforest type showed a significantly higher RGR than the other rainforest types, which all showed a similar low RGR. Consequently, the only significant difference between

the climate groups was the higher RGR of the temperate group when grown at 14°C/6°C (Table 5.5).

The rate of increase in RGR at 30°C showed strong correlations with variables of mean and maximum temperature (Table 5.6). The strongest correlation was between the annual maximum temperature and the rate of increase in RGR at 30°C. However, the rate of increase in RGR at 30°C increased with an increase in the value of all the temperature parameters.

Table 5.2 Growth temperature for maximum RGR (GT_{opt}) and the rate of change in RGR at 30°C (G_{R30}) for the individual species. The day growth temperature for maximum net photosynthesis is also included for comparison. Values are means of two runs with standard errors in brackets. 30⁺ = the temperature for maximum growth was above 30°C. Letters denoted non-significant groupings of means.

Species	GT_{opt} for maximum RGR (°C)	G_{R30} ($\mu\text{g g}^{-1} \text{day}^{-1} \text{°C}^{-1}$)	GT_{opt} for max. net photosynthesis (°C)
<i>E. lucida</i>	29.6 (1.2)	-3.5 (10.4) ^c	18.7 (0.1) ^e
<i>N. cunninghamii</i>	25.7 (0.4)	-15.8 (1.5) ^{bc}	21.5 (0.1)
<i>A. smithii</i>	30 ⁺	7.0 (4.7) ^{bc}	19.5 (0.1) ^e
<i>T. laurina</i>	29.1 (0.4)	-2.7 (1.4) ^{bc}	25.4 (0.1) ^c
<i>S. woollsii</i>	30 ⁺	8.5 (0.0) ^{bc}	24.2 (0.2) ^d
<i>H. trifoliolata</i>	30 ⁺	41.6 (2.5) ^a	24.5 (0.2) ^{cd}
<i>C. australe</i>	30 ⁺	78.7	26.3 ^{ab}
<i>A. scholaris</i>	30 ⁺	20.3 (1.0) ^{ab}	27.3 (0.2) ^a
Species	<i>F</i>	46.5	579
	<i>p</i>	< 0.01	< 0.01
Cabinet	<i>F</i>	5.25	2.04
	<i>p</i>	0.06	0.20

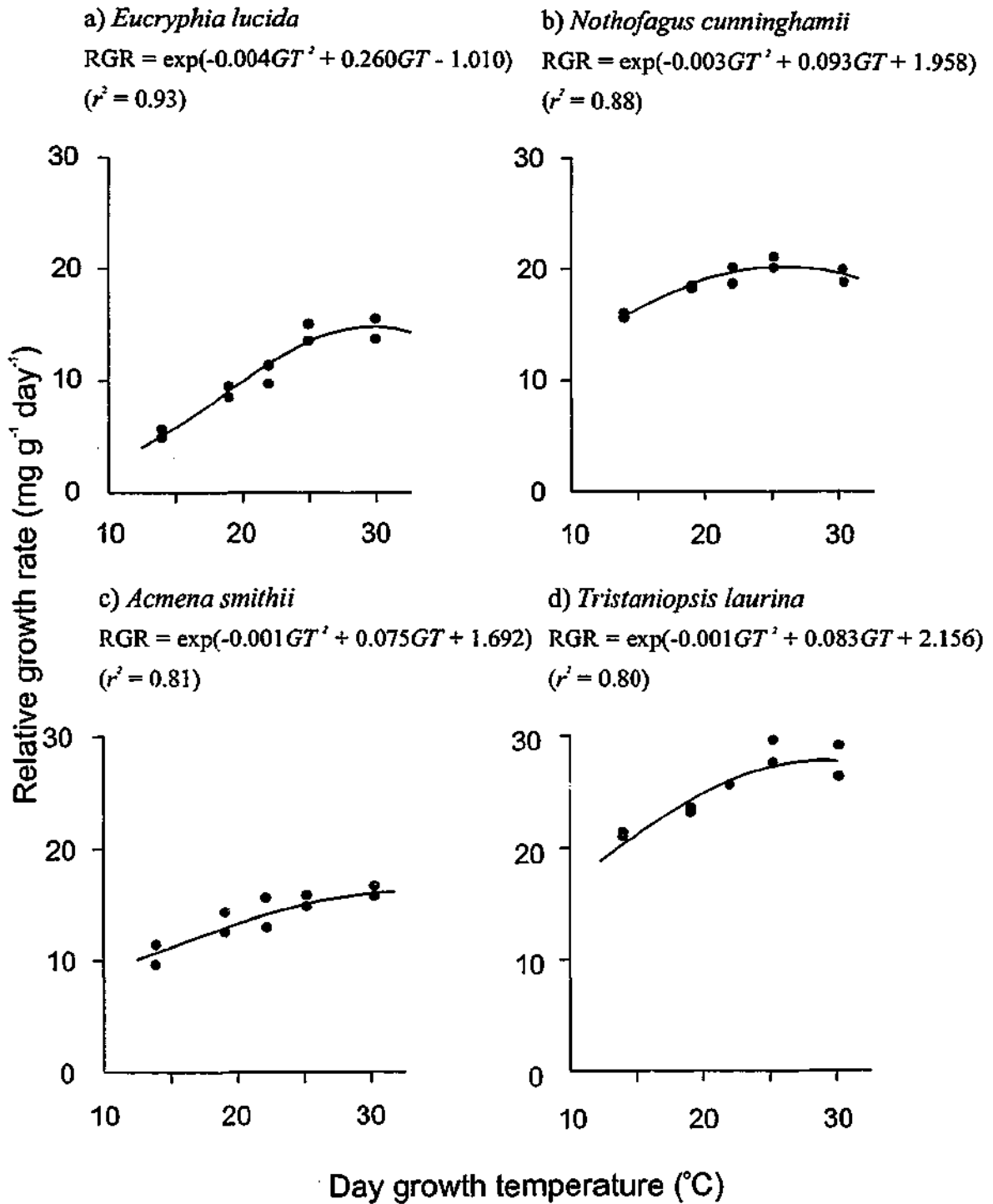


Figure 5.2a-d Relationship of relative growth rate with day growth temperature for the temperate species. Points are the mean values for each run of the experiment.

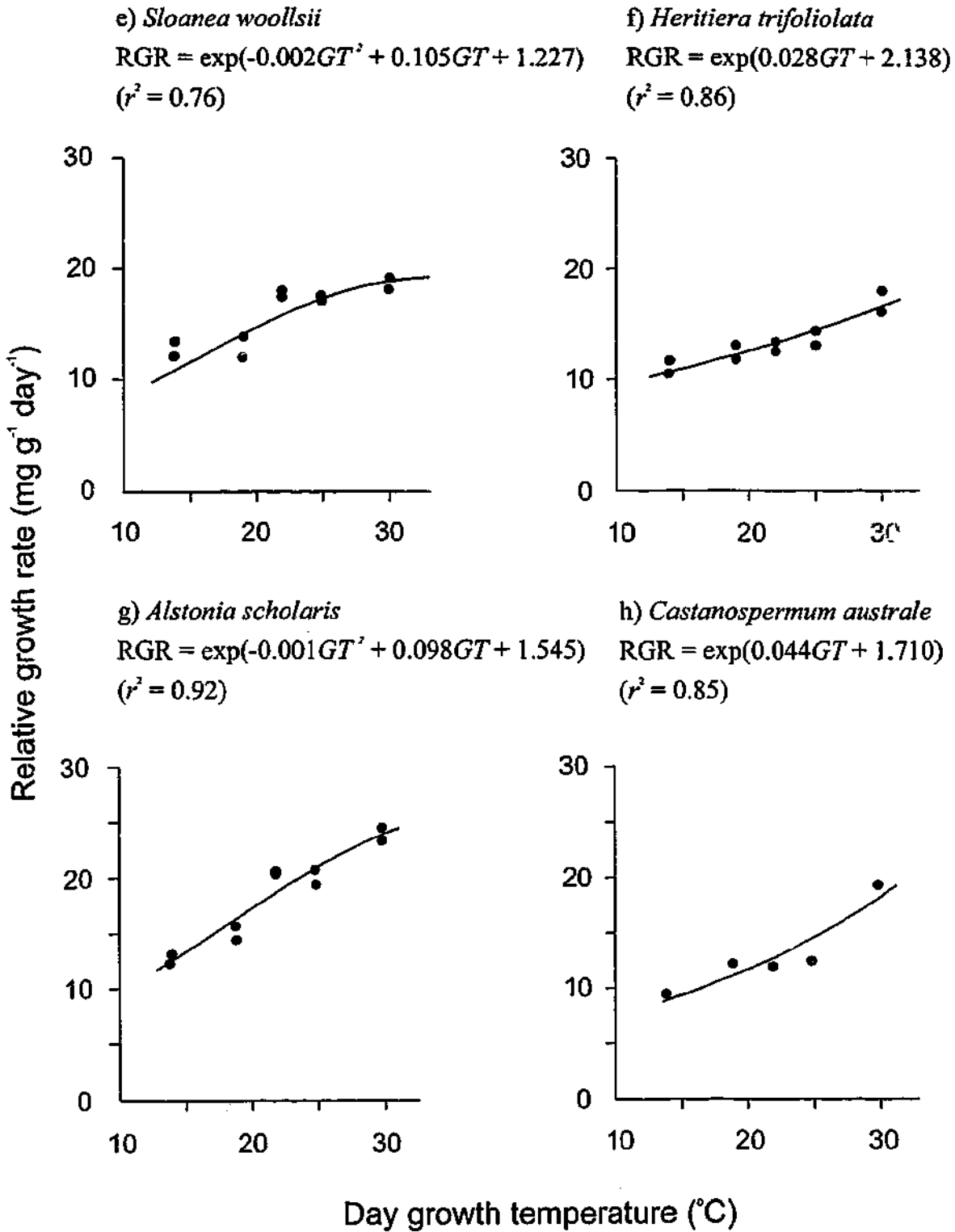


Figure 5.2e-h Relationship of relative growth rate with day growth temperature for the tropical species. Points are the mean values for each run of the experiment.

Table 5.3 Growth temperature for maximum RGR (GT_{opt}) and the rate of change in RGR at 30°C (G_{R30}) for the individual species. The day growth temperature for maximum net photosynthesis is also included for comparison. Values are means of two species with standard errors in brackets. 30^+ = the temperature for maximum growth was above 30°C. Letters denoted non-significant groupings of means.

Species	GT_{opt} for maximum RGR (°C)	G_{R30} ($\mu\text{g g}^{-1} \text{ day}^{-1} \text{ }^{\circ}\text{C}^{-1}$)	GT_{opt} for max. net photosynthesis (°C)
Cool-temperate	27.7 (2.0)	-9.6 (6.2)	20.1 (0.8)
Warm-temperate	29.1 – 30 ⁺	2.1 (4.9)	22.4 (1.7)
Subtropical	30 ⁺	25.1 (16.6)	24.4 (0.1)
Tropical	30 ⁺	49.5 (29.2)	27.0 (0.4)
<i>F</i>		2.30	3.08
<i>P</i>		0.22	0.15

Table 5.4 Relative growth rates ($\text{mg g}^{-1} \text{ day}^{-1}$) of rainforest types grown under different temperature regimes. Values are means of two runs with standard errors given in brackets. Letters denoted non-significant groupings of means.

Rainforest type	Temperature regime (day °C/night °C)				
	14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C
Cool-temperate	12.3 (0.1) ^a	16.0 (0.3) ^{ab}	18.2 (0.7)	20.4 (0.7)	19.8 (0.9) ^b
Warm-temperate	16.8 (0.6)	19.7 (0.6) ^a	21.1 (1.1)	23.4 (0.7)	23.4 (0.6) ^{ab}
Subtropical	12.2 (0.0) ^a	13.2 (0.9) ^b	16.3 (0.1)	16.4 (0.4)	19.3 (0.8) ^b
Tropical	13.7 (0.6) ^a	16.4 (0.3) ^{ab}	21.2 (2.4)	20.9 (1.7)	26.3 (0.9) ^a
Rainforest type <i>F</i>	42.0	15.0	3.17	6.92	12.6
<i>p</i>	0.01	0.03	0.18	0.07	0.03
Cabinet <i>F</i>	3.71	0.04	1.09	0.30	0.03
<i>p</i>	0.15	0.86	0.37	0.62	0.88

Table 5.5 Relative growth rates ($\text{mg g}^{-1} \text{ day}^{-1}$) of climate groups grown under different temperature regimes. Values are means of two runs with standard errors given in brackets. Letters denoted non-significant groupings of means.

Climate group		Temperature regime (day °C/night °C)				
		14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C
Temperate		14.6 (0.4)	17.8 (0.5)	18.7 (0.5)	21.9 (0.0)	21.6 (0.2)
Tropical		13.0 (0.3)	14.8 (0.3)	18.8 (1.2)	18.7 (0.6)	22.8 (0.0)
Climate group	<i>F</i>	499	14.5	0.72	25.9	44.9
	<i>p</i>	0.03	0.16	0.55	0.12	0.09
Cabinet	<i>F</i>	77.9	0.03	1.74	0.90	0.72
	<i>p</i>	0.07	0.90	0.41	0.52	0.55

Table 5.6 Results of Pearson correlations between G_{R30} and various temperature parameters from climate profiles of species. Temperature parameters included the annual (A) and highest monthly (Hi) values for mean temperature (MT), maximum temperature (MaxT) of the species' profiles and maximum temperature for the species' collection site (cs). See Table 2.3 for derivation of parameters.

Temperature parameter	Pearson's correlation coefficient	<i>p</i>
MTA	0.82	0.01
MTHi	0.77	0.03
MaxTA	0.77	0.02
MaxTHi	0.74	0.03
MaxTA (cs)	0.84	0.01
MaxTHi (cs)	0.79	0.02

Effect of temperature on the conversion of assimilate

Values of net assimilation rate (NAR) ranged from 2.1 to 7.7 g m⁻² day⁻¹ among the species (Table 5.7). Most species showed their highest NAR under the higher growth temperatures. The values of NAR for *E. lucida* and *A. scholaris* was more than doubled between the day growth temperatures of 14°C and 30°C. All the rainforest types, except the subtropical rainforest type, showed a significant increase in NAR with increasing temperature (Figure 5.3). The cool-temperate rainforest type showed the highest value of NAR at all growth temperatures but these values were not significantly different from the other rainforest types (Table 5.8).

Effect of temperature on allocation of biomass

The leaf area ratios (LARs) of the species ranged from 3.2 m² kg⁻¹ of *N. cunninghamii* at 19°C to 8.1 m² kg⁻¹ of *C. australe* at 22°C (Table 5.9). *Alstonia scholaris* and *Sloanea woollsii* were the only species to show significant changes in LAR with temperature. The tropical species showed different trends in LAR with *A. scholaris* showing a decrease in LAR with increasing growth temperature whereas *C. australe* produced a greatly increased LAR when grown at 22°C/14°C. Consequently, the cool-temperate and warm-temperate rainforest types showed no significant change in LAR with growth temperature (Figure 5.4). The subtropical rainforest type showed a curvilinear response with a maximum LAR around 22°C whereas the tropical rainforest type showed a decrease in LAR with increasing temperature. The subtropical and tropical rainforest types tended to have greater values of LAR however this was only significantly for the tropical rainforest type when grown at 14°C/6°C (Table 5.10).

The leaf weight ratios (LWRs) of the species vary from 0.27 to 0.51 g g⁻¹ (Table 5.11). At all growth temperatures, *N. cunninghamii* had one of the lowest leaf weight ratios at 0.28 to 0.32 g g⁻¹. The only rainforest type to show a significant change in LWR with temperature was the tropical rainforest type, which showed a decrease in LWR with increasing growth temperature (Figure 5.5). However, the cool-temperate rainforest type showed a slight trend of increasing LWR with increasing growth temperature. Overall, there was a significant difference in LWR between the rainforest types (Table 5.12). However, there was also a significant effect of cabinet within growth temperatures, with the trends between cabinets being different.

Table 5.7 Net assimilation rate ($\text{g m}^{-2} \text{ day}^{-1}$) for the species grown under different temperature regimes. Values are means of two runs with standard errors given in brackets except for *C. australe* for which the means are of six subreplicate plants from the second run. Results of one-way ANOVA within species are given and letters denote non-significant groupings of means.

Species	Temperature Regime (day °C/night °C)					<i>F</i>	<i>p</i>
	14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C		
<i>E. lucida</i>	2.20 (0.35) ^b	2.99 (0.26) ^{ab}	2.51 (0.19) ^{ab}	4.08 (0.76) ^{ab}	4.49 (0.14) ^a	5.93	0.04
<i>N. cunninghamii</i>	4.60 (0.56)	6.33 (0.23)	5.31 (0.84)	6.31 (0.66)	6.05 (0.34)	1.72	0.28
<i>A. smithii</i>	2.46 (0.44)	3.41 (0.34)	3.46 (0.05)	3.49 (0.33)	4.33 (0.77)	2.13	0.21
<i>T. laurina</i>	3.17 (1.11)	3.34 (0.76)	3.60 (1.06)	5.15 (1.72)	4.19 (0.92)	0.48	0.75
<i>S. woollsii</i>	3.21 (0.03)	2.67 (0.07)	2.40 (0.16)	2.76 (0.52)	3.88 (0.51)	2.69	0.13
<i>H. trifoliolata</i>	2.69 (1.17)	2.69 (1.19)	3.84 (1.22)	3.88 (1.39)	4.28 (1.62)	0.31	0.86
<i>C. australe</i>	3.71	4.77	3.43	4.57	5.82		
<i>A. scholaris</i>	1.73 (0.11) ^b	2.20 (0.14) ^b	2.91 (0.06) ^{ab}	3.32 (0.37) ^{ab}	4.49 (0.50) ^a	13.5	0.01

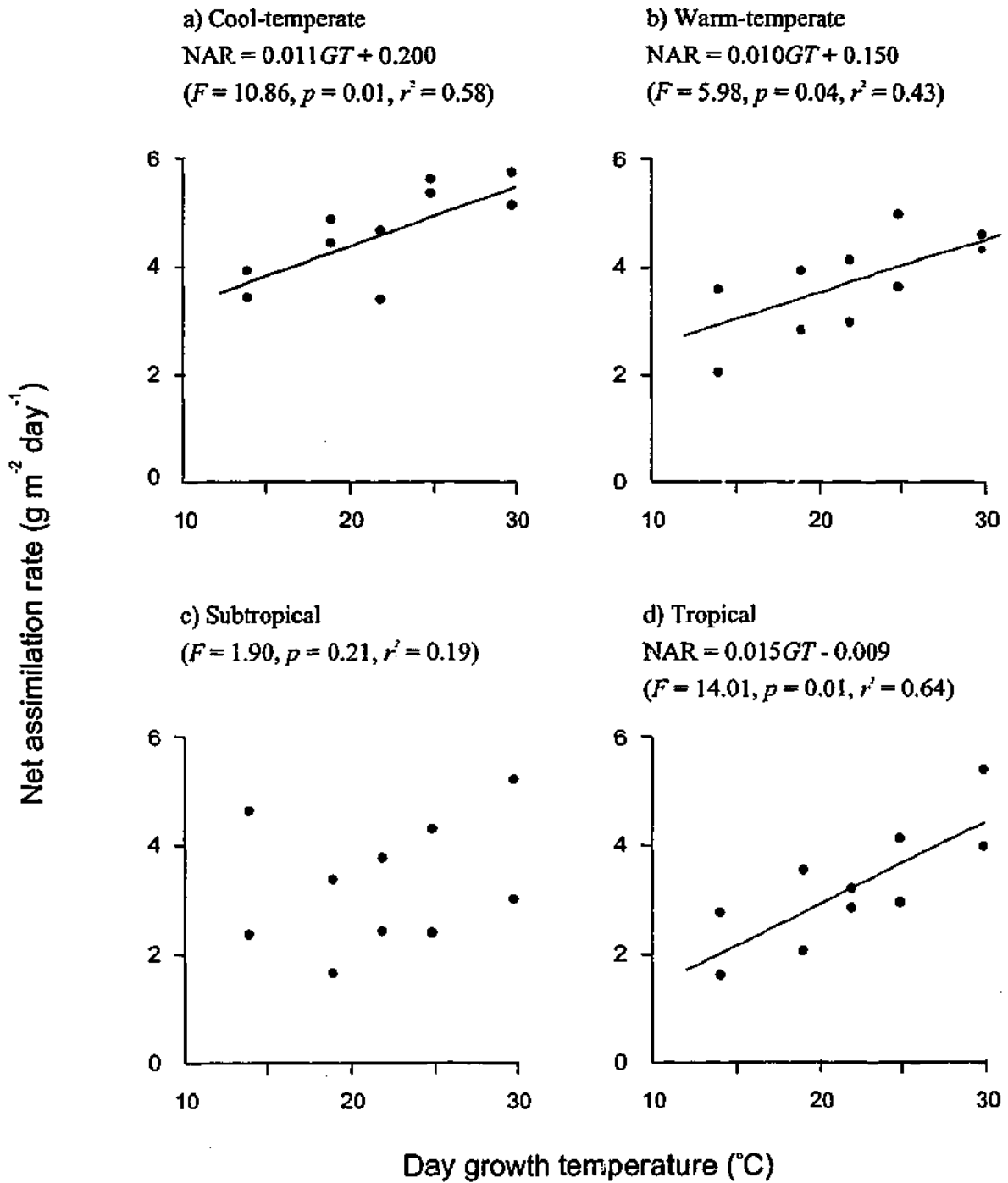


Figure 5.3 Relationships between net assimilation rate and day growth temperature for rainforest types. Points are the mean values for each run of the experiment

Table 5.8 Net assimilation rate ($\text{g m}^{-2} \text{ day}^{-1}$) of rainforest types grown under different temperature regimes. Values are means of two runs with standard errors given in brackets.

		Temperature regime (day °C/night °C)				
Rainforest type		14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C
Cool-temperate		3.40 (0.45)	4.66 (0.25)	3.91 (0.52)	5.19 (0.05)	5.27 (0.24)
Warm-temperate		2.82 (0.77)	3.38 (0.55)	3.53 (0.56)	4.32 (0.70)	4.26 (0.07)
Subtropical		2.95 (0.57)	2.68 (0.56)	3.12 (0.69)	3.32 (0.96)	4.08 (1.07)
Tropical		2.20 (0.58)	2.81 (0.74)	3.03 (0.18)	3.54 (0.59)	4.70 (0.71)
Rainforest type	<i>F</i>	0.51	2.11	0.46	1.40	0.71
	<i>p</i>	0.71	0.28	0.73	0.39	0.61
Cabinet	<i>F</i>	< 0.01	0.17	0.03	0.39	1.36
	<i>p</i>	0.96	0.71	0.87	0.57	0.33

Table 5.9 Leaf area ratios ($\text{m}^2 \text{kg}^{-1}$) for the species grown under different temperature regimes. Values are means of two runs with standard errors given in brackets except for *C. australe* for which the means are of six subreplicate plants from the second run. Results of one-way ANOVA are given and letters denote non-significant groupings of means.

Species	Temperature Regime (day °C/night °C)					<i>F</i>	<i>p</i>
	14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C		
<i>E. lucida</i>	3.91 (1.58)	4.04 (0.90)	4.56 (0.77)	5.28 (0.39)	4.46 (1.05)	0.28	0.88
<i>N. cunninghamii</i>	3.94 (1.43)	3.17 (0.75)	3.97 (1.34)	3.58 (1.04)	3.44 (0.88)	0.09	0.98
<i>A. smithii</i>	4.56 (1.39)	3.86 (0.95)	4.31 (0.02)	4.19 (0.04)	3.76 (0.49)	0.18	0.94
<i>T. laurina</i>	4.40 (0.01)	4.40 (0.87)	4.62 (0.38)	3.72 (0.12)	4.29 (0.39)	0.53	0.72
<i>S. woollsii</i>	3.49 (0.22) ^c	7.14 (0.11) ^a	6.86 (0.28) ^a	6.00 (0.05) ^{ab}	4.85 (0.41) ^{bc}	36.3	< 0.01
<i>H. trifoliolata</i>	5.47 (0.15)	5.40 (0.36)	5.40 (0.55)	5.08 (0.10)	5.19 (0.03)	0.29	0.87
<i>C. australe</i>	5.87	5.36	8.14	5.51	6.80		
<i>A. scholaris</i>	6.64 (0.30) ^a	6.13 (0.61) ^{ab}	6.54 (0.33) ^{ab}	5.20 (0.19) ^{ab}	4.48 (0.26) ^b	6.49	0.03

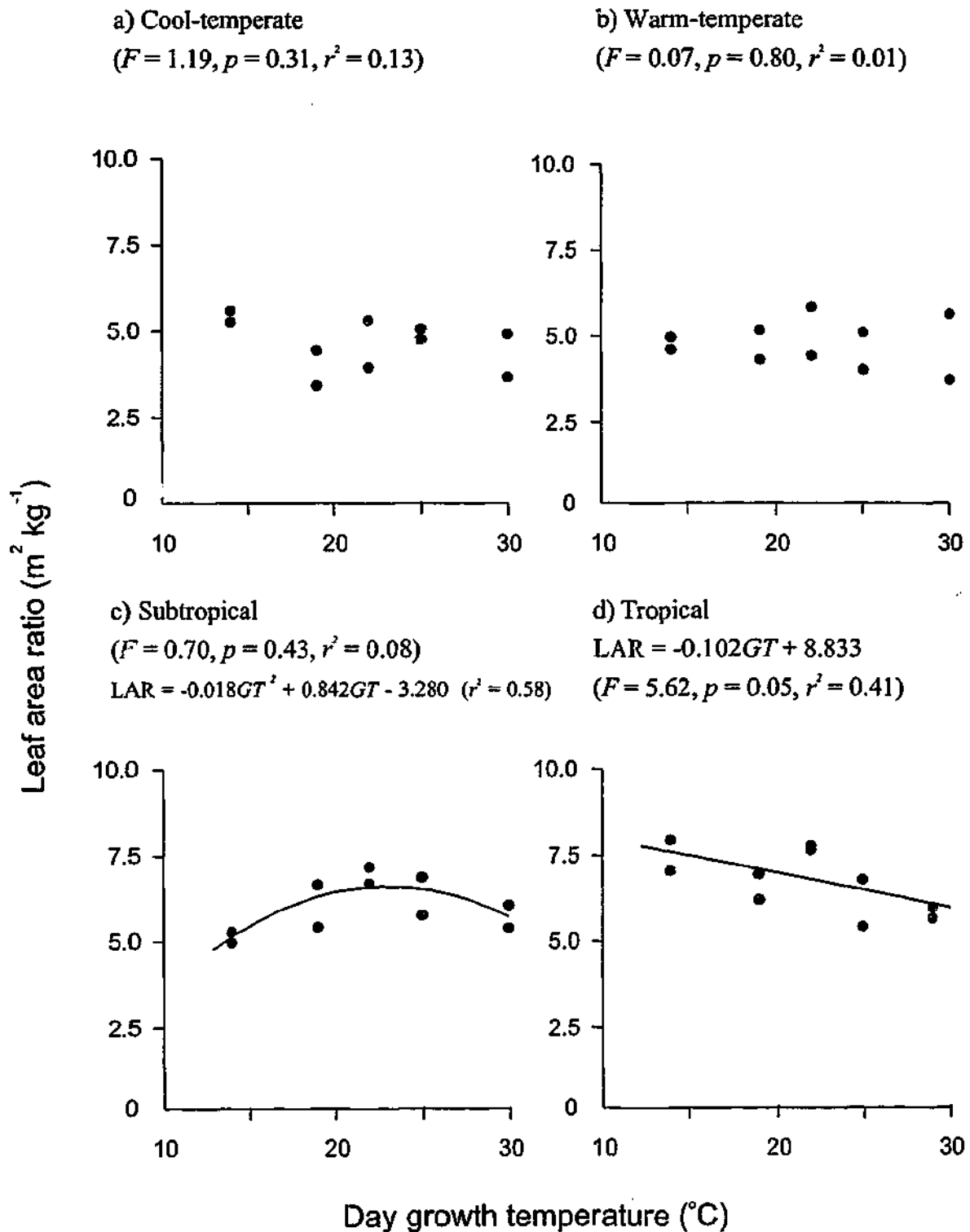


Figure 5.4 Relationships between leaf area ratio and day growth temperature for rainforest types. A quadratic curve was also fitted to the data for the subtropical rainforest type. Points are the mean values for each run of the experiment

Table 5.10 Leaf area ratio ($\text{m}^2 \text{kg}^{-1}$) of rainforest types grown under different temperature regimes. Values are means of two runs with standard errors given in brackets. Letters denoted non-significant groupings of means.

Rainforest type	Temperature regime (day °C/night °C)				
	14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C
Cool-temperate	5.55 (0.04) ^b	3.93 (0.51)	4.63 (0.68)	4.90 (0.15)	4.30 (0.62)
Warm-temperate	4.67 (0.02) ^b	4.60 (0.43)	5.00 (0.71)	4.42 (0.54)	4.54 (0.96)
Subtropical	4.97 (0.16) ^b	5.89 (0.62)	6.79 (0.24)	6.17 (0.55)	5.57 (0.33)
Tropical	7.35 (0.45) ^a	6.42 (0.38)	7.57 (0.07)	5.95 (0.69)	5.67 (0.16)
Rainforest type <i>F</i>	33.6	4.20	5.91	12.9	1.17
<i>p</i>	0.01	0.13	0.09	0.03	0.45
Cabinet <i>F</i>	2.30	0.08	0.08	17.3	0.40
<i>p</i>	0.23	0.79	0.79	0.03	0.57

Table 5.11 Leaf weight ratios (g g^{-1}) for the species grown under different temperature regimes. Values are means of two runs with standard errors given in brackets except for *C. australe* for which the means are of six subreplicate plants from the second run.

Species	Temperature Regime (day °C/night °C)					<i>F</i>	<i>p</i>
	14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C		
<i>E. lucida</i>	0.27 (0.06)	0.38 (0.02)	0.42 (0.04)	0.44 (0.01)	0.42 (0.05)	2.93	0.13
<i>N. cunninghamii</i>	0.32 (0.10)	0.28 (0.06)	0.29 (0.08)	0.29 (0.08)	0.30 (0.08)	0.02	> 0.99
<i>A. smithii</i>	0.38 (0.06)	0.38 (0.03)	0.38 (0.01)	0.37 (0.01)	0.37 (0.01)	0.04	> 0.99
<i>T. laurina</i>	0.46 (0.04)	0.45 (0.00)	0.47 (0.02)	0.43 (0.00)	0.47 (0.00)	0.65	0.65
<i>S. woollsii</i>	0.42 (0.04)	0.42 (0.03)	0.43 (0.02)	0.40 (0.03)	0.42 (0.03)	0.08	0.99
<i>H. trifoliolata</i>	0.34 (0.00)	0.44 (0.10)	0.51 (0.03)	0.49 (0.01)	0.46 (0.06)	1.47	0.34
<i>C. australe</i>	0.46	0.45	0.50	0.40	0.44		
<i>A. scholaris</i>	0.44 (0.03)	0.39 (0.01)	0.37 (0.00)	0.37 (0.03)	0.32 (0.00)	5.41	0.05

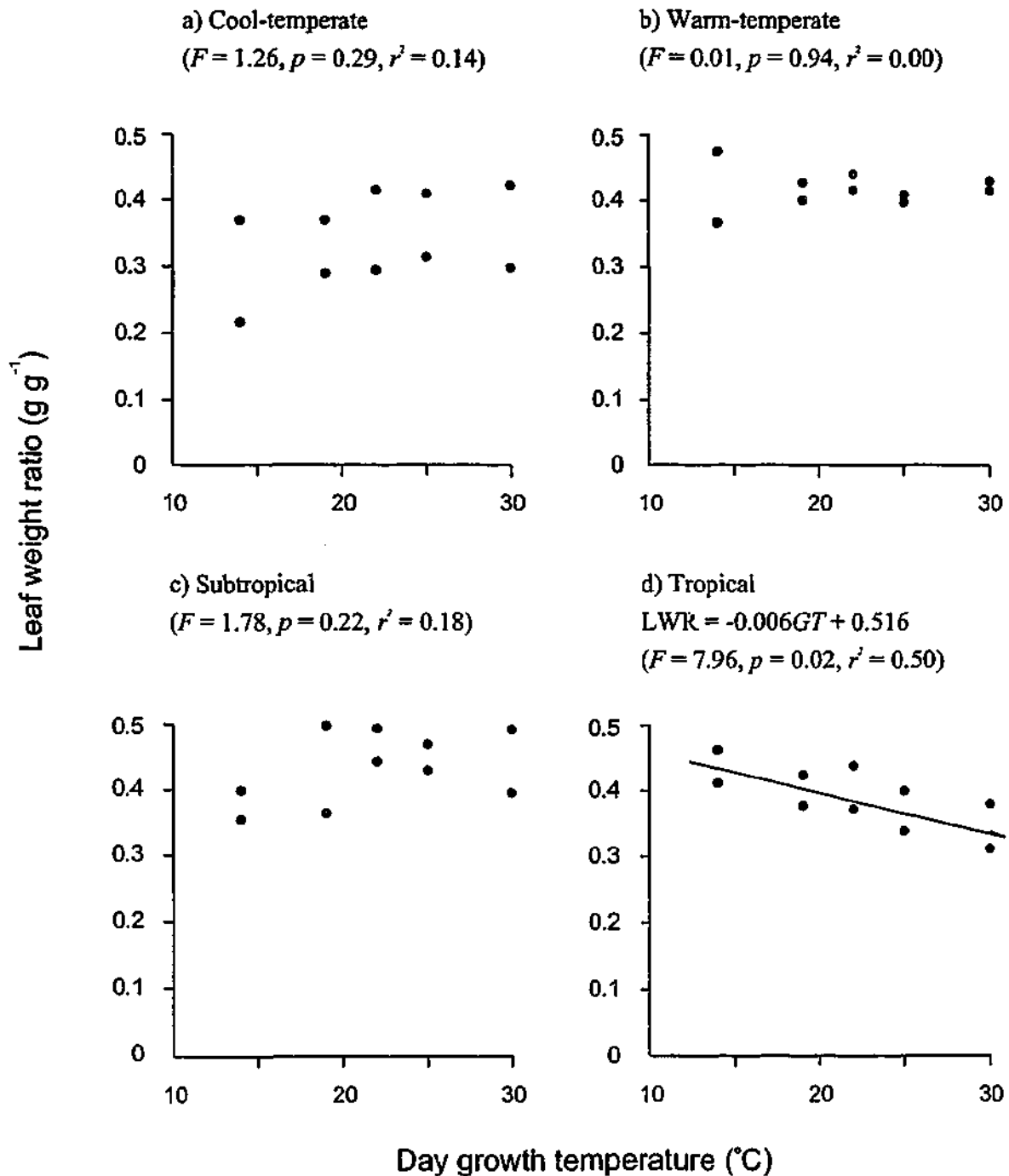


Figure 5.5 Relationships between leaf weight ratio and day growth temperature for rainforest types. Points are the mean values for each run of the experiment

Table 5.12 Results of a split-plot ANOVA comparing values of leaf weight ratio for rainforest types

Hypothesis test	<i>F</i>	<i>p</i>
growth temperature	0.11	0.97
species	16.5	< 0.01
growth temperature × species	1.90	0.12
cabinet (growth temperature)	10.2	< 0.01

At all growth temperatures, the SLA of the tropical species, *A. scholaris* and *C. australe*, were among the highest at 14 to 19 m² kg⁻² respectively (Table 5.13). The values of SLA for the remaining species ranged from 9 to 14 m² kg⁻². The rainforest types showed no significant changes in SLA with temperature (Table 5.14). However, the tropical rainforest type consistently had one of the highest SLA at all growth temperatures.

The root/shoot ratios measured from the species at different growth temperatures ranged from 0.17 to 0.85 (Table 5.15). Most of this variation was among species, with *Acmena smithii* exhibiting one of the highest root/shoot ratios (0.76-0.85) at all growth temperatures whereas *A. scholaris* consistently had one of the lowest root/shoot ratios (0.17-0.45). The remaining variation was due to the root/shoot ratios of the two tropical species doubling between the growth temperatures of 14°C and 30°C. The rainforest types differed in root/shoot response to temperature (Figure 5.6). The cool-temperate and warm-temperate rainforest types showed no significant change in their root/shoot ratio with temperature. In contrast, the subtropical rainforest type showed a decrease in root/shoot ratio with temperature, while the tropical rainforest type showed an increase in root/shoot ratio with temperature. Both these response were better fitted by nonlinear models than linear models. The warm temperate rainforest type had one of the largest root/shoot ratios at all temperatures however this was only significant at 25°C (Table 5.16).

Table 5.13 Specific leaf area ($\text{m}^2 \text{kg}^{-1}$) of the species grown under different temperature regimes. Values are means of two runs with standard errors given in brackets except for *C. australe* for which the means are of six subreplicate plants from the second run.

Species	Temperature Regime (day °C/night °C)					<i>F</i>	<i>p</i>
	14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C		
<i>E. lucida</i>	10.4 (0.5)	11.7 (2.3)	11.7 (0.8)	11.6 (0.5)	11.1 (1.6)	0.16	0.95
<i>N. cunninghamii</i>	12.3 (0.8)	11.2 (0.1)	12.2 (0.1)	12.4 (0.0)	11.7 (0.1)	2.33	0.19
<i>A. smithii</i>	10.1 (0.3)	10.5 (1.9)	11.6 (0.0)	11.8 (0.2)	10.5 (1.1)	0.59	0.69
<i>T. laurina</i>	9.8 (0.6)	9.9 (1.6)	10.0 (0.1)	8.9 (0.0)	9.3 (0.5)	0.37	0.82
<i>S. woollsii</i>	14.2 (1.1)	13.7 (0.1)	13.5 (0.9)	13.5 (0.7)	13.3 (0.9)	0.18	0.94
<i>H. trifoliolata</i>	11.1 (0.7)	12.5 (1.5)	14.2 (0.2)	12.8 (0.2)	11.2 (0.5)	2.71	0.15
<i>C. australe</i>	14.9	13.6	18.5	16.0	18.1		
<i>A. scholaris</i>	16.0 (0.1)	16.8 (1.2)	17.1 (0.3)	15.2 (1.8)	15.1 (1.0)	0.78	0.58

Table 5.14 Specific leaf area ($\text{m}^2 \text{kg}^{-1}$) of rainforest types grown under different temperature regimes. Values are means of two runs with standard errors given in brackets. Letters denoted non-significant groupings of means.

Rainforest type	Temperature regime (day °C/night °C)				
	14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C
Cool-temperate	11.9 (0.1) ^{ab}	11.4 (1.2) ^{ab}	11.9 (0.5) ^{ab}	12.0 (0.3) ^{ab}	11.4 (0.7) ^{ab}
Warm-temperate	10.0 (0.5) ^b	10.2 (0.1) ^b	10.8 (0.0) ^b	10.3 (0.1) ^b	9.9 (0.8) ^b
Subtropical	12.6 (0.2) ^a	13.1 (0.7) ^{ab}	13.8 (0.3) ^a	13.2 (0.5) ^{ab}	12.2 (0.7) ^{ab}
Tropical	15.8 (0.3)	15.7 (0.1) ^a	17.6 (0.1)	15.8 (1.1) ^a	16.1 (0.0) ^a
Rainforest type <i>F</i>	95.0	19.8	176	21.5	14.1
<i>p</i>	< 0.01	0.02	< 0.01	0.02	0.03
Cabinet <i>F</i>	3.25	4.00	3.72	3.00	0.34
<i>p</i>	0.17	0.14	0.15	0.18	0.60

Table 5.15. Root/shoot ratios (g g^{-1}) for the species grown under different temperature regimes. Values are means of two runs with standard errors given in brackets except for *C. australe* for which the means are of six subreplicate plants from the second run.

Species	Temperature Regime (day °C/night °C)					<i>F</i>	<i>p</i>
	14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C		
<i>E. lucida</i>	0.47 (0.06)	0.60 (0.09)	0.53 (0.14)	0.40 (0.01)	0.57 (0.09)	0.74	0.60
<i>N. cunninghamii</i>	0.53 (0.06)	0.63 (0.06)	0.57 (0.03)	0.56 (0.01)	0.57 (0.10)	0.35	0.83
<i>A. smithii</i>	0.85 (0.15)	0.82 (0.16)	0.76 (0.08)	0.83 (0.04)	0.82 (0.03)	0.11	0.97
<i>T. laurina</i>	0.63 (0.17)	0.63 (0.05)	0.47 (0.08)	0.68 (0.04)	0.45 (0.06)	1.19	0.42
<i>S. woollsii</i>	0.64 (0.10)	0.56 (0.07)	0.55 (0.10)	0.57 (0.04)	0.48 (0.12)	0.35	0.83
<i>H. trifoliolata</i>	0.72 (0.02)	0.55 (0.11)	0.41 (0.06)	0.43 (0.03)	0.46 (0.09)	3.26	0.11
<i>C. australe</i>	0.42	0.48	0.47	0.46	0.58		
<i>A. scholaris</i>	0.17 (0.01)	0.24 (0.00)	0.29 (0.01)	0.34 (0.04)	0.45 (0.05)	23.1	< 0.01

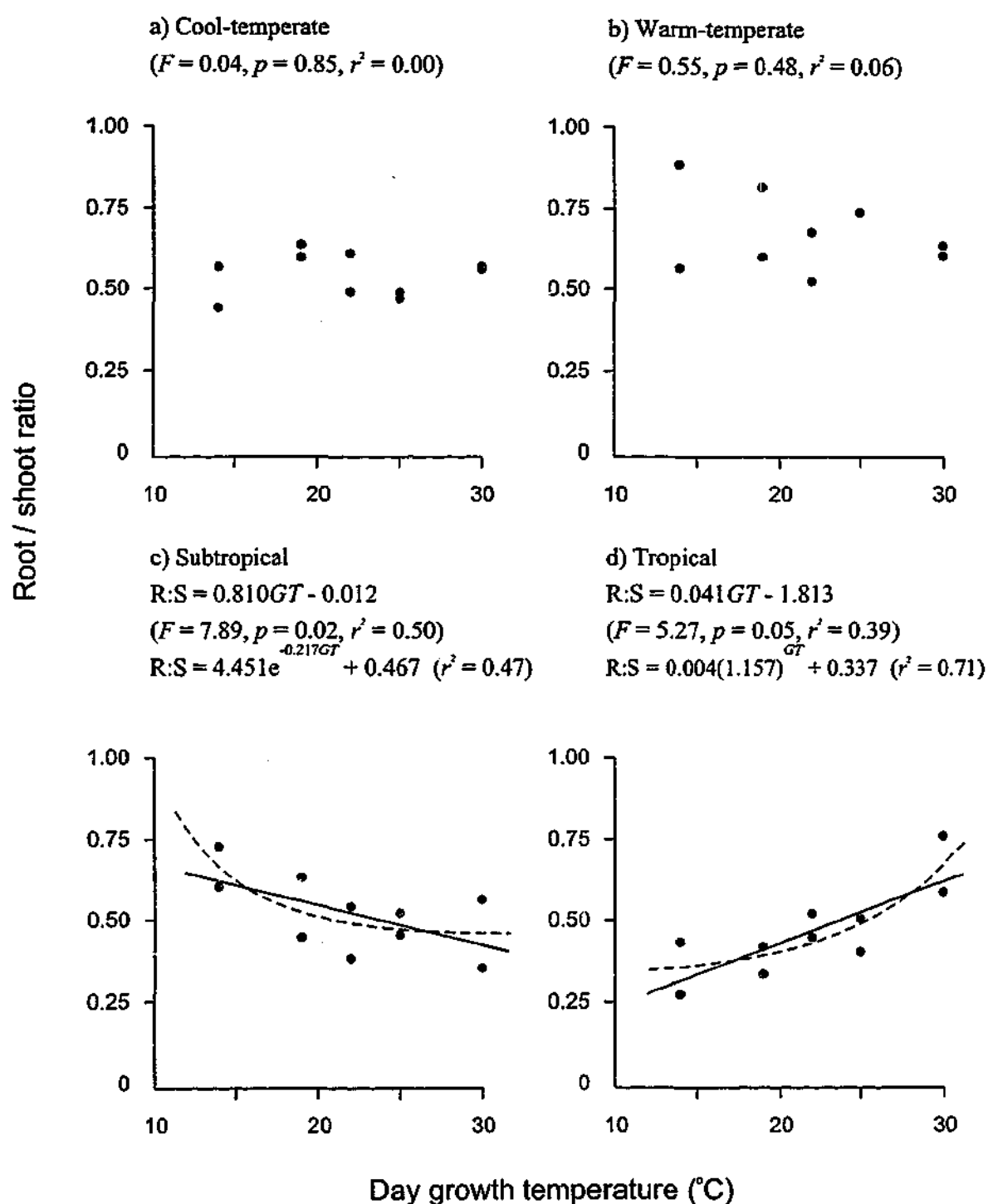


Figure 5.6 Relationships between root/shoot ratio and day growth temperature for rainforest types. For the subtropical and tropical rainforest types non-linear curves (dashed line) were also fitted. Points are the mean values for each run of the experiment

Table 5.16 Root/shoot ratios (g g^{-1}) of rainforest types grown under different temperature regimes. Values are means of two runs with standard errors given in brackets. Letters denote non-significant groupings of means.

Rainforest type	Temperature regime (day °C/night °C)				
	14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C
Cool-temperate	0.50 (0.06)	0.62 (0.02)	0.55 (0.06)	0.48 (0.01) ^a	0.57 (0.00)
Warm-temperate	0.74 (0.16)	0.72 (0.11)	0.62 (0.08)	0.75 (0.00)	0.63 (0.02)
Subtropical	0.68 (0.06)	0.55 (0.09)	0.48 (0.08)	0.50 (0.03) ^a	0.47 (0.11)
Tropical	0.37 (0.08)	0.39 (0.04)	0.50 (0.04)	0.47 (0.05) ^a	0.69 (0.09)
Rainforest type <i>F</i>	3.41	11.1	9.76	32.9	3.12
<i>p</i>	0.17	0.04	0.05	0.01	0.19
Cabinet <i>F</i>	1.70	9.82	40.5	3.86	3.93
<i>p</i>	0.28	0.05	0.01	0.14	0.14

Correlations between relative growth rate and components of growth

Pearson correlations of relative growth rates and the various growth variables revealed the changes associated with increased growth at high temperatures (Table 5.17).

The cool-temperate rainforest type showed a poor correlation between maximum photosynthesis and relative growth rate in comparison to the other rainforest types. The relative growth rates of the cool-temperate and warm-temperate rainforest types showed strong positive correlations with their net assimilation rates. In contrast, the subtropical and tropical rainforest types had high correlations between their relative growth rates and their root/shoot ratios. The subtropical rainforest type showed a negative correlation of relative growth rate with root/shoot ratio and the tropical rainforest type showed a highly positive correlation between root/shoot ratio and relative growth rate. In addition, the tropical rainforest type showed a strong correlation between relative growth rate and leaf weight ratio.

Table 5.17 Pearson correlation values of growth variables with relative growth rate for the rainforest types. Probabilities are given in brackets and variables with the prefix \log_e were log-transformed to improve normality of the data.

	Pmax	\log_e LAR	NAR	\log_e R/S	LWR	\log_e SLA
Cool-temperate	0.06 (0.86)	-0.22 (0.54)	0.69 (0.03)	-0.10 (0.78)	0.51 (0.13)	0.24 (0.50)
Warm-temperate	0.64 (0.05)	0.09 (0.80)	0.84 (<0.01)	0.01 (0.92)	-0.26 (0.46)	0.17 (0.66)
Subtropical	0.58 (0.08)	0.32 (0.37)	0.60 (0.07)	-0.70 (0.02)	0.58 (0.08)	-0.15 (0.69)
Tropical	0.79 (0.01)	-0.39 (0.26)	0.59 (0.05)	0.89 (<0.01)	-0.80 (0.01)	0.35 (0.32)

DISCUSSION

Effect of temperature on relative growth rate

Although temperatures for maximum growth could not be determined for many of the species, it was clear that the temperate species showed maximum growth at lower temperatures than the tropical species (Table 5.2). The temperate species showed maximum growth between 26°C and 30°C whereas maximum growth for the tropical species is above 30°C. Globally, trees show a similar separation between the temperature for maximum growth of temperate (15-25°C: Brix 1971; Hellmers & Rook 1973; Schaffer & Andersen 1994a) and tropical trees (25-35°C: Opeke 1982; Schaffer & Andersen 1994b). Previous studies of trees in Australia have found temperate species show maximum growth at day temperatures between 21°C and 27°C whereas trees from the tropical regions of Australia show maximum growth between 27°C and 33°C (Table 5.18). Interestingly, many tree species that grow both in the tropical and temperate regions of Australia have shown maximum growth at temperatures similar to those of tropical species. The warm-temperate species in the present study, which are distributed from warm-temperate climates through to tropical climates, showed growth at similar high temperatures. The higher temperatures for maximum growth in tropical species compared with temperate species reflect the higher temperatures experienced in the tropics of Australia (Table 2.6a).

The temperatures for maximum growth shown by the temperate species in this study are higher than previous findings in Australia. However, this could be explained by several differences between this study and past studies of the effect of temperature on the growth of trees. Firstly, previous studies in Australia have concentrated on the genus *Eucalyptus*, which may have distinct responses from other genera. Secondly, the majority of these Australian studies used aboveground biomass as a measure of growth, which does not include changes in allocation to roots with temperature. The only other Australian study that used relative growth rate as a measure of growth was by Sa-ardavut (1984). However, the species in the present study showed the same trends in relative growth rate and aboveground biomass with temperature. Thirdly, none of these other studies used curve fitting, which improves the accuracy of the determination of maxima.

Table 5.18a The temperature regime (day °C/night °C) for maximum growth of temperate species from other Australian studies. The latitudinal ranges were obtained from Boland *et al.* (1994) and Brooker and Kleinig (1996). Asterisks denote temperatures for maximum growth that were also the highest growth regime use in the experiment. Growth measures included aboveground biomass (AG), total biomass (TOT) and relative growth rate (RGR).

Species	Latitudinal range (°S)	Temperature for maximum growth	Number of temperatures used	Growth measurement	Source
<i>Banksia ornata</i>	35-37	27/22	3	TOT	Groves (1978)
<i>Eucalyptus blaeklyi</i>	28-37	25/20	5	AG	Scurfield (1961)
<i>Eucalyptus coccifera</i>	41-43	24/19	3	AG	Paton (1980)
<i>Eucalyptus globulus</i>	31-38	25/20	5	TOT	Scurfield (1961)
<i>Eucalyptus gunnii</i>	41-43	24/19	3	AG	Paton (1980)
<i>Eucalyptus nitens</i>	31-38	21/16	4	TOT	Shepherd (1976)
<i>Eucalyptus pauciflora</i>	28-43	24/19	5	TOT	Green (1969)
<i>Eucalyptus perriniana</i>	36-43	24/19	3	AG	Paton (1980)
<i>Eucalyptus polyanthemus</i>	33-38	25/20	5	TOT	Scurfield (1961)
<i>Eucalyptus regnans</i>	37-43	24/19	8	TOT	Cremer (1975)
<i>Eucalyptus rodwayi</i>		24/19	3	AG	Paton (1980)
<i>Eucalyptus urnigera</i>	42-43	24/19	3	AG	Paton (1980)
<i>Eucalyptus vernicosa</i>	42-43	24/19	3	AG	Paton (1980)
<i>Eucalyptus viminalis</i>	28-43	24/19 = 33/28 *	3	AG	Paton (1980)

Table 5.18b The temperature regime (day °C/night °C) for maximum growth of widespread and tropical species from other Australian studies. The latitudinal ranges were obtained from Boland (1994) and Brooker (1996). Asterisks denote temperatures for maximum growth that were also the highest growth regime use in the experiment. Growth measures included aboveground biomass (AG), total biomass (TOT) and relative growth rate (RGR).

Species	Latitudinal range (°S)	Temperature for maximum growth	Number of temperatures used	Growth measurement	Source
<u>Widespread species</u>					
<i>Banksia serrata</i>	26-39	33/28 *	3	TOT	Groves (1978)
<i>Eucalyptus camaldulensis</i>	13-38	30/25	5	RGR	Sa-ardavut <i>et al.</i> (1984)
<i>Eucalyptus maculata</i>	25-38	24/19	-	AG	Specht (1985)
<i>Eucalyptus tereticornis</i>	15-38	33/28 *	3	AG	Paton (1980)
<u>Tropical species</u>					
<i>Banksia serratifolia</i>	20-32	33/28 *	3	TOT	Groves (1978)
<i>Eucalyptus alba</i>	11-24	33/28*	3	AG	Paton (1980)
<i>Eucalyptus deglupta</i>		33/28*	3	AG	Paton (1980)
<i>Eucalyptus drepanophylla</i>		27/22	-	AG	Specht (1985)
<i>Eucalyptus grandis</i>	25-33	30/25	3	TOT	Morris (1977)
<i>Flindersia brayleyana</i>	16-19	29/22 *	3	AG	Herwitz (1993)
<i>Toona australis</i>	13-35	29/22 *	3	AG	Herwitz (1993)

A consistent problem in this and other studies was that the highest temperatures used were not supraoptimal for the growth of tropical species. Consequently, the temperatures for maximum growth could not be accurately determined for tropical species.

The temperatures for maximum growth determined in this study were also considerably higher, particularly for the temperate species, than those predicted by previous growth models (Table 5.19). However, the temperature for maximum growth determined from the regression equations was the day temperature whereas Specht (1986) and Nix (1982) were predicting the mean daily temperature for growth. Converting the results to mean daily temperatures for maximum growth (Table 5.19) showed that maximum growth still occurred at values considerably higher than those predicted by Specht (1986) and Nix (1982).

The temperatures for maximum growth predicted by Nix (1982) represent the mean annual temperatures at which the various rainforest type dominate, whereas maximum growth is more likely to be correlated with the temperature of the growing season. Information on the growing season of rainforest species in Australia is scarce (Hyland, pers. comm.). The growing seasons of the temperate species *Acmena smithii* and *Nothofagus cunninghamii* are known to be winter to spring and spring respectively (Howard 1973; Ashton & Frankenberg 1976). Growing seasons have been found to be between spring and summer for several rainforest tree species in eastern Australia (Lowman 1992). Therefore, in the absence of knowledge of the growing seasons for the other species it is a fair assumption that they would show maximum growth at temperatures representative of the warmest months of the year. Interestingly, the temperatures for maximum growth were also higher than the maximum temperature of the warmest month. In particular, the temperature for maximum growth of the cool-temperate rainforest type is 8.5°C higher than the maximum temperature of the warmest month (Table 5.19). The remaining rainforest types have temperatures for maximum growth, although not clearly determined, at least 4°C higher than the temperatures of the warmest months of their climates. Thus, it would appear that these rainforest species, particularly the cool-temperate species, are maximizing their growth towards temperatures higher than those commonly experienced in the field. This is a trend that has been observed in other controlled environment studies (eg. Went 1953).

Table 5.19 Comparison of temperatures for maximum growth (GT_{\max}) determined by this study with temperatures predicted by models and of climate profiles.

Rainforest type	Cool-temperate	Warm-temperate	Subtropical	Tropical
GT_{\max} (maximum temperature)	27.6	29.1+	30+	30+
GT_{\max} (mean temperature)	24.9	26.4+	27.3+	27.3+
<u>Model predictions</u>				
Mean daily temperature for maximum growth (Nix 1982)	10 - 14	10 - 14	19 - 22	26 - 28
Mean daily temperature for maximum shoot growth (Specht 1986)	15	20	25	30
<u>Climate profile</u>				
Mean annual temperature	9.2	16.3	17.1	21.9
Mean temperature of the warmest month	13.7	21.2	21.8	25.4
Maximum temperature of the warmest month	19.1	26.4	27.1	30.1

There are several possible explanations for why the temperature for maximum growth is higher than the mean maximum temperature of the warmest month. Firstly, temperatures experienced by trees in the field may be higher than those recorded by meteorological stations. In particular, seedlings in large canopy gaps or canopies of mature trees exposed to full sunlight are likely to experience temperatures several degrees higher than those measured in the shade by weather stations. Leaves of plants are often several degrees above ambient temperature (eg. Davidson 1969). Secondly, extrapolation from controlled environments to the field, where temperature varies continuously, is difficult. In the field, other factors such as water, nutrients and irradiance are often limiting and are likely to modify the influence of temperature on growth (Evans 1963). Thirdly, maximum growth at temperatures higher than those of the average climate may confer a competitive advantage. In particular, this strategy

would allow temperate species, whose growth is limited by the length of the warm season, to take advantage of warmer years. Similarly, species from arctic climates show improved growth at temperatures warmer than their mean climates (Chapin 1983; Xiong *et al.* 2000). Fourthly, seedlings may have higher temperatures for maximum growth than mature trees. Eldridge (1969) found in the cool-temperate species *Eucalyptus regnans* that the temperature for maximum growth decreased by 10°C in the first six months after germination. Finally, the large difference between the temperature for maximum growth and the temperature of the warmest month may reflect stronger selection for other strategies, such as herbivore defence, frost resistance or drought resistance. For example, temperate grasses, which have invaded warmer regions, still show moderate temperatures for maximum growth (Cooper 1964; Calder 1973; Hodgkinson & Quinn 1976). In this case, rapid growth and seed set during the wetter, cooler months, before the onset of the summer drought, ensures survival without needing to compete strongly with the summer grasses.

This apparent lack of strong selection for maximum growth at temperatures representative of a species' climate may reflect its lack of importance to the distribution of species. The performance of a species at temperatures representative of its climate are likely to be more important than the temperature at which it has maximum growth. Several authors have emphasized the importance of tolerance of low temperatures in explaining the distribution of plants (eg. Larcher & Bauer 1981; Woodward 1987). However, there is little evidence of the distribution of species being directly determined by tolerance limits (eg. Pigott & Huntley 1981). In contrast, many species can be grown outside their distributional limits, showing reduced growth beyond their cold limits but often showing their greatest growth rate at their warm limits (Schenk 1996; Loehle 1998). In particular, *Castanospermum australe* which is naturally restricted to tropical Australia, New Caledonia and the New Herbrides is successfully cultivated in temperate Australia and South Africa (Han *et al.* 1997; Abu-Zeyad *et al.* 1999, personal observation). Therefore, the distributions of species are likely to be the outcome of competition and not only an intolerance of climate extremes.

Growth at extreme temperatures

Differences in relative growth rates among species are likely to be more important than differences in the temperature for maximum growth to the competitive exclusion of rainforest trees. Species may simply be excluded from a climatic region because their growth rate under the prevailing temperature conditions is lower than that of the dominant species. However, a species could also be excluded from an area due to a lack of adaptation to local predators and pathogens or an absence of appropriate pollinators and seed dispersers.

If the absence of temperate species from the tropics were due to competitive exclusion by plants with higher growth rates, relative growth rates of species at high temperatures would be predicted to decline with increasing latitude of origin. The tropical rainforest type had the highest growth rate at 30°C giving support to why it dominates the tropics (Table 5.4). However, the warm-temperate rainforest type had a growth rate at 30°C which was higher than the subtropical rainforest type and similar to the tropical rainforest type. This is consistent with the presence of the warm-temperate species in both warm-temperate and subtropical rainforests. In addition, the tropical rainforest type contained a species, *C. australe*, that was determined to be shade-tolerant in Chapter 3. Shade-tolerant species are known to have lower growth rates than shade-intolerant species (Kitajima 1996). Therefore, *C. australe* would have lowered the growth rate of the tropical rainforest type at 30°C. However, the warm-temperate species *Tristaniopsis laurina* had a growth rate at 30°C equal to that of the other tropical species *Alstonia scholaris*. It is not surprising the warm-temperate rainforest type had a high growth rate as both component species were from the Myrtaceae, which includes the fast growing species of the genus *Eucalyptus*. What is surprising is that the subtropical rainforest type had a low growth rate at 30°C similar to that of the cool-temperate rainforest type.

The low growth rate of the subtropical rainforest type may mean that these plants were not growing under optimal conditions. Kitajima (1996) surveyed the literature on tropical trees to find that the mean growth rate of shade-tolerant species was $21 \pm 2 \text{ mg g}^{-1} \text{ d}^{-1}$ and that of shade-intolerant species was $59 \pm 7 \text{ mg g}^{-1} \text{ d}^{-1}$. Therefore, the growth rates at 30°C of the subtropical rainforest type at $19 \text{ mg g}^{-1} \text{ d}^{-1}$ and the tropical rainforest

type at $26 \text{ mg g}^{-1} \text{ d}^{-1}$ are low compared with the growth rates of other shade-intolerant tropical tree species. However, Kitajima's survey did include two members of the Moraceae which were shade-intolerant and coincidentally had growth rates of 19 and $26 \text{ mg g}^{-1} \text{ d}^{-1}$. In addition, this survey did not include any species from Australia or from the same families as in this study. I am not aware of any published values of relative growth rate for tropical rainforest trees of Australia. The majority of the growth rates in Kitajima's (1996) survey were of plants growing in the field. Therefore, the lower growth rates reported here may reflect a response to growth in controlled environment cabinets. Growth rates of *E. lucida* and *N. cunninghamii* have been shown to be around $30 \text{ mg g}^{-1} \text{ day}^{-1}$ when grown outside in full sunlight (Read 1995). In contrast, the maximum growth rates for *E. lucida* and *N. cunninghamii* were 17 and $24 \text{ mg g}^{-1} \text{ day}^{-1}$ respectively when grown in controlled environment cabinets in this study. Therefore, the growth rates of all the species, in the controlled environment cabinets may be lower than what would be expected in the field. This reduction in growth rate may have been relatively greater in the two subtropical species.

If the distribution of rainforest trees in Australia were determined by competitive exclusion, the temperate species would be predicted to have higher growth rates at low temperatures than tropical species. In general, tropical and subtropical species show poor growth or die at temperatures in a critical range from 7 to 14°C (Evans *et al.* 1985). In this study, the tropical and subtropical rainforest types showed 40 to 50% reductions in growth rate at $14^{\circ}\text{C}/6^{\circ}\text{C}$ compared with those at $30^{\circ}\text{C}/22^{\circ}\text{C}$. In addition, the leaves of the two tropical species were paler when grown at $14^{\circ}\text{C}/6^{\circ}\text{C}$ than at the other temperatures suggesting possible photoinhibition. However, the reduced growth rates of subtropical and tropical rainforest type at $14^{\circ}\text{C}/6^{\circ}\text{C}$ were not significantly different from that of the cool-temperate rainforest type (Table 5.4). Similarly, studies of cool and warm populations of single species only found differences in growth rates at high temperatures (Woodward 1975; Pearcy 1976; Körner & Woodward 1987). The warm-temperate rainforest type had a significantly higher growth rate than the other rainforest types at $14^{\circ}\text{C}/6^{\circ}\text{C}$, which again reflects the high growth rates of the family Myrtaceae to which they belong.

Higher growth rates of temperate species than tropical species at low temperatures have not been shown by species of *Banksia* and *Eucalyptus* (Groves 1978; Paton 1980). The only other study of growth responses to temperature in rainforest species found that a widespread tropical species, which experiences lower temperatures, had a lower growth rate at low temperatures than the more restricted tropical species (Herwitz 1993).

However, this anomaly is easily explained by the 'widespread' species in this study, *Toona australis* being winter deciduous and therefore does not actively growing during the cooler months. In light of the lack of difference in the temperature for maximum growth of temperate species of *Eucalyptus* Scurfield (1961) suggested that tolerance of extreme temperatures may be more important to their distribution. Since then several studies have investigated frost tolerance of temperate trees of Australia in order to explain their distribution (eg. Paton 1980; Read & Hill 1988a; Kirkpatrick & Gibson 1999). These studies have shown that species from colder environments (lower latitudes or higher altitudes) show greater frost resistance.

Comparison of temperatures for maximum growth and maximum net photosynthesis

The temperature for maximum growth was consistently higher than the temperature for maximum net photosynthesis (Table 5.2). In particular, the temperature for maximum growth of the cool-temperate rainforest type is 28°C but the temperature for maximum net photosynthesis is 20°C. This difference could be explained by a lack of direct relationship between photosynthesis and growth or an ability to lower leaf temperature towards the optimum for net photosynthesis.

Small leaves tend to be cooler than large leaves under high irradiance due to their thinner boundary layer allowing greater heat exchange (Parkhurst *et al.* 1968). The strong coupling between leaf and air temperature in small leaves means they tend to be close to ambient temperature. Plants can theoretically lower leaf temperatures by 10 to 15°C below ambient temperature using evaporative cooling (Jackson *et al.* 1981). Mahan (1988) proposed that plants maintain constant leaf temperatures, which are optimal for enzyme function, using evaporative cooling. For evaporative cooling of leaves to be effective there must be a sufficient supply of radiant energy and water, and a significant vapour pressure deficit (Mahan & Upchurch 1988). These conditions were met in the warmer controlled environment cabinets of this experiment. However, many

small leaves do not depart more than 2 or 3°C from air temperature (Gates 1980). Therefore, the cool-temperate species are unlikely to have lowered leaf temperatures to the temperature for maximum net photosynthesis (20°C) in the warmer cabinets.

The relationship between net photosynthetic rate and relative growth rate of plants is quite variable and the correlation is commonly quite poor (Körner 1991; Pereira 1994). This at first seems counterintuitive, as plant growth is ultimately dependent on photosynthesis for its energy source. However, the growth response of a plant is also dependent on the optimum temperatures for translocation and distribution of assimilates, cell division and elongation, storage processes, stomatal aperture and respiration of various organs (Evans *et al.* 1985; Pereira 1994). Gas exchange gives an instantaneous measure of plant performance, whereas growth is the integration of performance over a longer time scale and reflects morphological changes in plants (Pereira 1994). The relative growth rate of a plant is the product of the rate of assimilation per unit of leaf surface (NAR) and the area of the photosynthetic system relative to the plant's mass (LAR). Therefore, there are two further explanations for the discrepancy between the maximum temperature for growth and net photosynthesis. At the temperature for maximum growth rate, there could have been a greater allocation of biomass to photosynthetic tissue or a more efficient conversion of assimilate into biomass.

Effect of temperature on the conversion of assimilate

All rainforest types showed their highest value of NAR at 30°C (Table 5.8), which corresponds with the high temperatures for maximum growth. For the temperate rainforest types, it seems contradictory that NAR is higher at high temperatures when the net photosynthetic rate is decreasing. The net assimilation rate is largely the balance of photosynthesis and respiration in the entire plant (Lambers & Dijkstra 1987). In addition, NAR may also be affected by the rates of growth enzymes and losses of material such as root turnover and aboveground mortality. Therefore, the increased growth rate shown by the temperate rainforest types at high temperatures, without an increase photosynthetic rate, may be due to any of the above factors.

It is unlikely that the higher values of NAR for the temperate rainforest types at 30°C/22°C were a result of decreased respiration rates. The rate of respiration increases exponentially with instantaneous temperature. Plants show acclimation of respiration, with the overall respiration response to temperature being lower in leaves grown at high temperatures compared with leaves grown at low temperatures (Amthor 1989).

However, when respiration rates at their respective growth temperatures are compared, warm-grown plants usually show respiration rates equal to cold-grown plants (Rook 1969; Billings *et al.* 1971; Körner & Larcher 1988). Thus, plants show homeostasis of respiration, tending towards a certain rate regardless of the growth temperature (Amthor 1989). Although actual rates of respiration may not change with growth temperature, changes in the amount of respiring tissues, such as stems and roots, with temperature are likely to be important to growth rate.

The higher growth rate of the temperate species under the 30°C/22°C regime may have been a result of increased enzyme activity at these temperatures. Basic metabolic rates of plants tend to increase exponentially between 10°C and 30°C (Atwell *et al.* 1999). The efficiency of conversion of assimilate into biomass has been shown to increase with temperature in many agricultural plants (eg. McCree & Amthor 1982; Breeze & Elston 1983). The importance of excessive respiration rates during warm nights in reducing growth rates is often emphasised. However, studies of temperate trees have only shown decreases in growth rate with night temperatures above 23°C (Hellmers 1966; Brix 1971; Hellmers & Rook 1973; Hawkins & Sweet 1989). Therefore, in this experiment the 30°C/22°C regime may have provided more optimal conditions for most species than the 25°C/17°C regime simply because of the warmer night temperature. In particular, although the temperate rainforest types were producing greater amounts of carbon under the 22°C/14°C regime, the carbon produced under the 30°C/22°C regime may have been converted more rapidly into biomass due to the higher night temperature.

Effect of temperature on allocation of biomass

It has long been recognised that it is the amount rather than the activity of photosynthetic tissues that determines growth rate in most cases (Jarvis & Leverenz 1983; Osmond 1987). Similarly, improvement in crop yields has been achieved through greater allocation to the harvested organs and not by improved photosynthetic rates (Gifford *et al.* 1984; Evans *et al.* 1985). The area of the photosynthetic apparatus (LAR) can be increased by increasing the amount of leaves (LWR) or increasing the amount of area per unit mass in leaves (SLA). The amount of biomass that can be allocated to photosynthetic tissues is limited by the need for sufficient root mass to supply the water and nutrients necessary to maintain growth. As previously mentioned, the rates of the various growth processes have different temperature optima. Plants are predicted to respond to these differences by allocating new biomass to the rate that is most limiting (Brouwer 1983). Consequently, growth is predicted to be at a maximum when all rates are equally limiting (Bloom 1985). In this study, only the two tropical rainforest types showed significant changes in allocation with temperature.

The tropical rainforest types showed different changes in the area of photosynthetic tissue (LAR) with temperature. The subtropical rainforest type showed a maximum LAR at moderate temperatures. Most studies have found a linear increase in LAR with growth temperature (Woledge & Jewiss 1969; Treharne & Nelson 1975; Woodward 1979; Kleinendorst & Veen 1983). However, all these studies only used two or three cool to moderate temperatures, which would not have revealed a possible decline in LAR at high temperatures. Warren-Wilson (1967) studied growth over a similar temperature range to this study and found that rape also showed a maximum LAR at moderate temperatures. In contrast, the tropical rainforest type showed a decline in LAR with growth temperature. The higher LAR of the tropical rainforest type at 14°C/6°C was a result of a greatly reduced growth of the roots.

The tropical rainforest type was the only rainforest type to show a significant change in the relative amount of leaves (LWR) with temperature. The allocation of dry matter to leaves is insensitive to temperature in seedlings of many species (Warren-Wilson 1966; Woodward 1979; Marcelis 1994) although some species show increases in LWR with temperature (Warren-Wilson 1967; Brix 1971). In contrast, the tropical rainforest type

showed a decrease in LWR with increasing temperature. Therefore, none of the rainforest types achieved their maximum growth rate at higher temperatures because of a significantly increased allocation to photosynthetic tissues. Furthermore, the SLA of the rainforest types was unaffected by temperature. This is in contrast to most species, which show an increase in SLA associated with an increase in LAR with increasing temperature (Woledge & Jewiss 1969; Treharne & Nelson 1975; Woodward 1979; Kleinendorst & Veen 1983). However, increases in SLA with temperature can also result in no change in LAR (Morgan *et al.* 1985).

Only the two tropical rainforest types showed significant changes in root/shoot ratio with increasing temperature. The subtropical rainforest type showed a 30% decrease in root/shoot ratio between 14°C/6°C and 30°C/22°C. This is consistent with decreases in root/shoot ratio with temperature shown by seedlings of other tree species (Hellmers & Rook 1973; Good & Good 1976; Gowin *et al.* 1980; Hawkins & Sweet 1989; Stoneman & Dell 1993). In contrast, the tropical rainforest type showed an 85% increase in root/shoot ratio over the same temperature range. This is surprising as root growth tends to be at a minimum when overall growth is at a maximum (Grace 1988). The greater respiration rate of roots than shoots usually means that an increase in root/shoot ratio decreases overall growth (Körner 1991). Davidson (1969) proposed that root/shoot ratio is at a minimum when the temperature is optimal for root function. Therefore, root/shoot ratio is often considered a reflection of the relative activities of the two systems (Brouwer 1983; Ågren & Ingestad 1987).

The differences among the rainforest types in the response of root/shoot ratio to increasing temperature may reflect different reactions to low temperature. Root growth follows a typical temperature response curve, with tropical species showing higher temperatures for maximum growth than temperate species (Bowen 1991; Kaspar & Bland 1992). The reduced root/shoot ratio of the tropical rainforest type at 14°C may reflect a higher optimum temperature for root growth. In addition, root/shoot ratio increases with the age of seedlings (Hermann 1977), so the cold temperatures may have slowed the overall development of the tropical rainforest type. The increased root/shoot ratio of the subtropical rainforest type at low temperatures is likely to be the result of reduced root activity at low temperatures. Low soil temperatures are known to reduce uptake of water and nutrients whereas high soil temperatures increase respiration

(Hermann 1977). In contrast, the lack of response of root/shoot ratio to temperature in the temperate rainforest types may reflect a broader tolerance of roots to temperatures. Cold climate species have a higher capacity of for phosphorus absorption at low temperatures than species from warm climates (Chapin 1974; McNaughton *et al.* 1974). Furthermore, when nutrient status is high the root/shoot ratio may not change as much with temperature (Berry & Raison 1981).

Overall growth responses of rainforest types

The temperate rainforest types showed no significant changes in allocation with temperature. The increase in growth at higher temperatures was achieved instead by an increase in NAR. However, this increase in NAR with growth temperature is not easily explained due to the reduction in maximum net photosynthesis at high temperatures. Increases in growth rate at temperatures that decrease net photosynthesis have been explained in other species by homeostasis of aboveground respiration, an increase in LWR and a decrease in root/shoot ratio (Teskey & Will 1999; Xiong *et al.* 2000). However, this does not explain the response of the temperate rainforest types as there was no significant change in allocation and homeostasis of respiration alone would not account for the difference. Therefore, maximum growth at high temperatures may be a result of increased activity of metabolic enzymes.

In contrast, the tropical rainforest types showed changes in allocation with temperature. The subtropical rainforest type showed an increased LAR at 22°C/14°C and a decrease in root/shoot ratio with increasing temperature. Therefore, the increased growth of the subtropical rainforest type at 30°C was achieved by a reduction in allocation to roots and consequently root respiration. In contrast, the tropical rainforest type reduced allocation to photosynthetic tissues (LAR, LWR) and increased allocation to respiring tissues (root/shoot ratio) with increasing temperature. The increased RGR at high temperatures was achieved by an increased NAR due to an increase net photosynthetic rate at high temperatures.

In conclusion:

1. Temperate species had maximum growth at lower temperatures than tropical species
2. At 30°C/22°C, there was considerable overlap in the growth rate of tropical and temperate species. Only the tropical rainforest type showed a higher growth rate than the cool-temperate rainforest type.
3. Only the subtropical rainforest type showed increased allocation to photosynthetic tissues at the temperature for maximum growth.

CHAPTER 6

Response of Net Photosynthesis to Acclimation Temperature

The few studies of phenology in rainforest trees of Australia have shown differences in seasonal growth patterns between tropical and temperate species. Temperate species tend to show a bimodal pattern of growth beginning at a threshold temperature during late winter to spring, reaching a peak in spring, then decreasing over summer, followed by a second lower peak in autumn (Specht 1981). However, species with determinate growth, such as *Nothofagus cunninghamii*, rarely show this second growth flush (Howard 1973). By comparison, tropical rainforest species generally show a longer growth period throughout the wet season from late spring to early autumn, with little growth during the winter dry season (Frith & Frith 1985; Basset 1991; Lowman 1992). However, a bimodal pattern was observed in a lowland forest of the wet tropics, which peaked during the summer wet season and again when the trees flowered during the dry season (Hopkins & Graham 1989). Therefore, growth patterns of Australian rainforest trees follow global trends with growth being related to temperature in temperate species and to water availability in tropical species (Reich 1995).

In Chapter 2, temperature was shown to be more seasonal for temperate species than tropical species. Therefore, temperate species produce new leaves during a spring flush which are subsequently exposed to warm summer and cool winter temperatures. In contrast, tropical species produce new leaves over a greater portion of the year, which are then exposed to a smaller range of temperatures. Therefore, seasonal adjustments in mature leaves are likely to be less important in tropical species compared with temperate species.

In the field, temperate species tend to maintain a similar rate of maximum net photosynthesis over the warmer months (Lange *et al.* 1974; Slatyer & Morrow 1977; Drew & Ledig 1981; Pereira *et al.* 1986). In contrast, tropical species show peaks in maximum net photosynthesis, which are related to rainfall and not temperature (Lugo *et*

al. 1978). Numerous studies of temperate species have found seasonal shifts in the temperature for maximum net photosynthesis shown by leaves in the field (Monson 1984; Slatyer & Morrow 1977; Strain *et al.* 1976; Regehr & Bazzaz 1976; Lange *et al.* 1974; Neilson *et al.* 1972). Leaves tend to shift their temperature for maximum net photosynthesis towards the mean temperature of the season (Strain *et al.* 1976) or the previous weeks (Slatyer & Morrow 1977). However, for acclimation to be adaptive, species must also show a similar maximum rate under the new temperature. Species which have broad temperature response curves tend not to shift their response with the seasons (van der Heyden & Lewis 1990; Battaglia *et al.* 1996).

The seasonal responses of net photosynthesis have been reproduced in plants exposed to a series of growth temperatures in controlled environment cabinets. Many of these studies have concluded that species from more variable climates have a greater *acclimation potential* - the ability to maintain maximum net photosynthesis when exposed to a wide range of growth temperatures (Berry & Björkman 1980). Therefore, temperate species are likely to have greater acclimation potential due to their exposure to greater seasonal variations in temperature than tropical species. Most of these studies have used two to three acclimation temperatures (e.g. Tranquillini *et al.* 1986; Ferrar *et al.* 1989; Battaglia *et al.* 1996; Goldstein *et al.* 1996; Teskey & Will 1999) which does not give an indication of their full acclimation potential. For example, Ferrar *et al.* (1989) concluded that there was a lack of relationship between the climatic origin of *Eucalyptus* species and their acclimation potential from only two measurements at extreme temperatures. Presently, the studies of acclimation to temperature in temperate species greatly outnumber those in tropical species. This is because studies of tropical species have concentrated on irradiance and water status, which vary more than temperature in the tropics.

More comprehensive studies of rainforest tree species of Australia, using six to eight acclimation temperatures, have revealed important differences in acclimation potential, which relate to their climatic origin (Hill *et al.* 1988; Read 1990; Read & Busby 1990). Hill *et al.* (1988) found temperate species from high latitudes showed maximum net photosynthesis at lower acclimation temperatures than species from lower latitudes. All these temperate species showed maximum net photosynthesis over a wide range of acclimation temperatures. In contrast, tropical species in the genus *Nothofagus* showed

maximum net photosynthesis over a narrower range of acclimation temperatures than the temperate species (Read 1990). Furthermore, the temperate and tropical species of *Nothofagus* showed maximum net photosynthesis at similar acclimation temperatures. However, this is likely to be a reflection of the similarities in maximum temperatures during summer.

The majority of previous studies have used leaves developed under constant temperature conditions. However, in the field, plants are exposed to variation in day-to-day conditions. In addition, day-to-day variation in temperature is greater in temperate than tropical climates (Atwell *et al.* 1999, Table 2.18). Therefore, leaves of temperate species in particular would be predicted to show greater acclimation potential when developed under ambient conditions compared with constant conditions. A few studies have looked at leaves developed under ambient conditions and then exposed to a series of constant acclimation temperatures in controlled environment cabinets (e.g. Tranquillini *et al.* 1986; Hill *et al.* 1988). The acclimation potential of some species has been measured separately in leaves developed under ambient conditions and in controlled environment cabinets (e.g. Hill *et al.* 1988; Read & Busby 1990; Gunderson *et al.* 2000). However, these responses are not directly comparable, as other factors besides temperature are likely to have varied between the growth conditions. Therefore, no study has compared the effect of constant and fluctuating growth temperatures under the same experimental conditions on the subsequent acclimation potential over a range of growth temperatures.

This study aimed to test the following hypotheses:

1. Temperate species have a greater acclimation potential than tropical species.
2. Leaves growing under fluctuating temperature conditions will have a greater potential to acclimate to instantaneous temperatures than leaves grown under constant temperature conditions.
3. Leaves developed under fluctuating temperature conditions will have a greater potential to acclimate to new growth temperatures than leaves grown under constant temperature conditions.

These hypotheses were tested by measuring net photosynthesis in leaves developed under either a constant or fluctuating temperature regime in controlled environment cabinets. The response of net photosynthesis to instantaneous temperature was measured whilst the leaves were growing under the contrasting temperature regimes to test hypothesis 2. These leaves were then grown under a series of constant temperature regimes and the rate of maximum net photosynthesis measured at each temperature regime to test hypotheses 1 and 3.

METHODS

A subset of the eight species was used to measure acclimation due to the size and duration of the experiment. The cool-temperate species *Eucryphia lucida* and *Nothofagus cunninghamii* and the tropical species *Alstonia scholaris* and *Castanospermum australe* were chosen to give the greatest contrast. Seedlings were grown under two contrasting temperature regimes in the controlled environment cabinets. One set of seedlings was grown under a constant day/night temperature regime of 22°C/14°C. The other set of seedlings was grown under a fluctuating temperature regime in which the day/night temperature was changed daily to a random temperature regime between 17°C/11°C and 27°C/19°C. The temperature program included an equal number of all unit temperatures (17, 18, 19, 20, 21, 22, 23, 24, 25, 26 and 27°C) so that the mean day/night temperature over the experimental period was 22°C/14°C. Each treatment was contained within two replicate cabinets with four subreplicate seedlings of each species in each cabinet.

Seedlings were watered every two days and fertilizer was added to the soil every 14 days. Fertiliser was added in the form of FOGG-IT fish emulsion fertilizer (FOGG-IT Nozzle Company, San Francisco) diluted 1/500 with water to provide 98 mg L⁻¹ of nitrogen, 20 mg L⁻¹ of potassium, and 31 mg L⁻¹ of phosphorus. The seedlings were grown under lights and the day temperature for sixteen hours a day. Seedlings were raised on stands so that the first set of leaves initiated was exposed to an irradiance of 600-800 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ and the desired temperature regime. This also helped avoid shading of crown leaves by neighbouring seedlings. Plants were grown under these conditions for eight weeks until enough leaves had fully-expanded for the photosynthetic measurements to be carried out.

Instantaneous temperature dependence (ITD) curves were then measured on those leaves expanded under the treatment conditions. A total of eight ITD curves were measured for each species within each treatment. The evening before measurement the seedlings were watered to ensure they were fully hydrated during measurement. The measurement set-up was the same as used in the photosynthetic work in Chapter 3. The CO₂ concentration was 350 ppm, the irradiance level was 800 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ and the vapour pressure deficit was 1.1 kPa at all temperatures except at 32°C. However,

the lowest vapour pressure deficit that could be maintain at 32°C without water vapour condensing in the line was 1.5 kPa. Leaves were equilibrated at 22°C and then the temperature was dropped sequentially to 17°C and 12°C. The temperature was then returned to 22°C until the initial rate was reached. The temperature was then raised sequentially to 27°C and 32°C.

One subreplicate seedling of each species was removed from each cabinet after the ITD curves were completed to reducing^e crowding. This reduced the replication to three subreplicate seedlings per species per cabinet. The seedlings from the different treatments were then subjected to the sequence of constant temperature regimes shown in Table 6.1. It was decided that the acclimation temperatures should start at the highest temperature and then be progressively lowered for several reasons. Firstly, the lowest temperature was the most likely to damage leaves of the tropical species and therefore affect measurements at subsequent temperatures. Secondly, the initial change from 22°C to 30°C was the largest and therefore would give a conservative estimate of how long leaves would take to acclimate. Finally, the sequence is fairly representative of the seasonal changes in temperature experienced in climates of the temperate species.

Table 6.1 The sequence of acclimation temperature regimes used in the different treatments.

Treatment	Temperature regime (day/night°C)						
constant	30/22°C	26/18°C	22/14°C	18/10°C	14/6°C	22/14°C	
fluctuating	22/14°C	30/22°C	26/18°C	22/14°C	18/10°C	14/6°C	22/14°C

The acclimation response of seedlings was determined from measurements of the maximum net photosynthetic rate (P_{max}). The time taken to acclimate to a new temperature was determined when seedlings from each treatment were exposed to the first new growth temperature. That is, when the fluctuating treatment seedlings were subjected to a constant temperature regime of 22°C/14°C and when the constant treatment seedlings were subjected to a 30°C/22°C temperature regime. Previous

studies have found full acclimation has taken up to two weeks (Slatyer & Ferrar 1977; Badger *et al.* 1982; Hill *et al.* 1988). Consequently, P_{\max} was measured in the same leaf after 10 and 14 days of acclimation to the new temperature regime. Leaves were determined as fully acclimated if there was no significant difference ($p < 0.05$) between the consecutive readings.

After measurements were taken at 30°C/22°C, any shoots that were overshadowing the measurement leaves were pruned. The seedlings were then pruned after each measurement period. Removing fifty percent or more of the foliage of trees has been found to increase the net photosynthetic rate of the remaining leaves (Heichel & Turner 1983; Reich *et al.* 1993; Pinkard & Beadle 1998). Partial defoliation has been found to arrest the effects of aging on net photosynthesis (Mooney & Chiariello 1984). The leaves were measured at 22°C/14°C three times over the experiment to determine the effect of aging and pruning on net photosynthesis. The leaves of seedlings of *Castanospermum australe* began to pale and drop off after acclimation to 26°C/18°C, presumably in response to pruning. Consequently, seedlings of *C. australe* were removed from the experiment after the second measurement at 22°C/14°C.

Data analysis

The measurements of net photosynthesis at instantaneous temperatures obtained from each subreplicate seedling were regressed using the equation formulated by Ratkowsky *et al.* (1983), which was also used in Chapter 4 (equation 4.1). The maximum rate of net photosynthesis (P_{\max}), the temperature at which maximum net photosynthesis was shown (T_{opt}) and the span of instantaneous temperature over which at least 80% of P_{\max} was shown (T_{span}) were determined from these regression equations using the same methods as described in Chapter 4. The mean values of these parameters for each species within each cabinet were used for statistical analysis. Comparisons of growth temperature regime within a species were analyzed as a one-way ANOVA. Comparisons of species within a growth temperature regime were analyzed as a random complete block design with cabinet as the blocking variable.

The measurements of P_{\max} after 10 and 14 days of acclimation were analysed individually for each species as a repeated measures one-way ANOVA. For all species,

the maximum net photosynthetic rate of leaves recorded after transfer from a constant temperature regime of 22°C/14°C to 30°C/22°C was not significantly different at 14 days compared with 10 days (Table 6.2). Similarly, leaves grown under the fluctuating temperature regime showed no significant difference in maximum net photosynthesis recorded after 10 days acclimation under a constant 22°C/14°C compared with 14 days (Table 6.2). There was less than 1°C difference in the temperature for maximum net photosynthesis recorded at 10 days compared with 14 days after the growth temperature was changed in both treatments (Table 6.3). Therefore, leaves of all species were fully acclimated after fourteen days under a new growth temperature. Measurements were taken 14 days after acclimation to each of the subsequent growth temperatures.

The three sets of measurements of P_{\max} at 22°C/14°C were analyzed individually for each species as repeated measures one-way ANOVAs (Table 6.4). For all species, no significant difference was found between the initial and middle measurement or between the three measurements of P_{\max} at 22°C/14°C. However, having only two replicate cabinets in the repeated measures ANOVA means the statistical power of the analysis was low. Some species showed an obvious decline in the magnitude of maximum net photosynthesis recorded when acclimated to 22°C/14°C through the course of the experiment. In particular, leaves of *C. australe* showed declines in maximum net photosynthesis of 49% and 65% from the initial measurement compared with the second measurement in leaves grown under the constant and fluctuating temperature regimes respectively. The remaining species showed declines of 20% or less in net photosynthesis between the initial and second measurement at 22°C/14°C. To adjust for this decline in photosynthesis over the duration of the experiment, the measurements of P_{\max} during the middle acclimation to 22°C/14°C, 18°C/10°C and 14°C/6°C were normalised to the initial value at 22°C/14°C.

The mean values of P_{\max} obtained at each acclimation temperature were regressed using equation 4.1. Regressions were determined for each species from each cabinet. From these regression equations the highest rate of maximum net photosynthesis ($P_{AT\max}$), the acclimation temperature at which $P_{AT\max}$ was shown (AT_{opt}) and the span of acclimation temperatures over which at least 80% of $P_{AT\max}$ was shown (AT_{span}) were determined the same way as P_{\max} , T_{opt} and T_{span} respectively. These data were also analysed the same way as the instantaneous temperature dependence curves.

Table 6.2 Maximum net photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of leaves after 10 and 14 days of acclimation to a new growth regime. Acclimations included are of leaves grown under a constant temperature transferred to 30°C/22°C and leaves grown under fluctuating temperature transferred to a constant 22°C/14°C. Values are means of two cabinets with standard errors given in brackets.

Species	10 days	14 days	F	p
<u>fluctuating → 22/14</u>				
<i>E. lucida</i>	4.85 (0.11)	5.18 (0.01)	7.28	0.23
<i>N. cunninghamii</i>	5.99 (0.32)	6.03 (0.40)	0.18	0.74
<i>C. australe</i>	2.54 (0.03)	2.58 (0.18)	0.07	0.84
<i>A. scholaris</i>	7.54 (0.54)	7.42 (0.08)	0.07	0.84
<u>constant → 30/22</u>				
<i>E. lucida</i>	8.90 (0.71)	8.72 (0.80)	5.03	0.27
<i>N. cunninghamii</i>	6.21 (0.92)	5.89 (0.88)	58.57	0.08
<i>C. australe</i>	4.07 (0.03)	4.07 (0.50)	< 0.01	> 0.99
<i>A. scholaris</i>	8.34 (0.28)	8.92 (0.55)	0.48	0.62

Table 6.3 Temperature for maximum net photosynthesis (°C) of leaves after 10 and 14 days of acclimation to a new growth regime. Acclimations included are of leaves grown under a constant temperature transferred to 30°C/22°C and leaves grown under fluctuating temperature transferred to a constant 22°C/14°C. ANOVA was not possible in most cases due to either a lack of variation or multicollinearity. Values are means of two cabinets with standard errors given in brackets.

Species	constant → 30/22		fluctuating → 22/14	
	10 days	14 days	10 days	14 days
<i>E. lucida</i>	19.3 (0.3)	19.0 (0.3)	18.2 (0.2)	18.2 (0.2)
<i>N. cunninghamii</i>	19.3	19.7 (0.3)	18.7 (0.3)	18.7
<i>C. australe</i>	22.2 (0.2)	22.0	22.2 (0.2)	22.2 (0.2)
<i>A. scholaris</i>	25.8 (0.2)	26.0 (0.3)	22.2 (0.2)	22.3

Table 6.4 Comparison of maximum net photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) show by species when grown under a constant regime of 22°C/14°C at the beginning, middle and the end of the experiment. Values are means of two cabinets with standard errors given in brackets. The percentage of the initial net photosynthetic rate (%initial22) shown at the middle and end of the experiment are given. The results of repeated measures ANOVAs comparing the initial and middle (mid22/int22) and all three measurements (overall) are given for each species. Greenhouse-Geisser corrected probabilities (G-G) are given for the overall ANOVAs.

Species	Treatment	initial 22	middle 22	final 22	%initial 22		mid22/int22		overall		G-G
					middle	final	F	p	F	p	
<i>E. lucida</i>	constant	5.58 (0.21)	5.65 (0.10)	5.14 (0.22)	1.01	0.92	0.05	0.86	1.61	0.38	0.43
	fluctuating	9.68 (0.19)	7.79 (0.23)	7.92 (0.18)	0.80	0.82	19.4	0.14	20.2	0.06	0.14
<i>N. cunninghamii</i>	constant	7.79 (0.68)	6.52 (0.02)	6.09 (0.43)	0.84	0.78	3.85	0.30	7.32	0.12	0.23
	fluctuating	8.17 (0.07)	6.57 (2.07)	5.38 (0.02)	0.80	0.66	0.64	0.57	1.41	0.41	0.45
<i>C. australe</i>	constant	4.23 (0.56)	2.08 (0.37)		0.49		12.1	0.18			
	fluctuating	4.42 (0.78)	2.89 (0.04)		0.65		4.28	0.29			
<i>A. scholaris</i>	constant	8.05 (1.02)	8.99 (0.79)	9.87 (0.72)	1.12	1.23	0.27	0.69	0.88	0.53	0.52
	fluctuating	7.12 (0.28)	6.99 (0.31)	8.30 (0.93)	0.98	1.17	0.05	0.86	1.35	0.43	0.45

RESULTS

Response of net photosynthesis to instantaneous temperatures in leaves developed under constant or fluctuating growth temperature

Eucryphia lucida and *Castanospermum australe* were the only species that showed distinct differences in the response of net photosynthesis to instantaneous temperature between leaves grown under a constant compared with a fluctuating temperature regime (Figure 6.1). Leaves of *E. lucida* showed a significantly higher P_{\max} when grown under the fluctuating temperature regime compared with the constant temperature regime (Table 6.5). In contrast, *C. australe* showed a significantly lower P_{\max} in leaves grown under the fluctuating temperature regime compared with leaves grown under the constant temperature regime.

The contrasting growth temperature regimes had no significant effect on the instantaneous temperatures at which maximum net photosynthesis occurred (Table 6.6). The cool-temperate rainforest type showed maximum net photosynthesis at 18-19°C whereas the tropical rainforest type showed maximum net photosynthesis at 22°C. However, this difference was not significant under either growth temperature regime (Table 6.7).

For all the species, the span of instantaneous temperatures at which at least 80% of maximum net photosynthesis was shown (T_{span}) did not change significantly between the constant and fluctuating growth temperature regimes (Table 6.8). The important difference in T_{span} was between the rainforest types. The cool-temperate rainforest type showed a temperature span of 26°C which was significantly higher than the temperature span of 13-15°C shown by the tropical rainforest type under both growth temperature regimes (Table 6.9).

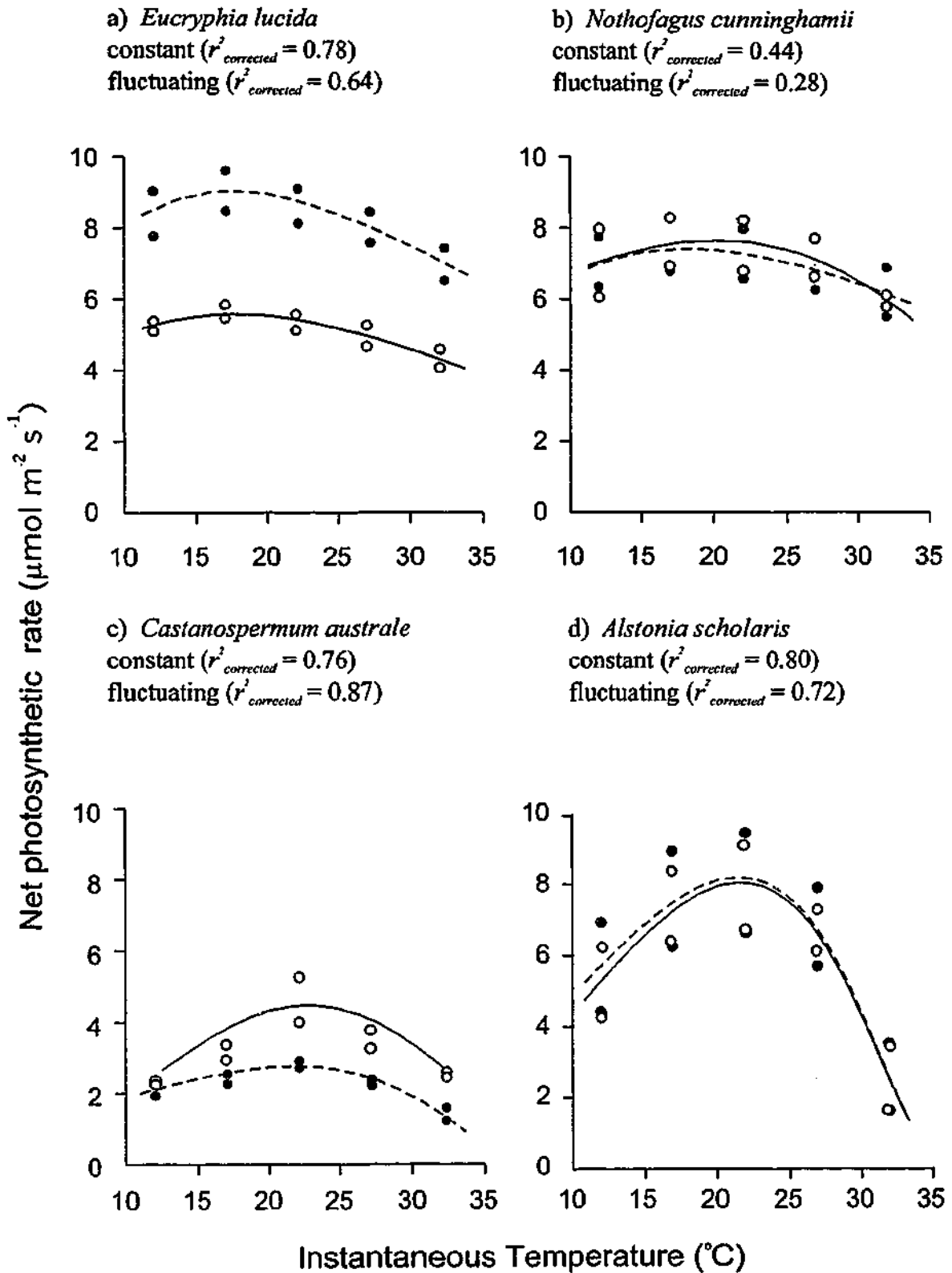


Figure 6.1 Average response of net photosynthesis to instantaneous temperature in leaves growing under a constant (—○—) and a fluctuating (---●---) temperature regime. Values are means for the two runs of the experiment.

Table 6.5 Maximum net photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of leaves when growing under a constant or fluctuating temperature regime. Values are means of two cabinets with standard errors given in brackets.

Species	Growth temperature		<i>F</i>	<i>p</i>
	constant	fluctuating		
<i>E. lucida</i>	5.58 (0.21)	9.06 (0.54)	36.7	0.03
<i>N. cunninghamii</i>	7.78 (0.65)	7.50 (0.72)	0.08	0.80
<i>C. australe</i>	3.80 (0.12)	2.66 (0.09)	54.7	0.02
<i>A. scholaris</i>	8.09 (0.99)	8.22 (1.36)	<0.01	0.95

Table 6.6 Temperature for maximum net photosynthesis ($^{\circ}\text{C}$) of leaves when growing under a constant or fluctuating temperature regime. Values are means of two cabinets with standard errors given in brackets.

Species	Growth temperature		<i>F</i>	<i>p</i>
	constant	fluctuating		
<i>E. lucida</i>	17.9 (0.5)	17.5 (0.5)	0.45	0.57
<i>N. cunninghamii</i>	19.5 (0.5)	18.4 (0.2)	5.38	0.15
<i>C. australe</i>	22.9 (0.0)	22.1 (0.4)	5.90	0.14
<i>A. scholaris</i>	21.6 (0.4)	22.0 (0.7)	0.25	0.67

Table 6.7 Temperatures for maximum net photosynthesis ($^{\circ}\text{C}$) for rainforest types of leaves growing under a constant or fluctuating temperature regime. Values are means of two cabinets with standard errors given in brackets.

Growth temperature		
Rainforest type	constant	fluctuating
cool-temperate	18.7 (0.5)	17.9 (0.3)
tropical	22.1 (0.6)	22.3 (0.2)
rainforest type	<i>F</i>	10.8
	<i>p</i>	0.19
cabinet	<i>F</i>	77.4
	<i>p</i>	0.07
	<i>F</i>	< 0.01
	<i>p</i>	0.04
	<i>F</i>	0.87
	<i>p</i>	0.95

Table 6.8 Span of instantaneous temperatures over which 80% of maximum net photosynthesis was shown ($^{\circ}\text{C}$) in leaves when growing under a constant or fluctuating temperature regime. Values are means of two cabinets with standard errors given in brackets.

Growth temperature				
Species	constant	fluctuating	<i>F</i>	<i>p</i>
<i>E. lucida</i>	25.1 (0.1)	24.7 (0.1)	8.00	0.11
<i>N. cunninghamii</i>	24.2 (0.1)	26.4 (1.6)	1.88	0.30
<i>C. australe</i>	13.1 (1.7)	16.8 (2.2)	1.93	0.30
<i>A. scholaris</i>	12.4 (1.0)	13.0 (0.7)	0.27	0.65

Table 6.9 Span of instantaneous temperatures over which 80% of maximum net photosynthesis was shown ($^{\circ}\text{C}$) in leaves of the rainforest types when growing under a constant or fluctuating temperature regime. Values are means of two cabinets with standard errors given in brackets.

		Growth temperature	
Rainforest type		constant	fluctuating
cool-temperate		24.7 (0.0)	25.6 (0.8)
tropical		12.7 (0.4)	14.9 (1.4)
rainforest type	<i>F</i>	1166	263
	<i>p</i>	0.02	0.04
cabinet	<i>F</i>	1.00	10.8
	<i>p</i>	0.50	0.19

Response of maximum net photosynthesis to acclimation temperature in leaves developed under constant or fluctuating growth temperature

All species showed a difference in the response of maximum net photosynthesis to acclimation temperature in leaves grown under a constant temperature regime compared with a fluctuating temperature regime (Figure 6.2). Differences were shown in the highest rate of maximum net photosynthesis (P_{ATmax}), the acclimation temperature at which P_{ATmax} was shown and the span of acclimation temperatures over which at least 80% of P_{ATmax} was shown.

The cool-temperate species showed significantly greater P_{ATmax} in leaves grown under the fluctuating temperature regime compared with the constant temperature regime (Table 6.10). In contrast, the tropical species showed a trend of a decreased P_{ATmax} in leaves grown under the fluctuating temperature regime compared with the constant temperature regime.

Nothofagus cunninghamii was the only species to show P_{ATmax} at a higher acclimation temperature in leaves grown under a fluctuating temperature regime compared with a constant temperature regime (Table 6.11). Consequently, there was no significant

change with growth temperature regime in the relationship of the acclimation temperature at which P_{ATmax} was shown between the rainforest types (Table 6.12). The cool-temperate rainforest type showed P_{ATmax} at an acclimation temperature of 23-24°C whereas the tropical rainforest type showed P_{ATmax} at 26°C.

All species, except *Nothofagus cunninghamii*, showed at least 80% of their highest rate of maximum net photosynthesis over a greater span of acclimation temperatures in leaves grown under a fluctuating temperature regime compared with leaves grown under a constant temperature regime (Table 6.13). However, this difference in AT_{span} was only statistically significant for *Alstonia scholaris*. In both leaves grown under the constant and the fluctuating temperature regime, the cool-temperate rainforest type showed close to its highest rate of maximum net photosynthesis over 16-18°C of acclimation temperature whereas the tropical rainforest type only showed a span of 8-12°C (Table 6.14). However, this difference was only significant between leaves grown under the constant temperature regime.

The species differed in their responses of the instantaneous temperature for maximum net photosynthesis (T_{opt}) to acclimation temperature (Figure 6.3). The two cool-temperate species showed minor changes in T_{opt} of 0.1°C/°C of acclimation temperature. The tropical species *C. australe* also showed minor changes, however these may be a result of measurement at only three acclimation temperatures. In contrast, *A. scholaris* showed a large increase in T_{opt} of 0.3-0.4°C/°C between the acclimation temperature of 14°C and 30°C. There was little difference within species in the changes of the temperature for maximum net photosynthesis between leaves grown under a constant temperature regime compared with a fluctuating temperature regime.

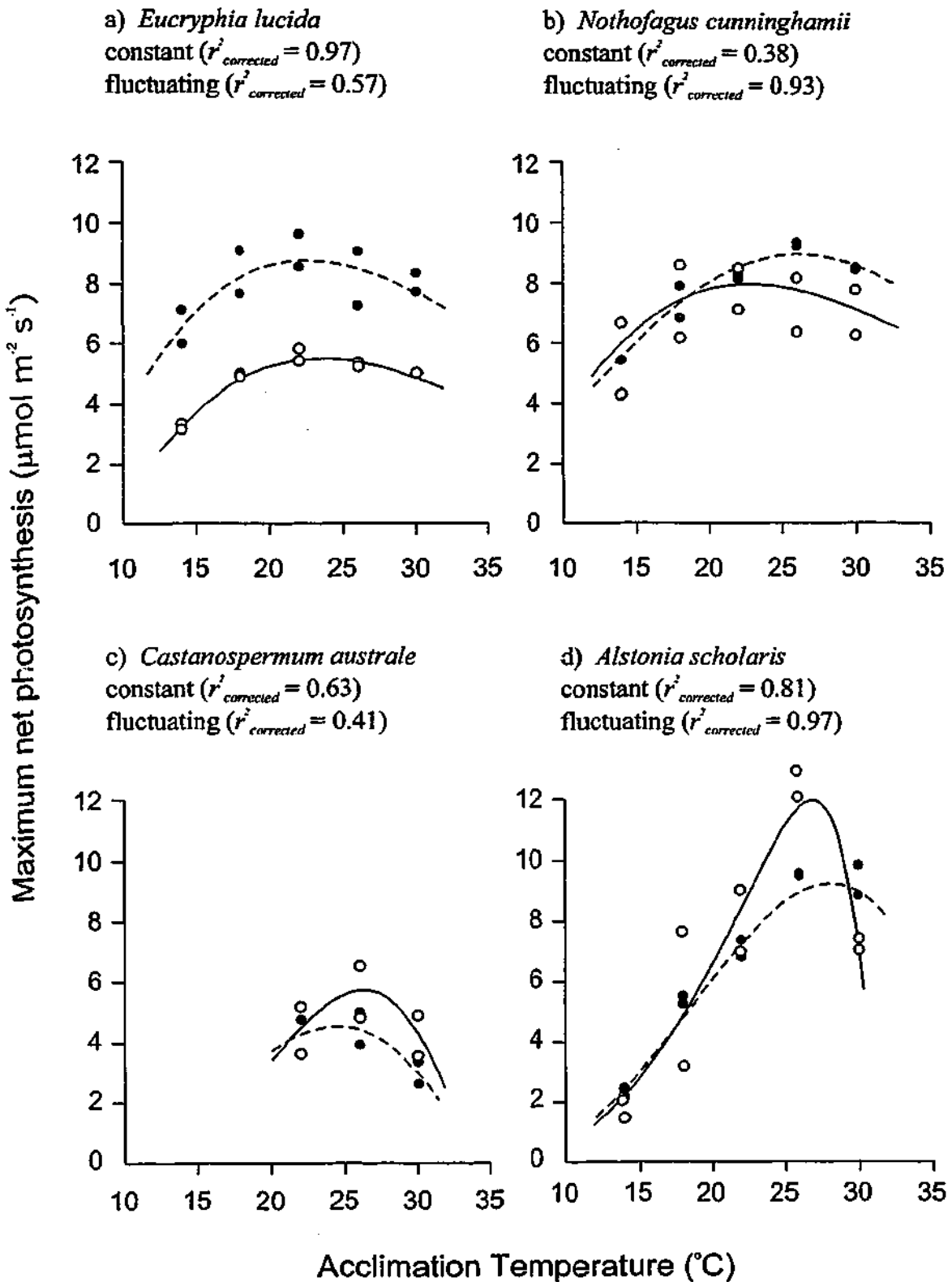


Figure 6.2 Average response of maximum net photosynthesis to acclimation temperature for leaves grown under a constant (—○—) and a fluctuating (---●---) temperature regime. Values are means for the two runs of the experiment.

Table 6.10 Highest rate of maximum net photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) shown across the range of acclimation temperatures ($P_{AT_{\text{max}}}$) in leaves grown under constant or fluctuating temperature regimes. Values are means of two cabinets with standard errors given in brackets.

Species	growth temperature		<i>F</i>	<i>p</i>
	constant	fluctuating		
<i>E. lucida</i>	5.44 (0.18)	8.86 (0.75)	19.9	0.05
<i>N. cunninghamii</i>	7.45 (0.31)	8.92 (0.30)	25.0	0.04
<i>C. australe</i>	5.70 (0.85)	4.48 (0.53)	1.44	0.35
<i>A. scholaris</i>	10.62 (1.70)	9.18 (0.43)	0.68	0.50

Table 6.11 Acclimation temperature ($^{\circ}\text{C}$) for maximum net photosynthesis ($P_{AT_{\text{max}}}$) in leaves grown under constant or fluctuating temperature regimes. Values are means of two cabinets with standard errors given in brackets.

Species	growth temperature		<i>F</i>	<i>p</i>
	constant	fluctuating		
<i>E. lucida</i>	23.4 (0.1)	22.5 (0.4)	4.45	0.17
<i>N. cunninghamii</i>	22.8 (0.8)	25.8 (0.4)	22.8	0.04
<i>C. australe</i>	26.1 (0.1)	25.6 (0.1)	12.5	0.07
<i>A. scholaris</i>	26.4 (0.5)	27.1 (0.4)	1.51	0.34

Table 6.12 Acclimation temperature ($^{\circ}\text{C}$) for maximum net photosynthesis (P_{ATmax}) in leaves of rainforest types grown under contrasting temperature regimes. Values are means of two cabinets with standard errors given in brackets.

Growth temperature		
Rainforest type	constant	fluctuating
cool-temperate	23.0 (0.3)	24.2 (0.4)
tropical	26.3 (0.3)	26.3 (0.2)
rainforest type	<i>F</i>	43.6
	<i>p</i>	0.10
cabinet	<i>F</i>	< 0.01
	<i>p</i>	> 0.99

Table 6.13 Span of acclimation temperatures ($^{\circ}\text{C}$) over which at least 80% of P_{ATmax} was shown (AT_{span}) by leaves grown under constant or fluctuating temperature regimes. Values are means of two cabinets with standard errors given in brackets.

Growth temperature				
Species	constant	fluctuating	<i>F</i>	<i>p</i>
<i>E. lucida</i>	15.7 (0.8)	17.8 (0.7)	4.13	0.15
<i>N. cunninghamii</i>	16.7 (1.5)	17.1 (2.9)	0.01	0.92
<i>C. australe</i>	7.6 (0.5)	13.3 (1.8)	9.09	0.09
<i>A. scholaris</i>	7.3 (0.2)	9.9 (0.5)	26.2	0.04

Table 6.14 Comparison of the span of acclimation temperatures ($^{\circ}\text{C}$) over which at least 80% of P_{ATmax} was shown by rainforest types within the temperature regimes. Values are means of two cabinets with standard errors given in brackets.

		Growth temperature	
Rainforest type		constant	fluctuating
cool-temperate		16.4 (0.9)	17.5 (1.1)
tropical		7.5 (0.4)	11.6 (1.2)
rainforest type	<i>F</i>	265	7.19
	<i>p</i>	0.04	0.23
cabinet	<i>F</i>	5.17	< 0.01
	<i>p</i>	0.26	0.97

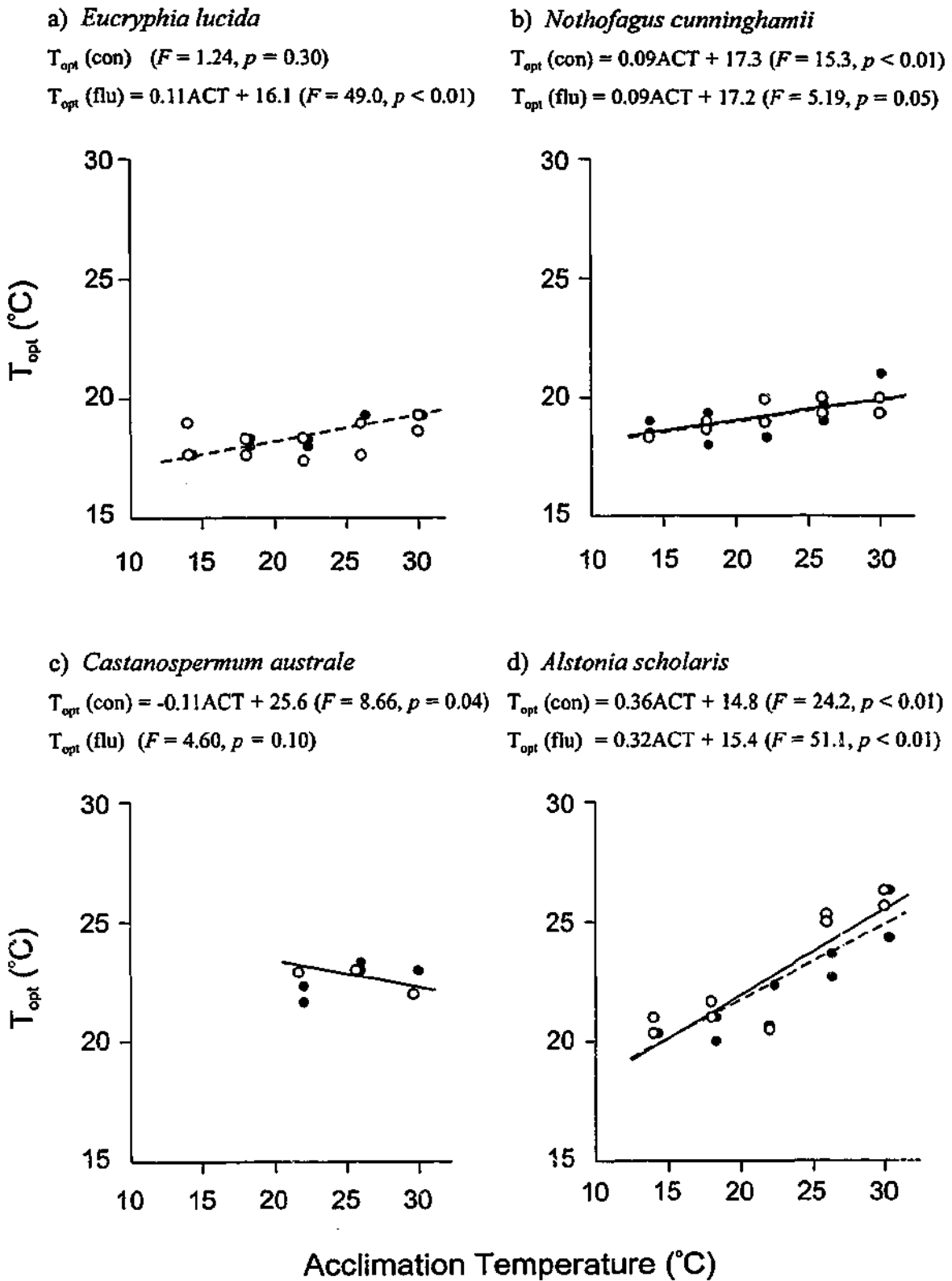


Figure 6.3 The relationship between the temperature for maximum net photosynthesis (T_{opt}) and acclimation temperature for leaves grown under a constant (—○—) and a fluctuating (---●---) temperature regime.

DISCUSSION

Response of net photosynthesis to instantaneous temperatures in leaves developed under constant or fluctuating growth temperature

There were few differences in the photosynthetic response to instantaneous temperature between leaves developed and growing under a constant or a fluctuating temperature regime (Figure 6.1). Two species showed a difference in the overall photosynthetic rate measured at instantaneous temperatures between leaves grown under a fluctuating temperature regime compared with those grown under a constant temperature regime. In contrast, there were distinct differences in photosynthetic responses to temperature between the rainforest types under both temperature regimes.

The cool-temperate species *Eucryphia lucida* showed a 62% higher maximum net photosynthetic rate in leaves grown under the fluctuating temperature regime compared with the constant temperature regime (Table 6.5). This increased photosynthetic rate of leaves under the fluctuating temperature regime compared with the constant temperature regime suggests development under more optimal temperatures. The fluctuating temperature regime exposed developing leaves to day temperatures ranging from 17°C to 27°C. Therefore, the fluctuating temperature regime included more temperatures closer to the growth temperature for maximum net photosynthesis of 19°C shown for *E. lucida* in Chapter 4 than the constant regime of 22°C. However, the increase in maximum net photosynthesis between the constant growth temperatures of 22°C and 19°C, shown in Chapter 4, was considerably smaller (9%) than that between the constant and fluctuating temperature regimes. Consequently, leaves developed under the fluctuating temperature regime showed a maximum net photosynthetic rate of $9.1 \pm 0.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, which is considerably higher than the $5.4 \pm 0.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ shown at the optimal growth temperature. Therefore, the mechanism for the increased net photosynthesis in leaves of *E. lucida* grown under a fluctuating temperature regime compared with a constant temperature regime remains uncertain. However, the response may be an adaptation to the greater day-to-day variation in temperature of temperate climates compared with tropical climates of Australia. Therefore, growing species from variable climates, such as *E. lucida*, under constant

temperature regimes is potentially underestimating their maximum net photosynthetic rate.

The tropical species *Castanospermum australe* showed the opposite response to *E. lucida*, with an overall decrease in net photosynthesis in leaves developed under the fluctuating temperature regime compared with the constant temperature regime. The stress of temperatures lower than 22°C in the fluctuating temperature regime may have outweighed the benefit of exposure to temperatures closer to the optimum growth temperature for maximum net photosynthesis for *C. australe* of 26°C. In addition, the reduction in net photosynthesis of leaves developed under a fluctuating temperature regime may be an effect of having to constantly acclimate to new daily temperatures. This response is consistent with the hypothesis that tropical species have a reduced acclimation potential compared with temperate species.

Studies that have measured photosynthetic responses to temperature in the same species growing in the field and in constant temperature regimes representative of field temperatures do not show consistent trends. Studies of Californian shrubs have shown show similar rates of net photosynthesis in the field and in controlled environments (Björkman *et al.* 1975; Mooney *et al.* 1976) although one species showed higher rates in the field (Pearcy & Harrison 1974; Pearcy 1977). In contrast, the alpine species *Eucalyptus pauciflora* showed lower rates of photosynthesis in the field compared with rates in constant temperature regimes representative of field temperatures (Slatyer & Ferrar 1977; Slatyer & Morrow 1977). Of course, these differences in photosynthetic rates between the field and controlled environments may reflect differences in water stress, nutrient availability, irradiance levels and leaf age rather than temperature conditions. However, studies where these factors were not limiting have shown photosynthetic rates of temperate species in the field are higher or similar in the field compared with controlled environments (Battaglia *et al.* 1996; Gunderson *et al.* 2000). These findings support the possibility of other temperate species that show higher photosynthetic rates when grown under fluctuating temperatures compared with constant temperatures.

There was no significant difference in the instantaneous temperature for maximum net photosynthesis (T_{opt}) between leaves developed under a constant or a fluctuating

temperature regime (Table 6.6). Therefore, the T_{opt} of leaves did not respond to the amount of fluctuation in temperature but instead to the mean daily temperature. This is consistent with the finding in *Eucalyptus pauciflora* that the temperature for maximum net photosynthesis was strongly correlated with the mean maximum temperature of the ten days prior to measurement (Slatyer & Morrow 1977). Similarly, leaves of *Quercus rubra* showed the same T_{opt} when acclimated to three constant temperature regimes with the same mean daily temperature but different amplitudes of diurnal change (Chabot & Lewis 1976). Furthermore, when leaves were acclimated to different constant temperature regimes in the present study, they only showed minor shifts in the instantaneous temperature for maximum net photosynthesis. Therefore, it is unlikely that shifts in the temperature for maximum net photosynthesis would occur under the daily temperature changes of the fluctuating temperature regime.

None of the species showed a significant difference in the span of instantaneous temperatures over which maximum net photosynthesis was maintained (T_{span}) between leaves developed under the contrasting or fluctuating temperature regimes (Table 6.8). Higher values of T_{span} are expected in leaves developed under fluctuating temperature conditions compared with constant temperature conditions, due to exposure to a greater range of temperatures. However, the cool-temperate species *E. lucida* and *Nothofagus cunninghamii* showed close to maximum net photosynthesis over the large spans of 24-26°C. Therefore, an adjustment of T_{span} was not necessary to tolerate the wider range of temperatures in the fluctuating temperature regime compared with the constant temperature regime. The tropical species do not experience large temperature fluctuations in the field, so they were not expected to adjust to the fluctuating temperature regime. The greater values of T_{span} shown by the cool-temperate rainforest type compared with the tropical rainforest type is consistent with values shown under a constant temperature regime of 22°C/14°C (Table 4.12). The greater span of the cool-temperate rainforest type is likely to be an adaptation to the greater day-to-day and seasonal variation in temperature of the temperate climate compared with the tropical climate of Australia.

Response of maximum net photosynthesis to acclimation temperature in leaves developed under constant or fluctuating growth temperature

The response of maximum net photosynthesis to acclimation temperature differed between the cool-temperate and tropical species (Figure 6.2). Firstly, the acclimation response of the cool-temperate species was improved in leaves grown under the fluctuating temperature regime compared with leaves grown under the constant temperature regime, whereas the acclimation response of the tropical species was reduced. Secondly, the cool-temperate species showed a greater acclimation potential than the tropical species.

The cool-temperate species showed a significant increase in the highest maximum net photosynthetic rate shown across the range of acclimation temperatures in leaves developed under a fluctuating temperature regime compared with a constant temperature regime (Figure 6.2). Therefore, exposure to a wide range of temperatures during the development of leaves in cool-temperate species, such as in the field, improves their net photosynthesis compared with a constant temperature regime. The cool-temperate species differed in the range of acclimation temperatures over which maximum net photosynthesis was increased in leaves developed under the fluctuating temperature regime compared with the constant temperature regime. *Eucryphia lucida* showed an increased rate of maximum net photosynthesis over the whole range of acclimation temperature in leaves developed under the fluctuating temperature regime, whereas *N. cunninghamii* only showed increased maximum net photosynthesis over the warm acclimation temperatures.

In previous studies, the highest rate of maximum net photosynthesis for *E. lucida* and *N. cunninghamii* was shown at an acclimation temperature of 21-22°C in leaves developed under ambient conditions or a constant temperature of 20°C (Hill *et al.* 1988; Read & Busby 1990). In the present study, these species showed their highest rate of maximum net photosynthesis (P_{ATmax}) at a similar acclimation temperature of 23°C when developed under a constant day/night temperature regime of 22°C/14°C. In contrast, when leaves of *N. cunninghamii* were developed under the fluctuating temperature regime P_{ATmax} was shown at the much higher acclimation temperature of 26°C. Interestingly, leaves of *N. cunninghamii* show P_{ATmax} at 21-22°C when developed

under ambient conditions, with mean monthly temperatures ranging from 15°C to 22°C (Hill *et al.* 1988), and at 26°C when grown under temperatures fluctuating between 17°C and 27°C in this study. Therefore, leaves of *N. cunninghamii* appear to shift their acclimation response towards the highest temperature during their development. This would be advantageous for this species as it produces a single flush of leaves in early spring when maximum temperatures fluctuate around 20°C, which are then exposed to summer temperatures in the middle to high twenties.

Development of leaves of the cool-temperate species under a fluctuating temperature regime did not increase the span of acclimation temperatures over which maximum net photosynthesis was shown (AT_{span}) compared with leaves developed under the constant temperature regime (Table 6.13). However, the cool-temperate species already showed values of AT_{span} of 16–18°C in leaves developed under a constant temperature regime. Therefore, the wide tolerance of maximum net photosynthesis to acclimation temperature in the cool-temperate species means further increases in the span of the response in leaves developed under the fluctuating temperature regime would be of little advantage.

The tropical species showed a non-significant decrease in the highest rate of maximum net photosynthesis shown across the range of acclimation temperatures in leaves developed under the fluctuating temperature regime compared with the constant temperature regime (Figure 6.2). The tropical species showed no difference in the acclimation temperature at which the highest rate of maximum net photosynthesis was shown between leaves developed under the two temperature regimes. Both species showed an increase in the span of acclimation temperatures at which the highest maximum net photosynthetic rate was shown in leaves developed under a fluctuating temperature regime compared with a constant temperature regime, although this was only significant for *Alstonia scholaris*. Overall, the tropical species showed a trend of a decreased and broader response of maximum net photosynthesis to acclimation temperature in leaves grown under a fluctuating temperature regime compared with a constant temperature regime. The greater acclimation potential of leaves of tropical species grown under a constant temperature regime compared with a fluctuating temperature regime reflects the small day-to-day and seasonal variation in temperature of their climates.

Acclimation temperature spans for maximum net photosynthesis (AT_{span}) of the rainforest types were of a similar magnitude to previous studies on Australasian rainforest species (see Table 6.15). However, the temperature spans of *E. lucida* and *N. cunninghamii* in this study of 16-18°C and 17°C respectively were higher than the temperature spans of 10-11°C and 14°C respectively reported previously (Hill *et al.* 1988; Read & Busby 1990). The differences in the temperature spans of these two species among studies may be a result of the greater number of acclimation temperatures used in the previous studies allowing a finer resolution of the response.

Table 6.15 Comparison of the span of acclimation temperatures (°C) over which at least 80% of maximum net photosynthesis was shown by rainforest types in various studies (excluding shade-tolerant species).

rainforest type		
temperate	tropical	source
9-14		Hill <i>et al.</i> (1988)
10-17		Read & Busby (1990)
14-17	8-11	Read (1990)
16-18	7-13	present study

The cool-temperate rainforest type showed greater values of AT_{span} than the tropical rainforest under both temperature regimes. A comparison of *Nothofagus* species also found that the temperate species showed maximum photosynthesis over a greater span of acclimation temperatures than the tropical species (Read 1990). Similarly, the cool-temperate rainforest type showed close to its highest maximum net photosynthetic rate over a greater span of growth temperatures than the tropical group in Chapter 4. The greater tolerance of maximum net photosynthesis to growth temperature in the cool-temperate species compared with the tropical species is likely to be an adaptation the greater temperature fluctuation in the field during development. In contrast, the greater tolerance of maximum net photosynthesis to acclimation temperatures in the cool-temperate species compared with the tropical species is likely to be an adaptation the greater seasonal fluctuations in temperature of the temperate climate.

The tropical species *A. scholaris* showed the greatest shifts in the instantaneous temperature for maximum net photosynthesis (T_{opt}) with acclimation temperature (Figure 6.3). However, these greater shifts in T_{opt} were associated with greater declines in maximum net photosynthesis at low acclimation temperatures than the temperate species. Therefore, these greater shifts are not a reflection of a greater acclimation potential. The same trend was found for shifts in the temperature for maximum net photosynthesis with growth temperature in Chapter 4. The greater span of instantaneous temperatures at which maximum net photosynthesis is shown by cool-temperate species than tropical species diminishes the importance of shifting T_{opt} towards the new growth temperature.

A survey of the literature shows the magnitude of the shift in the temperature for maximum net photosynthesis with an increase in acclimation temperature ranges from 0 to 1°C/°C in tree species (Table 6.16). This survey shows that temperate species tend to show greater shifts in T_{opt} than tropical species. However, the responses of temperate species range from no shifts to large shifts in T_{opt} . However, these smaller shifts in the temperature for maximum net photosynthesis are often related to a broader response of net photosynthesis to instantaneous temperatures (van der Heyden & Lewis 1990; Battaglia *et al.* 1996).

It is often argued that acclimation is more likely to occur in evergreen species that occupy a wide range of thermal environments or are exposed to large seasonal variations in temperature (Berry & Björkman 1980). In comparison, species from environments in which growth is restricted to one season or seasonal temperature variations are small showed a limited capacity for acclimation (Kemp & Williams 1980; Goldstein *et al.* 1996). Therefore, the ability of the cool-temperate rainforest type to acclimate successfully to a greater span of temperatures than the tropical rainforest type is likely to be a reflection of differences in their climates. That is, the cool-temperate species come from a climate that has a greater seasonal variation in temperature than the tropical rainforest type.

Table 6.16 Shifts in the temperature for maximum net photosynthesis with increasing acclimation temperature ($^{\circ}\text{C } ^{\circ}\text{C}^{-1}$) recorded in previous studies of trees.

	α ($^{\circ}\text{C } ^{\circ}\text{C}^{-1}$)	source
<u>Temperate</u>		
<i>Acer saccharum</i> *	0.93	Gunderson <i>et al.</i> (2000)
<i>Atherosperma moschatum</i>	0	Read & Busby (1990)
<i>Athrotaxis selaginoides</i>	0	Read & Busby (1990)
<i>Ceratopetalum apetalum</i>	0.38	Hill <i>et al.</i> (1988)
<i>Doryphora sassafras</i>	0.38	Hill <i>et al.</i> (1988)
<i>Eucalyptus globulus</i>	0.12	Battaglia <i>et al.</i> (1996)
<i>Eucalyptus incrassata</i>	0.58	Ferrar <i>et al.</i> (1989)
<i>Eucalyptus pauciflora</i>	0.52-0.58	Ferrar <i>et al.</i> (1989)
<i>Eucryphia lucida</i>	0	Read & Busby (1990)
<i>Eucryphia moorei</i>	0.38	Hill <i>et al.</i> (1988)
<i>Lagarostrobos franklinii</i>	0	Read & Busby (1990)
<i>Larix decidua</i> *	0.67	Tranquillini <i>et al.</i> (1986)
<i>Nothofagus cunninghamii</i>	0	Read (1990)
<i>Nothofagus gunnii</i> *	0	Read (1990)
<i>Nothofagus moorei</i>	0.10-0.19	Read (1990)
<i>Phyllocladus aspleniifolius</i>	0	Read & Busby (1990)
<i>Pinus taeda</i>	1.0	Teskey & Will (1999)
mean = 0.30		
<u>Tropical</u>		
<i>Acacia harpophylla</i>	0	Downes & Connor (1973)
<i>Eucalyptus miniata</i>	0	Ferrar <i>et al.</i> (1989)
<i>Nothofagus carrii</i>	0	Read (1990)
<i>Nothofagus cf. carrii</i>	0.19	Read (1990)
<i>Nothofagus cf. crenata</i>	0.19	Read (1990)
<i>Nothofagus grandis</i>	0.19	Read (1990)
<i>Nothofagus perryi</i>	0	Read (1990)
<i>Nothofagus pseudoresinosa</i>	0.10	Read (1990)
<i>Nothofagus pullei</i>	0.10	Read (1990)
mean = 0.09		

* deciduous species

The acclimation potentials of the two rainforest types reflect the combination of differences in their phenology and temperature conditions. Temperate rainforest species of Australia tend to only produce leaves during late winter and spring (eg. Howard 1973; Ashton & Frankenberg 1976). By comparison, tropical species produce leaves over a longer period during the wet season from spring to autumn (Frith & Frith 1985; Lowman 1992). The climates of rainforest species of Australia differ in the greater seasonal and day-to-day variation of temperature experienced by temperate species compared with tropical species. Therefore, leaves of temperate species are developed under and subsequently exposed to greater temperature variation than those of tropical species. Therefore, the strategy of cool-temperate species would be to produce leaves in spring that can acclimate to the full annual variation in temperature. In contrast, tropical species would not need to rely on acclimation as they are exposed to smaller seasonal variations in temperature and produce new leaves throughout most of the year.

In conclusion to the specific hypotheses:

1. Temperate species showed an ability to acclimate to a wider range of growth temperatures than tropical species
2. Leaves of the temperate species *Eucryphia lucida* developed under fluctuating temperature conditions showed a greater potential to acclimate to instantaneous temperatures than leaves developed under constant temperature conditions
3. Leaves of temperate species developed under fluctuating temperature conditions showed a greater potential to acclimate to new growth temperatures than leaves grown under constant temperature conditions.

Part C

Vapour Pressure Deficit

CHAPTER 7

Response of Net Photosynthesis to Water Vapour Pressure Deficit

Rainforests are mainly found along the eastern edge of Australia in areas where the annual precipitation exceeds 1500 mm, although precipitation can be as low as 800 mm (Francis 1981; Webb & Tracey 1981a). Differences in the annual precipitation among the rainforest types of Australia are often quoted (eg. Webb & Tracey 1981a; Williams *et al.* 1984). In the case of the species in this study, the warm-temperate species have the lowest values of annual precipitation (1300 mm), and the highest values of annual precipitation were found among the cool-temperate and tropical species (1700 - 2100 mm, Table 7.1). The more important difference is the change in the seasonality of precipitation with latitude. In the tropics of the north, the majority of the annual precipitation falls during the summer months. In contrast, the temperate climate in south receives the majority of its rain during the cooler months of winter. At intermediate latitudes precipitation is uniform throughout the year (Bureau of Meteorology 1989). The difference in precipitation patterns among the rainforest species is shown in Figure 7.1.

The change in seasonality of precipitation with latitude means that temperate species receive considerably less precipitation than tropical species during summer when temperatures are more optimal for growth. Consequently, the water balance (precipitation minus evaporation) is negative for temperate species and positive for tropical species during summer. The lack of difference in soil moisture compared with water balance during summer between temperate and tropical species shown in Chapter 2 suggests that the important difference in water stress is the greater evaporative demand of the temperate summer. Therefore, tropical and temperate rainforest trees of Australia are likely to have different strategies to tolerate atmospheric water deficit.

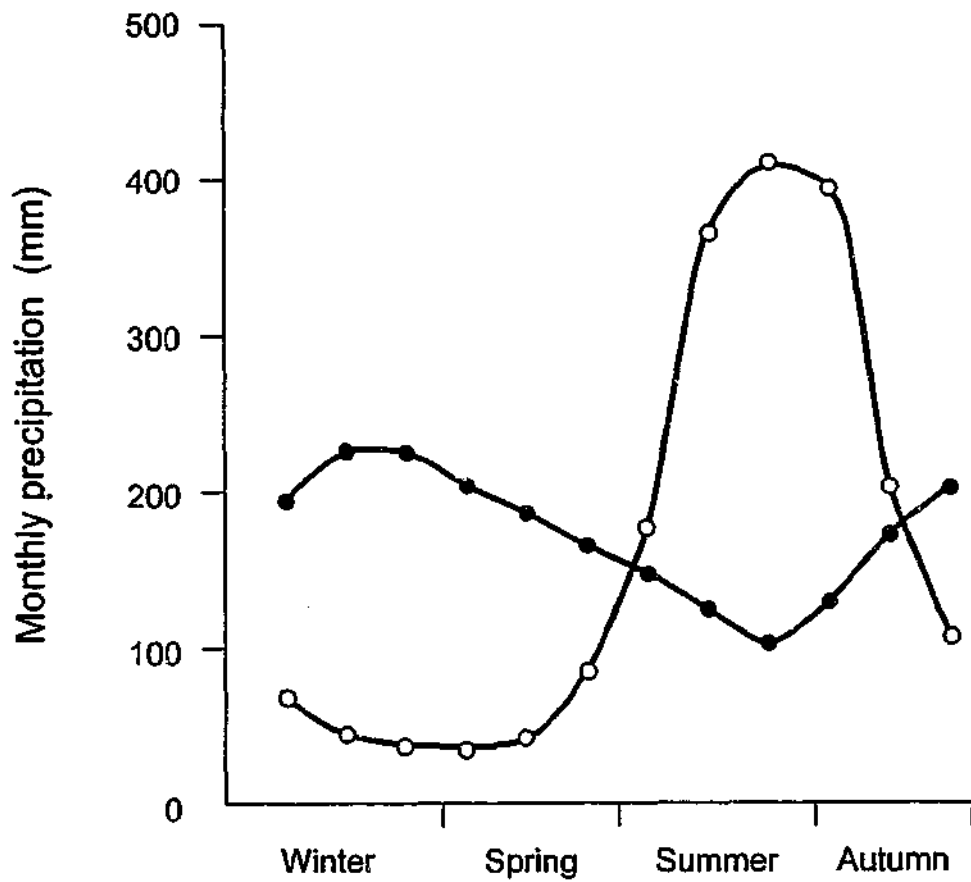


Figure 7.1 Variation in the seasonality of monthly precipitation for rainforest species of eastern Australia. Precipitation patterns shown are the winter-dominant precipitation of *Eucryphia lucida* (—●—) and the summer-dominant precipitation of *Alstonia scholaris* (—○—). Points are mean monthly precipitation from the climate profile of the species.

Table 7.1 Precipitation (mm) and Maximum VPD (kPa) from species profiles derived from ANUCLIM 5.0. Values of parameters are means of the values from individual site locations ($n > 60$).

species	precipitation			maximum VPD	
	annual	summer	winter	summer	winter
<i>E. lucida</i>	2079 (51)	374 (10)	645 (16)	0.70 (0.01)	0.23 (0.01)
<i>N. cunninghamii</i>	1674 (27)	298 (5)	527 (9)	0.86 (0.02)	0.23 (0.00)
<i>A. smithii</i>	1320 (24)	479 (12)	224 (4)	1.32 (0.02)	0.84 (0.01)
<i>T. laurina</i>	1314 (34)	445 (15)	238 (6)	1.24 (0.03)	0.82 (0.02)
<i>S. woollsii</i>	1387 (27)	529 (9)	221 (5)	1.31 (0.02)	0.86 (0.01)
<i>H. trifoliolata</i>	1750 (64)	679 (25)	253 (10)	1.29 (0.03)	0.99 (0.02)
<i>C. australe</i>	1655 (59)	737 (25)	173 (9)	1.42 (0.02)	1.18 (0.02)
<i>A. scholaris</i>	1978 (94)	956 (35)	150 (12)	1.44 (0.05)	1.24 (0.03)

Lowland rainforests in the tropics are among the wettest terrestrial habitats on earth (Walter 1971). However, plants in these rainforests can be exposed to water deficits on a regular diurnal and seasonal basis as well as severe water deficits during years of low precipitation (Robichaux *et al.* 1984; Park & Furukawa 1999). Australian tropical rainforests experience pronounced dry seasons during the winter and spring, which can last up to six months in some areas (Yates & Hutley 1995). However, soil water availability in wet, lowland tropical forests of northern Australia is predicted to be adequate during the dry season (Hopkins & Graham 1989). The tropical species in this study are also exposed to a higher VPD than the temperate species throughout the year (Table 7.1). Therefore, strategies to tolerate water stress should be just as important to tropical rainforest species of Australia as they are to the survival of temperate species.

Tree species that inhabit areas where drought periods do not exceed 3 to 4 months, such as eastern Australia, are likely to be avoiders of water stress (Ludlow 1989). Short-term water stress can be avoided by restricting water loss through stomatal closure (Cowan 1977; Ludlow 1980; Schulze 1986). A stomatal response to increasing vapour pressure deficit would be effective in reducing water loss under dry environments but it would also restrict photosynthesis (Hinckley *et al.* 1983; Richter & Wagner 1983). Therefore,

a low stomatal sensitivity to vapour pressure deficit would be an advantage in environments where high atmospheric deficits are not necessarily accompanied by soil water shortage (Maroco *et al.* 1997). However, a rapid stomatal response to vapour pressure deficit is likely to be highly effective in protecting species from wet environments against sudden desiccation (Körner & Bannister 1985). Water stress can be avoided for longer periods by maintaining access to water through a deeper and more extensive root system or osmotic adjustments (Jones *et al.* 1981).

Tropical species of *Nothofagus* show higher long-term water use efficiency than temperate species primarily due to a lower stomatal sensitivity to vapour pressure deficit in the temperate species (Read & Farquhar 1991). Furthermore, the temperate species *Nothofagus cunninghamii* shows an ability to keep its stomata open and make osmotic adjustments under mild water stress (Read 1998). Read (1991) proposed the temperate species have evolved mechanisms such as osmotic adjustment or a high root/shoot ratio that allow continued water uptake and high stomatal conductance during periods of mild water stress. In contrast, tropical rainforest species tend to have shallow roots (Doley 1981) and may not have access to a large water reserve. Consequently, tropical rainforest species are more susceptible to water deficits (Grubb 1977; Buckley *et al.* 1980). Furthermore, osmotic adjustments have only been reported in tropical trees from dry forests (Medina 1983; Myers *et al.* 1987; Sobrado 1986). Therefore, stomatal closure is likely to be an adequate response for tropical rainforest species during short periods of water stress.

Research so far has not shown consistent trends in stomatal sensitivity between species from different moisture environments (Bunce 1986). Stomatal responses to increasing VPD range from insensitive to highly sensitive in tree species from both wet and dry habitats (Rawson *et al.* 1977; Meinzer 1982; Turner *et al.* 1984; Hogan *et al.* 1994). However, tropical rainforest trees tend to show a high sensitivity of stomatal conductance to increasing VPD (Whitehead *et al.* 1981; Doley *et al.* 1987; Meinzer *et al.* 1993; Park & Furukawa 1999). These declines in stomatal conductance with increasing VPD usually lead to similar declines in net photosynthesis (Turner *et al.* 1984; Sandford & Jarvis 1986; Park & Furukawa 1999). However, some species show a decline in net photosynthesis without any decline in stomatal conductance with increasing VPD (Langenheim *et al.* 1984; Sharkey 1984). The response of stomata to

VPD in many species is also dependent on the growth conditions. Plants exposed to water stress adjust their response to VPD with a decreased stomatal sensitivity being the most common response (Ludlow 1980). In contrast, tropical trees tend to increase their stomatal sensitivity to VPD under water stress (El-Sharkawy & Cock 1984; Smith 1989; Doley *et al.* 1987). In the absence of soil water stress, plants grown under higher VPD have been shown to increase stomatal resistance to water vapour (Beardsell *et al.* 1973; Slavik 1973). Growth of plants at higher values of VPD has been shown to both increase and decrease net photosynthesis (Beardsell *et al.* 1973; Kawamitsu *et al.* 1993; Marsden *et al.* 1996).

This study aimed to investigate if tropical rainforest trees have a higher stomatal sensitivity to VPD than temperate species that leads to a significant reduction in net photosynthesis. The effect of growing leaves under a reduced VPD on this response was also determined. In particular the following hypotheses were tested:

1. Tropical species will show a significantly greater reduction in net photosynthesis with increasing VPD than the temperate species.
2. Leaves grown under low VPD will show a greater reduction in net photosynthesis with increasing VPD than plants grown under high VPD.

To test these hypotheses seedlings of the rainforest species were grown under either ambient conditions or low VPD in glasshouses. The response of net photosynthesis to VPD was measured in leaves developed during summer.

METHODS

Growth conditions

Seedlings were grown for a year, between March 1996 and March 1997, in glasshouses under two different vapour pressure deficits (VPD). One set of seedlings was grown under ambient conditions whilst the other set was grown under a constant low VPD. These seedlings were grown to determine photosynthetic responses to VPD, which are discussed in this chapter and growth responses to VPD, which are discussed in Chapter 8. Forty seedlings of each species were used with the exception of the species *Sloanea woollsii* and *Eucryphia lucida* for which only 16 and 20 seedlings respectively were used due to low numbers at the time of the experiment. Seedlings of each species were divided evenly across four glasshouses and positioned randomly within each glasshouse.

Each VPD treatment was housed within two separate glasshouses. The low VPD treatment was achieved using a misting system that was triggered off by an evaporative arm. The seedlings in the other two glasshouses were grown under ambient VPD. Plastic collars were attached to the base of the stem of seedlings from both treatments to ensure that the misting systems did not keep the soil of seedlings in the low VPD treatment constantly saturated. Pots were watered every two to seven days depending on the time of year. During summer, seedlings had to be watered twice as often in the ambient VPD treatment than in the low VPD treatment to ensure that soil moisture was consistent across the treatments. Fertiliser was added every fourteen days in the form of FOGG-IT fish emulsion fertilizer (FOGG-IT Nozzle Company, San Francisco) diluted 1/500 with water to provide 98 mg L⁻¹ of nitrogen, 20 mg L⁻¹ of potassium, and 31 mg L⁻¹ of phosphorus.

Irradiance in the glasshouses at midday on clear days ranged from 1266 ± 53 μmol quanta m⁻² s⁻¹ in March to 328 ± 44 μmol quanta m⁻² s⁻¹ in July. During the summer, the glasshouses were white-washed to reduce the air temperature, which reduced irradiance levels to 348 ± 34 μmol quanta m⁻² s⁻¹. On days over 30°C, sheets of 90% shade cloth

were placed over the glasshouses to help maintain temperatures close to ambient, which resulted in a reduction of irradiance levels to $108 \pm 12 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$.

Over the period that photosynthetic measurements were taken, the VPD within each glasshouse was randomly measured on eight separate days. This approach was used, as there was only two sets of dataloggers and four glasshouses to be measured. VPD was calculated from data obtained from temperature and humidity dataloggers during daylight hours. The values of daytime VPD are given in Table 7.2.

Table 7.2 Daytime conditions recorded in the glasshouses during the period of photosynthetic measurements. Values are means of two glasshouses with one standard error given in brackets. Results of one-way ANOVAs between treatments are given.

		treatment		<i>F</i>	<i>p</i>
		low VPD	ambient VPD		
VPD (kPa)	mean	0.45 (0.04)	1.36 (0.17)	28.0	0.03
	maximum	0.73 (0.07)	2.16 (0.21)	43.8	0.02
	minimum	0.17 (0.01)	0.35 (0.02)	84.7	0.01
temperature (°C)	mean	21.6 (1.9)	23.8 (0.5)	1.22	0.39
	maximum	24.6 (2.4)	26.9 (0.4)	0.89	0.44
	minimum	17.9 (0.9)	19.3 (0.0)	2.52	0.25

Net photosynthesis measurements

In January 1997, the response of photosynthesis to different values of instantaneous VPD was measured on a subset of the seedlings in the growth experiment. For each species, eight seedlings were measured from each of the treatments, with four subreplicates being taken from each glasshouse. Plants were brought over to the laboratory the night before measurement and watered. This ensured leaves were fully-hydrated and had not been exposed to large values of VPD on the day of measurement.

The measurement setup was the same as used in the photosynthetic study in Chapter 3. Leaves were equilibrated in the leaf chamber at an air temperature of 22°C, a VPD of 0.5 kPa and an irradiance level of 800 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$. The photosynthetic rate was then measured at progressively higher values of VPD in the order 0.8, 1.1, 1.3, 1.6, and 1.9 kPa. The leaf was allowed to equilibrate to each new VPD for ten minutes before measurement. The leaf area within the leaf chamber was measured by tracing the leaf after measurement and measuring the area of this trace using image analysis (BIOSCANTM Image Analyser).

Data Analysis

The form of the response of net photosynthesis to VPD varied among species and between treatments within a species. Responses of net photosynthesis to increasing VPD ranged from a distinct reduction to minor changes. The species showing only minor changes showed maximum net photosynthesis at low, intermediate or high values of VPD. The majority of these responses could be regressed successfully using the following exponential equation:

$$P = a(1 - e^{b \cdot \text{VPD}}) + c \quad (\text{equation 7.1})$$

where P is the net photosynthetic rate, VPD is the vapour pressure deficit, and a, b and c are fitting parameters. The responses that showed maximum net photosynthesis at an intermediate VPD were regressed using a simple quadratic equation. From these regressions the maximum net photosynthetic rate (P_{max}) within the measurement range was determined and the vapour deficit at which net photosynthesis was reduced to ninety percent of the maximum rate (VPD_{90}). Many species showed only minor changes in net photosynthesis across the measurement range of VPD and their values of VPD_{90} could not be determined. Therefore, it was not possible to perform statistical comparisons among species for this parameter. However, statistical comparisons of the percentage reduction in net photosynthesis over the measurement range were possible among taxonomic groups.

Regressions of the percent reduction in net photosynthesis shown by species when grown under ambient conditions against several climate variables were performed. The following twenty one climatic variables were chosen to describe the moisture environment:

annual precipitation (PTOT)	highest monthly mean VPD month (MVHi)
summer precipitation (PSum)	mean VPD of the hottest month (MVH)
summer/winter precipitation (PSW)	mean annual max. VPD (MaxVA)
lowest monthly precipitation (PLo)	summer max. VPD (MaxVSum)
precipitation of hottest month (PH)	highest monthly max. VPD (MaxVHi)
mean annual evaporation (EA)	max. VPD of hottest month (MaxVH)
summer evaporation (ESum)	mean annual water balance (WBA)
highest monthly evaporation (EHi)	summer water balance (WBSum)
evaporation of hottest month (EH)	lowest monthly water balance (WBLo)
mean annual VPD (MVA)	water balance of hottest month (WBH)
summer mean VPD (MVSum)	

A Pearson correlation was performed on these water variables using the mean values for each species (Table 7.3). A high level of correlation (>0.80) was found among many of the variables. Consequently, only a subset of these variables was used in the regressions. Summer maximum VPD (MaxVSum) was included, as it is directly relevant to the hypothesis being tested. Annual precipitation and the ratio of summer to winter precipitation were included because they were not correlated with MaxVSum and the majority of the other variables. Lowest monthly precipitation (PLo) was included because it was negatively correlated with MaxVSum. The variables WBSum and WBH were not included although they were not correlated with MaxVSum because they were highly correlated with PLo.

Table 7.3 Pearson correlation matrix of the water variables that describe the moisture environment of the species. Probabilities were adjusted using the Step-down Holm algorithm and correlations with a Pearson coefficient >0.95 were significant. Variables highly correlated with summer maximum VPD (MaxVSum) are highlight in bold.

	P TOT	P Sum	P SW	P Lo	P H	E A	E Sum	E Hi	E H	MV A	MV Sum	MV Hi	MV H	Max VA	Max V Sum	Max V Hi	Max V H	WB A	WB Sum	WB Lo	WB H
PTOT	-																				
PSum	-0.12	-																			
PSW	0.42	0.77	-																		
PLo	0.33	-0.96	-0.67	-																	
PH	0.11	0.96	0.87	-0.87	-																
EA	-0.22	0.98	0.74	-0.97	0.93	-															
ESum	-0.57	0.85	0.45	-0.91	0.73	0.92	-														
EHi	-0.01	0.98	0.85	-0.93	0.97	0.98	0.81	-													
EH	-0.40	0.95	0.59	-0.97	0.86	0.98	0.97	0.91	-												
MVA	-0.17	0.99	0.76	-0.97	0.94	1.00	0.88	0.99	0.97	-											
MVSum	-0.32	0.97	0.66	-0.99	0.89	0.99	0.94	0.95	0.99	0.99	-										
MVHi	0.01	0.98	0.87	-0.93	0.96	0.97	0.79	1.00	0.90	0.98	0.94	-									
MVH	-0.21	0.99	0.72	-0.98	0.93	0.99	0.89	0.97	0.97	1.00	0.99	0.97	-								
MaxVA	-0.24	0.99	0.70	-0.98	0.92	0.99	0.90	0.97	0.98	0.99	0.99	0.96	1.00	-							
MaxVSum	-0.39	0.96	0.60	-0.99	0.85	0.97	0.94	0.92	0.99	0.97	0.99	0.91	0.98	0.98	-						
MaxVHi	-0.17	0.99	0.73	-0.96	0.95	0.99	0.88	0.98	0.96	0.99	0.98	0.97	0.99	1.00	0.96	-					
MaxVH	-0.26	0.98	0.70	-0.99	0.90	0.97	0.88	0.96	0.96	0.98	0.98	0.95	0.99	0.99	0.99	0.98	-				
WBA	0.72	-0.77	-0.29	0.88	-0.60	-0.84	-0.97	-0.70	-0.92	-0.80	-0.88	-0.69	-0.82	-0.84	-0.91	-0.80	-0.84	-			
WBSum	0.55	0.76	0.94	-0.60	0.87	0.67	0.33	0.82	0.53	0.72	0.61	0.82	0.70	0.67	0.55	0.72	0.66	-0.17	-		
WBLo	0.09	-0.90	-0.84	0.91	-0.85	-0.93	-0.80	-0.94	-0.86	-0.93	-0.90	-0.96	-0.91	-0.90	-0.88	-0.89	-0.91	0.71	-0.71	-	
WBH	0.71	0.58	0.86	-0.38	0.76	0.48	0.12	0.64	0.33	0.52	0.39	0.65	0.49	0.47	0.33	0.53	0.44	0.06	0.94	-0.49	-

RESULTS

The species showed distinct differences in their response of net photosynthesis to instantaneous VPD (Figure 7.2). The four temperate species and one of the subtropical species showed little change in net photosynthesis in response to instantaneous VPD over the measurement range (Figures 7.2 a, b, d, & f). In contrast, the two tropical species showed a distinct reduction in net photosynthesis at high instantaneous high values of VPD (Figures 7.2 g & h).

There was an overall significant increase in the percentage reduction in net photosynthesis with increasing VPD in plants grown under low VPD compared with those grown under ambient conditions (Table 7.4). The trend was strongest in *Acmena smithii* and *Castanospermum australe* whereas *Tristaniopsis laurina* showed little change between growth conditions (Table 7.5). However, none of the individual comparisons of growth VPD within a species were statistically significant. In contrast, there were many significant differences among species within growth VPD treatments (Table 7.5). The two tropical species showed the greatest reductions in net photosynthesis with increasing VPD under both treatments. In contrast, the cool-temperate species *Nothofagus cunninghamii* showed minor increases in net photosynthesis with increasing VPD. The species *Eucryphia lucida*, *N. cunninghamii*, *T. laurina* and *Heritiera trifoliolata* showed less than a ten percent reduction in net photosynthesis across the measurement range in seedlings grown under both treatments. *Acmena smithii* was the only temperate species to show a 10% reduction in net photosynthesis within the measurement range and this was only shown in seedlings grown under a low VPD.

The rainforest types showed a trend of smaller reductions in net photosynthesis with increasing VPD when grown under ambient VPD compared with low VPD (Table 7.6). However, this reduction was only significant for the tropical rainforest type. Comparisons of the rainforest types showed that the tropical rainforest type showed the greatest reduction in net photosynthesis with increasing VPD under both ambient and low VPD (Table 7.6). The reduction in net photosynthesis with instantaneous VPD shown by the tropical rainforest type was significantly greater than all the other rainforest types when grown at low VPD. In contrast, the reduction in net photosynthesis with instantaneous VPD shown by the tropical rainforest type was only

significantly greater than the cool-temperate type when grown at ambient VPD. The tropical group showed a significantly greater reduction in net photosynthesis than the temperate group when grown at low VPD ($F = 40599, p < 0.01$) but not when grown at ambient VPD ($F = 54.6, p = 0.09$).

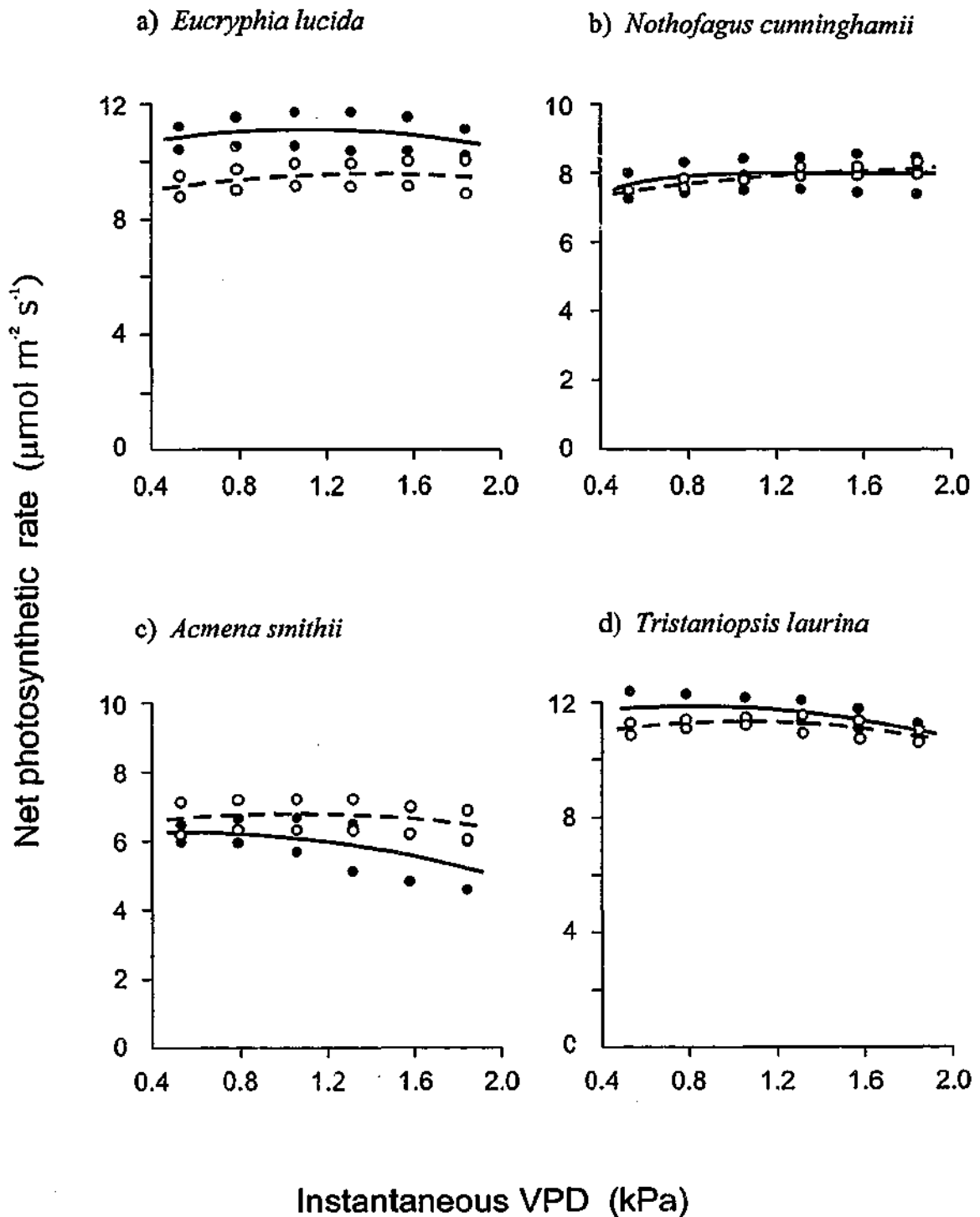


Figure 7.2 a-d Average response of net photosynthesis to instantaneous VPD in leaves of the species grown under an ambient (—○—) and a low (—●—) VPD regime. Values are means for the two runs of the experiment

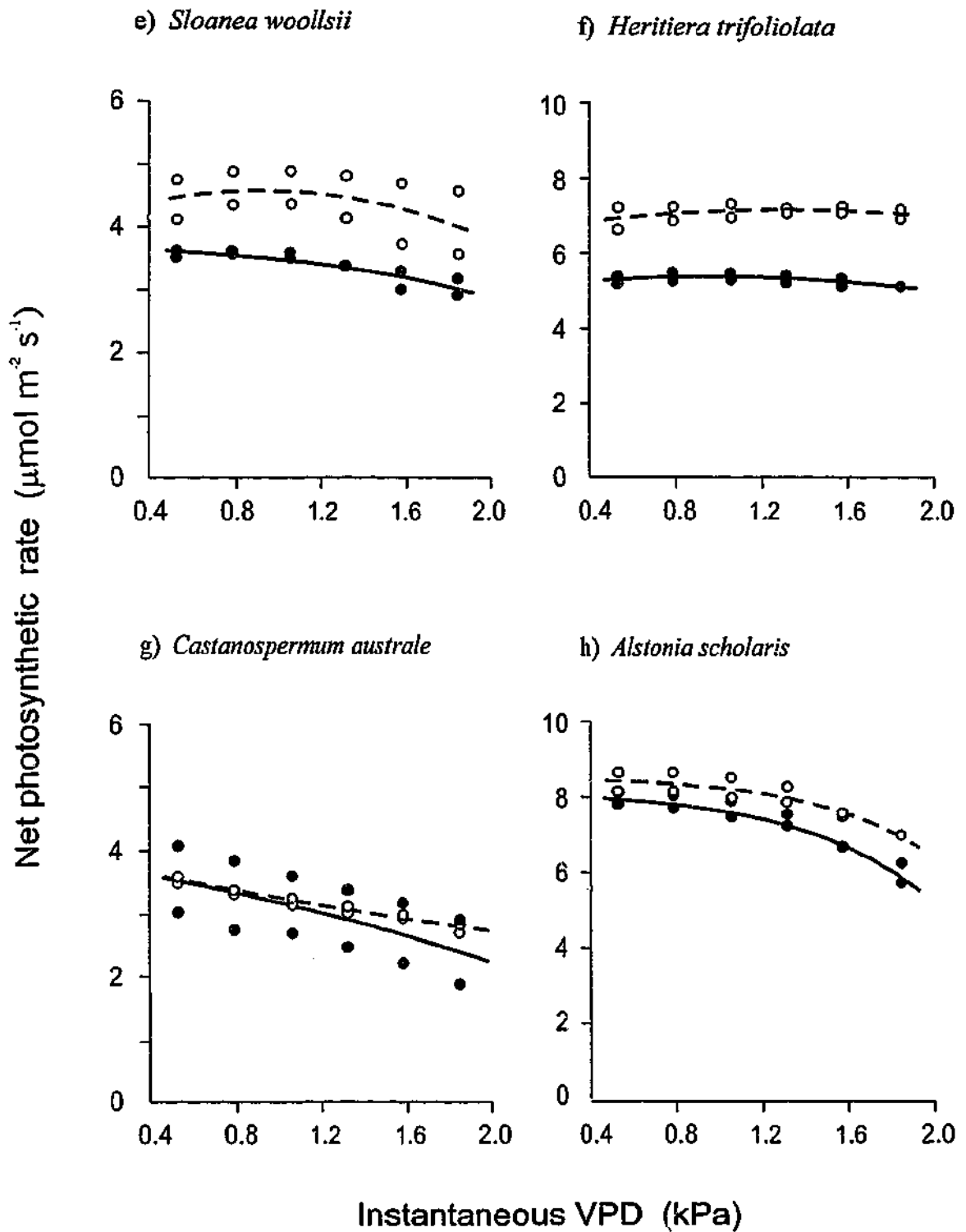


Figure 7.2 e-h Average response of net photosynthesis to instantaneous VPD in leaves of the species grown under an ambient (—○—) and a low (—●—) VPD regime. Values are means for the two runs of the experiment

Table 7.4 Results of the split-plot ANOVA for percentage change in net photosynthesis with increasing vapour pressure deficit for species grown under a low or ambient vapour pressure deficit.

Hypothesis test	<i>F</i>	<i>p</i>
VPD	53.3	0.02
species	14.1	< 0.01
VPD × species	0.68	0.68

Table 7.5 Percentage change in net photosynthesis with increasing vapour pressure deficit (% 1 kPa^{-1}) for species grown under a low or ambient vapour pressure deficit. Values are means of two glasshouses with standard errors in brackets. The results of randomized block ANOVAs comparing species within growth VPD are given. Letters denote non-significant groupings of means.

Growth VPD		
Species	low	ambient
<i>E. lucida</i>	-4.0 (1.3) ^{ab}	0.5 (3.7) ^{ab}
<i>N. cunninghamii</i>	1.0 (3.8) ^a	6.5 (1.3) ^a
<i>A. smithii</i>	-15.7 (5.4) ^{ab}	-4.5 (0.1) ^{ab}
<i>T. laurina</i>	-3.5 (2.5) ^{ab}	-4.5 (0.3) ^{ab}
<i>S. woollsii</i>	-14.8 (3.5) ^{ab}	-12.4 (6.1) ^{ab}
<i>H. trifoliolata</i>	-4.6 (1.5) ^{ab}	-3.1 (1.9) ^{ab}
<i>C. australe</i>	-27.1 (3.9) ^b	-17.8 (0.4) ^b
<i>A. scholaris</i>	-24.5 (5.8) ^b	-17.2 (2.5) ^b
species	<i>F</i> 6.65	8.84
	<i>p</i> 0.01	0.01
glasshouse	<i>F</i> < 0.01	0.46
	<i>p</i> 0.96	0.52

Table 7.6 Percentage change in net photosynthesis with increasing vapour pressure deficit (% kPa^{-1}) for the rainforest types grown under a low or ambient vapour pressure deficit. Values are means of two glasshouses with standard errors in brackets. The results of one-way ANOVA comparing growth VPD within rainforest types and randomized block ANOVA comparing rainforest types within growth VPD are given.

Rainforest type	Growth Vapour Pressure		One-way ANOVA	
	low	ambient	<i>F</i>	<i>p</i>
cool-temperate	-1.5 (1.2) ^a	3.5 (2.5) ^b	3.27	0.21
warm-temperate	-9.6 (1.4) ^a	-4.5 (0.2) ^{ab}	12.2	0.07
subtropical	-9.7 (1.0) ^a	-7.7 (2.1) ^{ab}	0.23	0.68
tropical	-25.8 (0.9)	-17.5 (1.5) ^a	22.6	0.04
Randomized block ANOVA				
rainforest type	<i>F</i>	56.5	18.1	
	<i>p</i>	< 0.01	0.02	
glasshouse	<i>F</i>	0.01	0.05	
	<i>p</i>	0.92	0.84	

The tropical species *Sloanea woollsii*, *C. australe* and *Alstonia scholaris* showed a 10% reduction in net photosynthesis at a VPD between 1.0 and 1.8 kPa (Table 7.7). These tropical species showed a 10% reduction in net photosynthesis at lower values of instantaneous VPD when grown under low VPD compared with ambient conditions however these differences were not significant. Similarly, the temperate species *Acmena smithii* only show a 10% reduction in net photosynthesis over the measurement range when grown under low VPD.

Both the subtropical species, *S. woollsii* and *H. trifoliolata*, showed a 30% increase in maximum net photosynthesis in plants grown under ambient conditions compared with plants grown at low VPD (Table 7.8). This difference was significant for *H. trifoliolata* but only nearly significant for *S. woollsii*. The remaining species showed much smaller changes in maximum net photosynthesis between the growth treatments and there was no consistent trend in the difference.

Table 7.7 VPD (kPa) at which net photosynthesis was reduced to 10% of the maximum net photosynthetic rate for the rainforest types. Values are means of two glasshouses with standard errors in brackets. The results of one-way ANOVAs comparing growth VPD within species are given. Species that did not show a 10% reduction in net photosynthesis over the measurement range are denoted as 'na'.

Species	Growth Vapour Pressure		<i>F</i>	<i>p</i>
	low	ambient		
<i>E. lucida</i>	na	na		
<i>N. cunninghamii</i>	na	na		
<i>A. smithii</i>	1.47 (0.35)	na		
<i>T. laurina</i>	na	na		
<i>S. woollsii</i>	1.52 (0.10)	1.79 (0.21)	1.38	0.36
<i>H. trifoliolata</i>	na	na		
<i>C. australe</i>	1.00 (0.02)	1.21 (0.07)	8.41	0.10
<i>A. scholaris</i>	1.38 (0.01)	1.60 (0.10)	4.66	0.16

Table 7.8 Maximum net photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for species grown under a low or ambient vapour pressure deficit. Values are means of two glasshouses with standard errors in brackets. The results of one-way ANOVAs comparing growth VPD within species are given.

Species	Growth Vapour Pressure		<i>F</i>	<i>p</i>
	low	ambient		
<i>E. lucida</i>	11.19 (0.81)	9.39 (0.14)	8.16	0.10
<i>N. cunninghamii</i>	7.75 (0.21)	7.44 (0.01)	2.41	0.26
<i>A. smithii</i>	6.36 (0.26)	6.76 (0.43)	0.61	0.52
<i>T. laurina</i>	11.95 (0.47)	11.35 (0.22)	1.33	0.37
<i>S. woollsii</i>	3.63 (0.03)	4.61 (0.28)	12.0	0.07
<i>H. trifoliolata</i>	5.38 (0.11)	7.16 (0.09)	158	0.01
<i>C. australe</i>	3.54 (0.55)	3.51 (0.03)	<0.01	0.96
<i>A. scholaris</i>	8.00 (0.16)	8.46 (0.28)	2.05	0.29

Regressions of the reduction in net photosynthesis with increasing VPD when grown at ambient VPD (PRP_{amb}) against several precipitation variables of the species revealed some interesting trends (Figure 7.3). There was no relationship between PRP_{amb} and the annual precipitation of the species climate profiles. Significant negative relationships were found between PRP_{amb} and summer maximum VPD summer precipitation and the ratio of summer to winter precipitation. In contrast, there was a significant positive relationship between PRP_{amb} and precipitation of the driest month.

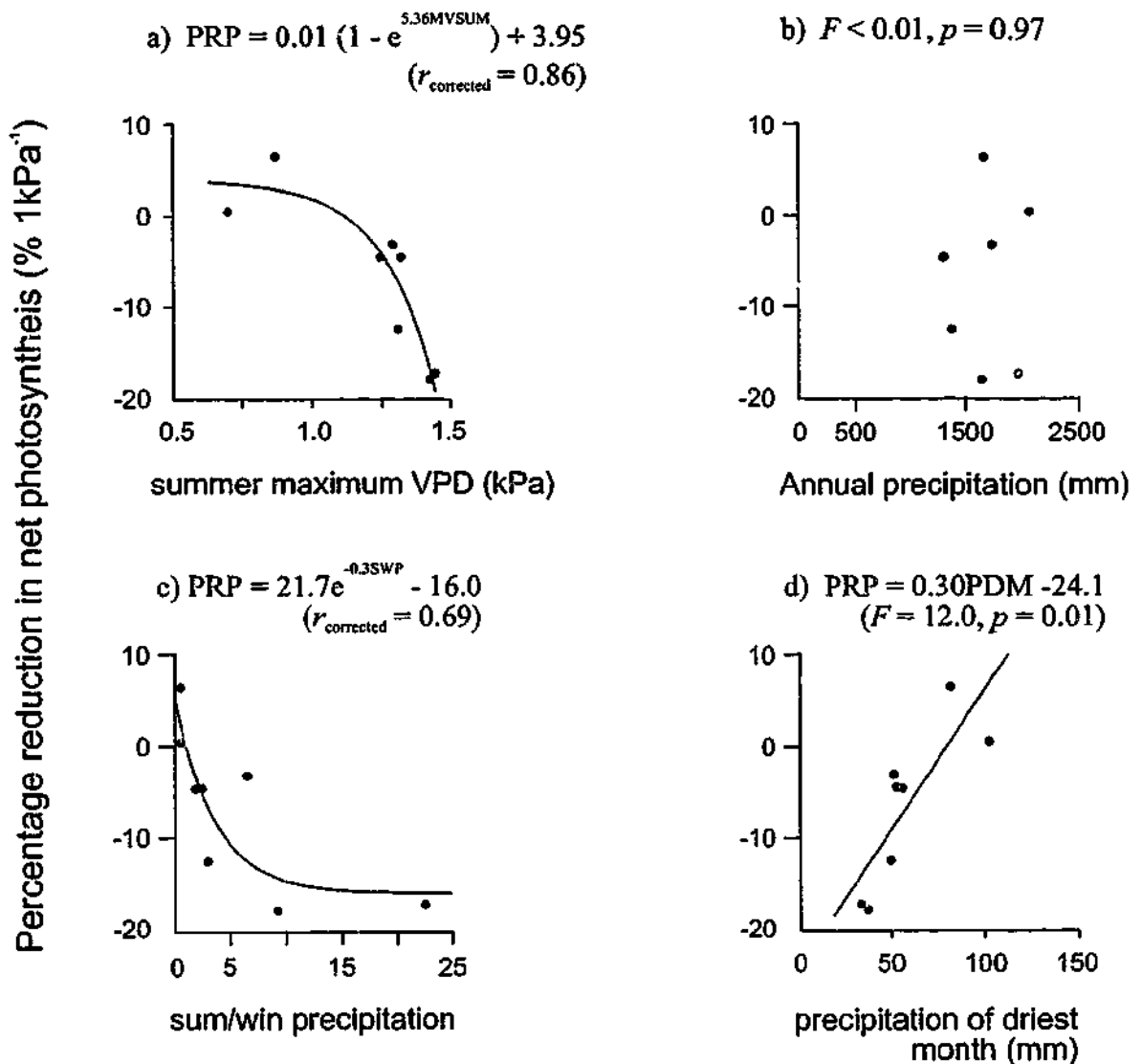


Figure 7.3 Relationships between the percentage reduction in maximum net photosynthesis with increasing VPD (PRP , % 1kPa⁻¹) and several climate variables from the climate profiles of the species. Points represent means for individual species.

DISCUSSION

Differences in the response of net photosynthesis to instantaneous VPD among taxa

The tropical group showed greater reductions in net photosynthesis over the VPD range of 0.5 to 1.9 kPa than the temperate group. However, this was only significant when the plants were grown under a low VPD. Therefore, the hypothesis that the tropical species would show significantly greater reductions in net photosynthesis with increasing VPD than the temperate species was only true under the low VPD conditions. Nevertheless, the tropical rainforest type showed significantly larger reductions (18 to 26%) in net photosynthesis with increasing VPD compared with the cool-temperate rainforest type, which show little change with increasing VPD, under both growth conditions (Table 7.6). These reductions in net photosynthesis of the tropical species occurred in well-watered plants, which indicates a direct response to the atmospheric water deficit.

Reductions in net photosynthesis with increasing VPD of the species grown under ambient conditions (PRP_{amb}) showed strong relationships with climate variables that describe summer moisture conditions (Figure 7.3). In contrast, there was no relationship between annual precipitation and PRP_{amb} , which is not surprising as the tropical and temperate groups included species covering a similar range of annual precipitation (Table 7.1). Values of PRP_{amb} increased with the amount of summer precipitation, the amount of summer precipitation compared with winter precipitation and the magnitude of maximum VPD during summer. In contrast, PRP_{amb} decreased with increasing precipitation of the driest month. This is because the tropical species, which showed the greatest values of PRP_{amb} , have lower precipitation during winter than the temperate species have during summer. Therefore, rainforest trees from areas with the highest precipitation and highest maximum VPD during summer showed the greatest reductions in net photosynthesis with increasing VPD.

These findings are consistent with previous findings in the rainforest genus *Nothofagus* (Körner & Bannister 1985; Read & Farquhar 1991). Species of *Nothofagus* from wet forest types in New Zealand showed a pronounced sensitivity of stomatal conductance to increasing VPD (Körner & Bannister 1985). In contrast, *Nothofagus* species from areas of winter-dominant precipitation maintain a higher stomatal conductance even

under mild water deficits than species from areas of summer-dominant precipitation (Read 1998). Furthermore, these species from winter-dominant precipitation areas showed greater long-term water-use efficiency, as measured by leaf carbon isotope discrimination, than the summer-dominant precipitation species (Read & Farquhar 1991). The greater sensitivity of net photosynthesis to VPD of the tropical species compared with the cool-temperate species found in this study is consistent with higher water-use efficiency in species from areas of summer-dominant than winter-dominant precipitation. That is, the stomatal closure of tropical species at lower VPD than the cool-temperate species means their stomata will be closed more often leading to higher water-use efficiency.

Park (1999) also found that tropical rainforest trees showed greater reductions in net photosynthesis with increasing VPD than temperate trees. A survey of the literature on trees and shrubs shows a non-significant trend ($F = 2.94$, $p = 0.10$) of greater reductions in net photosynthesis with increasing VPD in tropical species compared with temperate species (Table 7.9). The lack of a significant difference between these groups is probably due to both groups containing species from a range of precipitation environments. A more relevant comparison would be between tropical and temperate species from mesic environments. However, it was not possible to find accurate information of the precipitation of the majority of the species. Regardless of this, it is important to note that the tropical rainforest trees on average show greater reductions than other tropical trees or temperate trees. The greater sensitivity of photosynthesis to VPD suggests tropical rainforest trees are more susceptible to water deficits than temperate species.

In the wet tropics, roots tend to be concentrated in the surface soil and trees are therefore easily damaged by small water deficits (Grubb 1977; Buckley *et al.* 1980). Furthermore, the high leaf area indexes of tropical rainforests mean soil water deficits can develop rapidly in the absence of rain (Tenhunen *et al.* 1987). Therefore, the use of rapid stomatal closure to avoid water stress would be a successful strategy in tropical trees. Similarly, a higher sensitivity of stomatal conductance to VPD in herbaceous species has been found to be related to a higher leaf area to root mass (Bunce 1986). In the wet tropics, deep root systems are unnecessary to obtain water as the soil profile remains wet for the majority of the year (Doley 1981; Hopkins & Graham 1989).

Table 7.9a The percentage reduction in net photosynthesis with increasing VPD recorded in previous studies of well-watered temperate tree and shrub species.

Species	% reduction in net photosynthesis	VPD measurement range (kPa)	standardised reduction in net photosynthesis (% 1 kPa ⁻¹)	Source
<i>Arbutus unedo</i>	40	1.0-3.0	20	Turner (1984)
<i>Atriplex halimus</i>	0	0.8-2.7	0	Rawson (1977)
<i>Betula pendula</i> *	9	1.0-2.5	6	Osonubi (1980)
<i>Citrus sinensis</i>	8	0.7-2.1	6	Khairi (1976)
<i>Corylus avellana</i>	25	1.0-3.0	12.5	Turner (1984)
<i>Daphniphyllum macropodum</i>	17	1.0-2.5	11	Park (1999)
<i>Gmelina aroborea</i>	3	1.0-2.5	2	Osonubi (1980)
<i>Helianthus annuus</i>	16	1.0-3.0	8	Turner (1985)
<i>Nerium oleander</i>	25	1.0-3.0	12.5	Turner (1984)
<i>Nothofagus fusca</i>	16	1.0-2.0	16	Hollinger (1987)
<i>Pinus radiata</i>	45	1.0-2.0	45	Hollinger (1987)
<i>Pinus taeda</i>	20	1.0-2.2	17	Teskey (1986)
<i>Pistacia vera</i>	25	1.0-3.0	12.5	Turner (1984)
<i>Prunus dulcis</i>	10	1.0-3.0	5.0	Turner (1984)
<i>Pseudotsuga menziesii</i>	37.5	1.0-2.0	37.5	Hollinger (1987)
<i>Viburnum awabuki</i>	0	1.0-2.5	0	Park (1999)
			mean	13 ± 3

Table 7.9b The percentage reduction in net photosynthesis with increasing VPD recorded in previous studies of well-watered tropical tree and shrub species. * denotes rainforest tree species.

Species	% reduction in net photosynthesis	VPD measurement range (kPa)	standardised reduction in net photosynthesis (% 1 kPa ⁻¹)	Source
<i>Agathis robusta</i> *	25	1.0-3.0	c	Langenheim (1984)
<i>Elaeis guineensis</i>	40	1.0-3.0	20	Dufrene (1993)
<i>Eugenia grandis</i> *	35	1.0-2.5	23	Park (1999)
<i>Gossypium hirsutum</i>	10	1.0-3.0	5	Turner (1984)
<i>Macadamia integrifolia</i>	50	1.0-3.0	25	Lloyd (1991)
<i>Manihot esculenta</i>	30	1.0-2.0	30	El-Sharkawy (1984)
<i>Podocarpus neriifolius</i> *	60	0.4-2.0	37.5	Meinzer (1984)
<i>Podocarpus oleifolius</i> *	60	0.4-2.0	37.5	Meinzer (1984)
<i>Pongamia pinnata</i> *	45	1.0-2.5	30	Park (1999)
<i>Psychotria horizontalis</i>	0	0.5-2.0	0	Hogan (1994)
<i>Ricinus communis</i>	60	0.5-3.5	20	Dai (1992)
<i>Schima superba</i>	35	1.0-3.5	14	Sun (1986)
			mean	21 ± 3
			tropical rainforest trees	28 ± 5

In addition, the rapid decomposition of the litter layer under the humid and warm conditions of the tropics makes extensive root systems unnecessary for nutrient acquisition (Attiwill & Leeper 1987). Therefore, the use of stomatal closure to avoid water stress may be more cost effective than producing extensive root systems in the wet tropics.

Species from warm, wet environments, such as those of tropical rainforests of north-eastern Australia, tend to have larger xylem vessels than species from colder or drier environments (Tyree *et al.* 1994). Larger vessels improve hydraulic efficiency and reduce resistance to the flow of water to leaves (Tyree & Ewers 1991). However, large vessels are more susceptible to embolism (air blockage) during drought or freezing temperatures (Sperry & Tyree 1990; Sperry & Sullivan 1992). As temperatures are never freezing and droughts are short in the wet, lowland tropics, stomatal closure may be a more efficient strategy than increased hydraulic resistance to water flow.

A rapid stomatal response to VPD would lead to greater water-use efficiency under wet, tropical conditions. Rainforest species from the wet tropics, like those in this study, experience the combination of high precipitation and high values of maximum VPD during the summer (Table 7.1). Under these conditions, a stomatal response to VPD would lead to a reduction in net photosynthesis during the middle of the day. However, this would lead to small losses in productivity due to the longer period of warm temperatures, as well as the longer daylength, under a tropical climate relative to a temperate climate.

Midday stomatal closure is common in tropical rainforest species during the dry season (Fetcher *et al.* 1994). A stomatal response to VPD may lead to a slower depletion of the available soil water during the dry season. This is because most transpirational losses would occur during periods of the day when VPD is low and water-use efficiency is high. This higher water-use efficiency would lead to a greater total accumulation of photosynthate than would occur with no stomatal control (El-Sharkawy & Cock 1986). However, such a strategy would only be an advantage if species that use up soil water reserves are absent from the community (Bradford & Hsiao 1982). Furthermore, productivity during the dry season of tropical Australia is likely to be low due to reduced temperatures. Therefore, prolonged stomatal closure during this time would not lead to large losses in productivity.

A high stomatal sensitivity to VPD may not be a successful strategy in temperate rainforests where the warmer growth period is much shorter. Stomatal closure during a large portion of the day would lead to a reduction in dry matter accumulation due to reduced CO_2 diffusion and raised leaf temperatures. Temperate species are likely to have adaptations that extend access to water during the summer months. Firstly, temperate species may invest in deeper and more extensive root systems (Read & Farquhar 1991). Secondly, osmotic adjustments would help to maintain photosynthesis for longer during days of high evaporative demand (Richter & Wagner 1983). Thirdly, temperate species might also be less vulnerable to cavitation at low soil moisture than tropical species (Tyree & Ewers 1996). The additional advantages of maintaining unrestricted transpiration are that leaf temperatures can be maintained close to optimum for photosynthesis (Mahan *et al.* 1995) and the high water flow through the plant possibly increases nutrient uptake by the roots (Sarmiento *et al.* 1985). There may also be an advantage in reducing soil water reserves below levels that competing species can tolerate (Bunce *et al.* 1977).

There appears to be an inconsistency among different studies in the moisture environment of the species that show greater reductions in net photosynthesis with increasing VPD. As already mentioned, several studies, including this one, have found that species from more mesic environments show greater stomatal control (eg. Körner & Bannister 1985; Read & Farquhar 1991; Park & Furukawa 1999). In contrast, other studies have found species from drier environments show greater reductions in net photosynthesis with increasing VPD than species from more mesic environments (Johnson & Caldwell 1976; Teskey *et al.* 1994). It is possible that greater stomatal control is a successful strategy at both ends of the spectrum of water availability. Evergreen desert shrubs consist of both species that have poor stomatal control of water loss but can tolerate extreme water deficits (Odening *et al.* 1974) and species with tight stomatal control on water loss, which show midday stomatal closure (De Puit & Caldwell 1973; Björkman *et al.* 1980b). A rapid stomatal response in desert plants would lead to greater water-use efficiency and therefore greater photosynthetic gains from a restricted water supply. However, desert species are likely to show stomatal closure at much higher values of VPD than tropical rainforest species. Thus, stomatal control may be a successful strategy for avoiding the infrequent water stress of the wet tropics and increasing photosynthetic gains from a limited water supply in arid species.

Whether the responses of single leaves to increasing VPD translate into responses of whole trees has been questioned (eg. Eamus & Cole 1997). A plant may be able to supply the water requirements of a single leaf under increasing VPD but unable to supply a whole canopy under increasing VPD. Therefore, the smaller response of leaves in the temperate species may not translate into the response of the whole plant. However, a study of four herbaceous and six woody species found all species showed a similar decline in net photosynthesis whether a single leaf or the whole plant was exposed to increasing VPD (Turner *et al.* 1984). Only in a grass species, *Hordeum vulgare*, has a reduction in net photosynthesis with increasing VPD been shown when the whole plant was exposed to increasing VPD but not when a single leaf was exposed (Rawson *et al.* 1977). Therefore, it seems likely that the responses shown by single leaves of the rainforest trees are representative of the response of a whole canopy when soil water availability is high.

Effect of growth VPD on the response of net photosynthesis to instantaneous VPD

Most species showed a trend of greater reductions in net photosynthesis with increasing VPD when grown at low VPD compared with ambient VPD (Table 7.5). The tropical rainforest type showed a significant decrease in the reduction in net photosynthesis with increasing VPD when grown under ambient conditions (Table 7.6). Maximum values of VPD for the ambient and low VPD treatments were 0.8 and 2.0 kPa respectively (Table 7.2). Therefore, the reduced sensitivity of net photosynthesis to increasing VPD in leaves grown under ambient conditions compared with low VPD may be due to exposure to higher values of VPD.

Although both treatments were well-watered, the plants grown under ambient conditions may have had trouble maintaining the water potential of their leaves at midday during summer. Plants use secondary strategies, such as osmotic adjustment, when the primary defence of the stomatal response to VPD is ineffective (Mansfield & Davies 1981). Therefore, the reduced sensitivity to VPD under ambient conditions compared with low VPD may reflect a change in physiology such as an osmotic adjustment. Studies of three other species have shown no difference in the response of net photosynthesis to instantaneous VPD between leaves grown at different magnitudes of VPD (El-Sharkawy & Cock 1986; Kawamitsu *et al.* 1993). Two of these species

were grasses and the lack of change with growth VPD could reflect differences between the physiological capabilities of grasses and trees. The third species was cassava, the shrub crop originated from Central and South America which is successfully grown throughout the tropics of the world and is therefore likely to be tolerant of wide variations in VPD. Similarly, arid shrub species show no change in the response of stomatal conductance to increasing VPD when grown at contrasting magnitudes of VPD (Roy & Mooney 1982; Mooney & Chu 1983). However, the consistent response to VPD with changing growth VPD in these arid species may be a reflection of conservative strategies to water stress in arid species.

Both of the subtropical rainforest species showed a 30% increase in their maximum net photosynthetic rate when grown under ambient conditions compared with low VPD (Table 7.9). In contrast, other species have shown no change or a decrease in net photosynthesis when plants are grown at a higher VPD (Beardsell *et al.* 1973; El-Sharkawy & Cock 1986; Kawamitsu *et al.* 1993; Marsden *et al.* 1996). However, only Kawamitsu (1993) found maximum net photosynthesis at low VPD, and not just at growth VPD, decreased when grown at a higher VPD. They explained this response by the lower water status of leaves grown under long-term high VPD (Luo & Strain 1992). Similarly, reduced stomatal conductance has been found in plants grown under a high VPD compared with a low VPD (Slavik 1973). The increased net photosynthetic rate in leaves of the subtropical rainforest species when grown under higher VPD may be a result of a faster transpiration rate under ambient conditions increasing nutrient uptake and therefore the amount of photosynthetic enzymes.

The response of net photosynthesis to increasing VPD is more affected by soil water status than growth VPD. Soil water stress can increase, not change or reduce the sensitivity of stomata to VPD, with the latter being the most common response (Ludlow 1980). For example, species native to cloud forests in New Zealand show a reduced sensitivity to VPD when grown on drier sites (Jane 1983). This reduced sensitivity in water stressed plants is due more to a reduction in the maximum conductance rate achieved than an adjustment of the stomatal response (Ludlow 1980). In contrast, tropical trees tend to increase their stomatal sensitivity to VPD under water stress (El-Sharkawy & Cock 1984; Smith 1989; Doley *et al.* 1987). Species that show no stomatal response to VPD when well-watered often become responsive when exposed

to water stress (Maier & Teskey 1992; Tewolde *et al.* 1993). Stomatal closure occurs in these plants under water stress as they can no longer keep up the water demand to the leaves. In the field, midday stomatal closure becomes more pronounced^d as water stress increases (Tenhunen *et al.* 1987). The photosynthetic rate of tropical rainforest species has been shown to decline rapidly several after rain in the dry season (Odum *et al.* 1970; Doley *et al.* 1987).

From the above findings, certain predictions can be made about the response of the rainforest tree species in this study to water stress. All species are likely to show declines in maximum net photosynthetic rate under water stress. In particular, the tropical species are likely to show rapid declines in maximum net photosynthesis as drought proceeds. The species that were not responsive to VPD when well-watered are likely to become sensitive to VPD under water stress. However, species that are native to dry environments tend to show delayed stomatal closure in response to water stress (Bunce *et al.* 1977; Davies & Kozlowski 1977; Bahari *et al.* 1985; Ni & Pallardy 1991; Abrams 1990). Therefore, in the field the tropical species would show significant reductions in net photosynthesis under mild VPD well before soil moisture was low enough to cause stomatal closure in the temperate species.

In summary, the tropical species only showed significantly greater reductions in net photosynthesis with increasing VPD when grown under low VPD. In contrast, the tropical rainforest type showed significantly greater reductions than the cool-temperate rainforest type under both ambient and low VPD. These trends reflect different strategies to tolerate the higher values of VPD associated with summer temperatures between the tropical and temperate species. It is proposed that stomatal closure is a cost effective response to high values of VPD in tropical species. This is because large root systems are unnecessary due high water and nutrient availability in surface soils and the reduction in photosynthesis is compensated by a longer warm growing season of tropical species than temperate species. In contrast, the shorter warm growing season of temperate rainforest species means they can not afford reduced photosynthesis due to stomatal closure at high VPD. Therefore, temperate species are likely to use other strategies to maintain water status during summer such as producing larger root systems, increasing hydraulic resistance and making osmotic adjustments. Temperate and tropical species showed a similar response to growth under an increased VPD.

Most species showed a reduced sensitivity of net photosynthesis to increasing VPD and no significant change in the maximum net photosynthetic rate when grown under ambient conditions of a temperate summer compared with a lower VPD.

In conclusion to the specific hypotheses:

1. Tropical species showed significantly greater reductions in net photosynthesis with increasing VPD than the temperate species when grown under low VPD but not under high VPD. However, the tropical rainforest type showed greater reductions in net photosynthesis with increasing VPD than the cool-temperate rainforest type under both treatments.
2. Leaves grown under low VPD showed a greater reduction in net photosynthesis with increasing VPD than plants grown under high VPD.

CHAPTER 8

Growth under different vapour pressure deficit regimes

Tropical and temperate rainforest species of Australia experience different moisture climates during summer (Table 8.1). Firstly, during summer tropical species receive their highest precipitation whereas temperate species receive their lowest precipitation. Secondly, although the cool-temperate species receive the lowest summer precipitation, lower maximum temperatures result in the lowest values of maximum vapour pressure deficit (VPD) during summer among the species. Finally, the combination of higher precipitation and higher VPD of the tropical climate during summer results in a higher water balance (indicator of atmospheric drought) but similar soil moisture compared with temperate climate. Therefore, the main difference between the moisture climates during summer of temperate and tropical rainforest trees in Australia is the greater atmospheric drought experienced by temperate species.

In the previous chapter, the majority of tropical species showed significant reductions in net photosynthesis with increasing VPD when well-watered whereas the temperate species showed minor reductions (Figure 7.2). This reduced sensitivity of net photosynthesis to VPD in the temperate species is consistent with their lower levels of VPD during summer compared with the tropical species (Table 8.1). However, it also suggests they possess other adaptations to tolerate their low summer precipitation. A reduced sensitivity of stomatal conductance to increasing VPD has been found in plants with a smaller leaf area to root biomass or length ratios (Bunce 1981, 1986). Therefore, temperate rainforest species may allocate more biomass to roots than tropical species to maintain water status during the summer months. In addition, temperate rainforest species could possess other adaptations to maintain water status during summer such as osmotic adjustments and lower hydraulic conductivity.

Table 8.1 Summer moisture climates of the species derived from ANUCLIM 5.0. Values are means of variables calculated for site locations with standard errors in brackets. Summer values are the mean of values for the months December, January and February.

species	n	precipitation (mm)	max. temperature (°C)	max. VPD (kPa)	water balance (mm)	moisture index
<i>E. lucida</i>	112	374 (10)	17.9 (0.1)	0.70 (0.01)	6.1 (3.8)	0.96 (0.01)
<i>N. cunninghamii</i>	354	298 (5)	18.7 (0.1)	0.86 (0.02)	-30.6 (2.4)	0.83 (0.01)
<i>A. smithii</i>	291	479 (12)	26.1 (0.1)	1.32 (0.02)	-14.2 (4.9)	0.72 (0.01)
<i>T. laurina</i>	137	445 (15)	26.1 (0.2)	1.24 (0.03)	-27.8 (5.9)	0.72 (0.02)
<i>S. woollsii</i>	140	529 (9)	26.0 (0.2)	1.31 (0.02)	10.4 (3.7)	0.84 (0.01)
<i>H. trifoliolata</i>	98	679 (25)	27.3 (0.2)	1.29 (0.03)	63.4 (9.1)	0.86 (0.01)
<i>C. australe</i>	123	737 (25)	29.0 (0.2)	1.42 (0.02)	78.2 (8.6)	0.82 (0.01)
<i>A. scholaris</i>	61	956 (35)	30.2 (0.2)	1.44 (0.05)	144.4 (11.7)	0.83 (0.02)

The greater reductions in net photosynthesis with increasing VPD in well-watered plants shown by the tropical species than the temperate species suggests that the tropical species will experience substantial midday reductions in net photosynthesis during summer. These midday reductions in net photosynthesis in the tropical species may result in reductions in growth when soil water is still available. This is likely to be a successful strategy in the tropics due to the long warm growing season but not in the temperate climate where the growing season is considerably shorter.

Previous studies of the effects of VPD on growth in well-watered plants have concentrated on herbaceous crops. Reducing VPD from 2.0 to 1.0 kPa usually improves growth of these crops. In contrast, further reductions in VPD down to 0.2 kPa have little effect on growth (Hoffman 1979; Grange & Hand 1987). The few published studies of trees and shrubs have shown both increases in growth rate and no response to a decrease in VPD (Mortensen 1986; Salim 1989; Ball *et al.* 1997; Darlington *et al.* 1997).

The increase in growth of plants under lower VPD is attributed to changes in physiology. Firstly, lowering VPD will increase stomatal aperture leading to greater stomatal conductance and to an increased net photosynthesis. Secondly, the transpiration rate of leaves is known to decrease with decreasing VPD (Lösch 1979; Schulze & Hall 1982). Decreases in transpiration rate have been shown to increase cell turgor pressure (Shackel *et al.* 1987; Frensch & E.-D. 1988). Cell and leaf expansion rates are known to be dependent on cell turgor pressure (Cosgrove 1986). Expansion rates have been shown to increase with decreased VPD over short time scales (Ben Haj Salah & Tardieu 1996; Stirzaker *et al.* 1997; Clifton-Brown & Jones 1999). Therefore, the improved water status of leaves under low VPD may lead to increases in the rate of photosynthesis and growth.

Changes in allocation of biomass with VPD may explain the greater growth rate of plants under low VPD. Trees show an increased allocation to shoots when grown under a reduced VPD (Hogan *et al.* 1994; Marsden *et al.* 1996; Darlington *et al.* 1997). Increases in leaf area ratio and reductions in specific leaf area have been shown when plants are grown at low VPD (Grange & Hand 1987; van de Sanden & Veen 1992; Ball

et al. 1997). These reductions in allocation to non-photosynthetic tissues should lead to an increase in growth.

Studies of horticultural crops have shown detrimental effects of very low VPD (<0.5 kPa) on growth. Firstly, the increased water vapour can lead to increased incidence of plant diseases (Grange & Hand 1987). Secondly, the reduced transpiration associated with low VPD results in reduced water transport within the plant. This can lead to reduced uptake of nutrients from the soil and result in symptoms of nutrient deficiency (Bakker 1984; Murtadha *et al.* 1989; Salim 1989). Thirdly, the suppression of transpirational cooling under low VPD means leaf temperatures can rise to lethal levels (Lipton 1970; Bakker 1985).

The sensitivity of net photosynthesis to VPD shown by the tropical species suggests that their growth may be reduced at high VPD. Previous studies of the effect of VPD on the growth of plants show a general trend of reduced growth at higher VPD. However, this work has concentrated on herbaceous crops and may not translate into large differences in the growth of tree species. This experiment aimed to determine the growth responses of temperate and tropical rainforest trees to different values of VPD in the absence of soil water stress. The specific hypotheses were:

1. The growth rate of temperate species will be unaffected by VPD whereas tropical species will show a reduced growth rate under high VPD compared with low VPD.
2. Temperate species will allocate more biomass to roots than tropical species.

To test these hypotheses seedlings of the rainforest species were grown under either ambient conditions or low VPD in glasshouses.

METHODS

Seedlings of the eight species were grown for a year in glasshouses under either ambient VPD or a constant low VPD. A subset of these seedlings were also used for the photosynthetic measurements discussed in Chapter 7. For a detailed description of the growing conditions within the glasshouses refer to Chapter 7.

At the beginning of the experiment, ten seedlings of each of the species were harvested to determine initial biomass. For *Sloanea woollsii*, only eight seedlings were harvested due to the low numbers available. The seedlings were separated into leaves, petioles, stems and roots to be dried and weighed separately. The total leaf area of each seedling was measured from the fresh leaves using image analysis (BIOSCANTM Image Analyzer).

Each of the treatments was housed within two separate glasshouses. Ten seedlings of each species were placed randomly within each glasshouse. The two exceptions to this were *Eucryphia lucida* for which five seedlings were placed in each glasshouse and *S. woollsii* for which four seedlings were placed in each glasshouse. Seedlings were grown for a year and then harvested in the same manner as the initial harvest.

The vapour pressure deficit within each glasshouse was measured every two months using paired temperature and humidity dataloggers. Two sets of datalogger were available so measurements for each glasshouse were taken on two randomly selected days over four days each month. The seasonal changes in mean and maximum daytime VPD in the glasshouses are shown in Figure 8.1. The low VPD treatment maintained low values throughout the year whereas the ambient treatment showed higher values of VPD during the warmer months.

Data analysis

The biomass and leaf area data were used to calculate relative growth rates (RGR), root/shoot ratio, specific leaf area (SLA), leaf weight ratio (LWR), leaf area ratio (LAR) and net assimilation rate (NAR) using the equations listed in the methods of Chapter 5. These parameters were analysed as a split-plot design, with growth VPD as the effect between glasshouses and taxonomic as the effect within glasshouses.

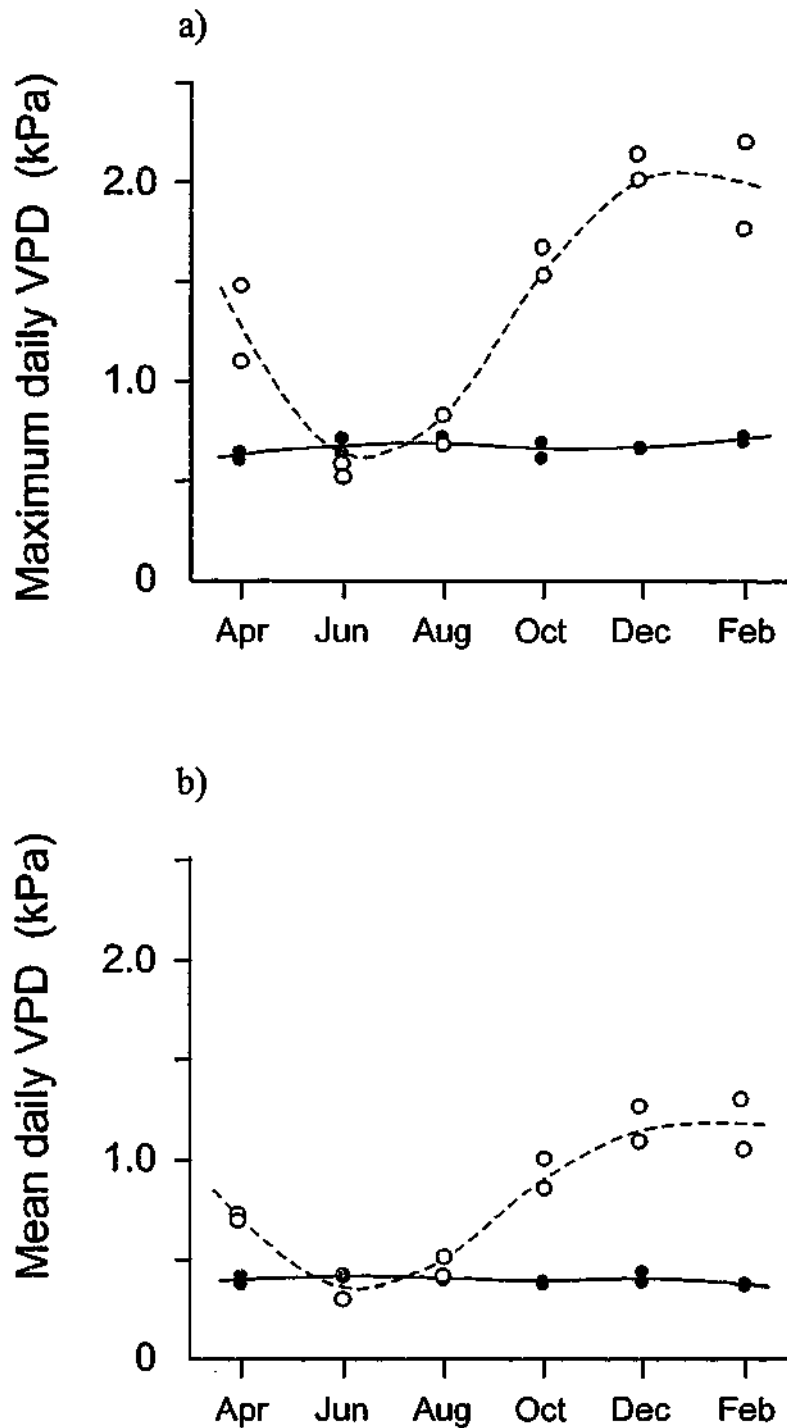


Figure 8.1 The values of a) maximum daytime VPD and b) mean daytime VPD recorded in the ambient (---○---) and the low VPD (—●—) glasshouses during the experiment. Smoother functions were fitted to show the seasonal trends in VPD. Points are means of two days for each glasshouse.

RESULTS

None of the growth parameters measured differed significantly between the ambient and low VPD growth regimes (Table 8.2). There was a trend of a greater relative growth rate in plants grown under low VPD compared with ambient VPD (Table 8.3).

However, this increase in relative growth rate with lowered VPD was less than 10% for all species. Similarly, many species showed an increase in the size of leaves when grown under low VPD compared with ambient VPD which was also less than 10% (Table 8.4). In contrast, significant differences were shown in all growth parameters among the species.

The temperate species showed some of the highest relative growth rates achieved over the year (Table 8.3). The cool-temperate and warm-temperate rainforest types showed significantly higher growth rates than the two tropical rainforest types under ambient conditions (Figure 8.2a). When grown under low VPD, the relative growth rate of the cool-temperate rainforest type was only significantly higher than that of the tropical rainforest type (Figure 8.2b). The relative growth rate of the temperate group was significantly higher than the tropical group when grown under ambient conditions ($F = 76643, p < 0.01$) whereas the rate of the temperate group was only nearly significantly higher when grown under low VPD ($F = 103, p = 0.06$).

The net assimilation rates of the temperate species were among the highest recorded (Table 8.5). Under ambient conditions, the net assimilation rates of the cool-temperate and warm-temperate rainforest types were among the highest (Figure 8.3a). A similar pattern was shown under low VPD but the difference among the rainforest types was only nearly significant (Figure 8.3b). Similarly, the net assimilation rate of the temperate group was significantly higher than the tropical group when grown under ambient conditions ($F = 257, p = 0.04$) whereas this difference was only nearly significantly higher when grown under low VPD ($F = 91.7, p = 0.07$).

Table 8.2 Results of split-plot ANOVAs for the various parameters measured during the growth experiment.

Parameter	Hypothesis test	<i>F</i>	<i>p</i>
RGR	vpd	1.42	0.36
	species	81.1	< 0.01
	vpd × species	0.29	0.95
NAR	vpd	1.20	0.39
	species	14.2	< 0.01
	vpd × species	0.76	0.63
LAR	vpd	0.45	0.57
	species	14.3	< 0.01
	vpd × species	2.12	0.11
leaf size	vpd	0.79	0.47
	species	1071	< 0.01
	vpd × species	0.43	0.87
LWR	vpd	0.08	0.80
	species	84.6	< 0.01
	vpd × species	4.54	0.01
SLA	vpd	1.19	0.39
	species	25.1	< 0.01
	vpd × species	2.72	0.05
Root/shoot	vpd	0.11	0.77
	species	23.3	< 0.01
	vpd × species	2.45	0.07
LA/root mass	vpd	0.03	0.88
	species	89.3	< 0.01
	vpd × species	6.31	< 0.01

Table 8.3 Relative growth rate ($\text{mg g}^{-1} \text{day}^{-1}$) of the species grown under ambient and low VPD. Values are means of two glasshouses with standard errors in brackets. The results of the random complete block ANOVA within each treatment are given. Letters denote non-significant groupings of means.

Growth VPD			
Species		ambient	low
<i>E. lucida</i>		10.32 (0.84) ^a	11.01 (0.26) ^{ab}
<i>N. cunninghamii</i>		10.07 (0.97) ^a	10.91 (0.55) ^{ab}
<i>A. smithii</i>		7.23 (0.07) ^b	7.89 (0.01) ^b
<i>T. laurina</i>		11.33 (0.25) ^a	11.95 (0.19) ^a
<i>S. woollsii</i>		7.99 (0.92) ^b	8.19 (0.50) ^b
<i>H. trifoliolata</i>		7.78 (0.33) ^b	7.84 (0.04) ^b
<i>C. australe</i>		3.73 (0.20)	3.90 (0.14)
<i>A. scholaris</i>		8.06 (0.05) ^b	8.71 (0.02) ^b
species	<i>F</i>	77.7	20.1
	<i>p</i>	< 0.01	< 0.01
glasshouse	<i>F</i>	1.19	5.78
	<i>p</i>	0.31	0.05

Table 8.4 Size of individual leaves (cm^2) of the species grown under ambient and low VPD. Values are means of two glasshouses with standard errors in brackets. The results of the random complete block ANOVA within each treatment are given. Letters denote non-significant groupings of means. The data were log-transformed for analysis whereas the data presented are untransformed.

Growth VPD		
Species	ambient	low
<i>E. lucida</i>	2.77 (0.03)	3.02 (0.07)
<i>N. cunninghamii</i>	0.90 (0.05)	0.96 (0.05)
<i>A. smithii</i>	8.86 (1.12) ^c	9.11 (0.22) ^c
<i>T. laurina</i>	7.07 (0.21) ^c	7.67 (0.74) ^c
<i>S. woollsii</i>	49.15 (0.43) ^a	46.29 (4.70) ^a
<i>H. trifoliolata</i>	16.43 (0.42) ^b	17.62 (1.15) ^b
<i>C. australe</i>	15.64 (1.04) ^b	15.36 (0.96) ^b
<i>A. scholaris</i>	45.38 (1.33) ^a	49.10 (3.77) ^a
species	<i>F</i>	735
	<i>p</i>	< 0.01
glasshouse	<i>F</i>	3.32
	<i>p</i>	0.11

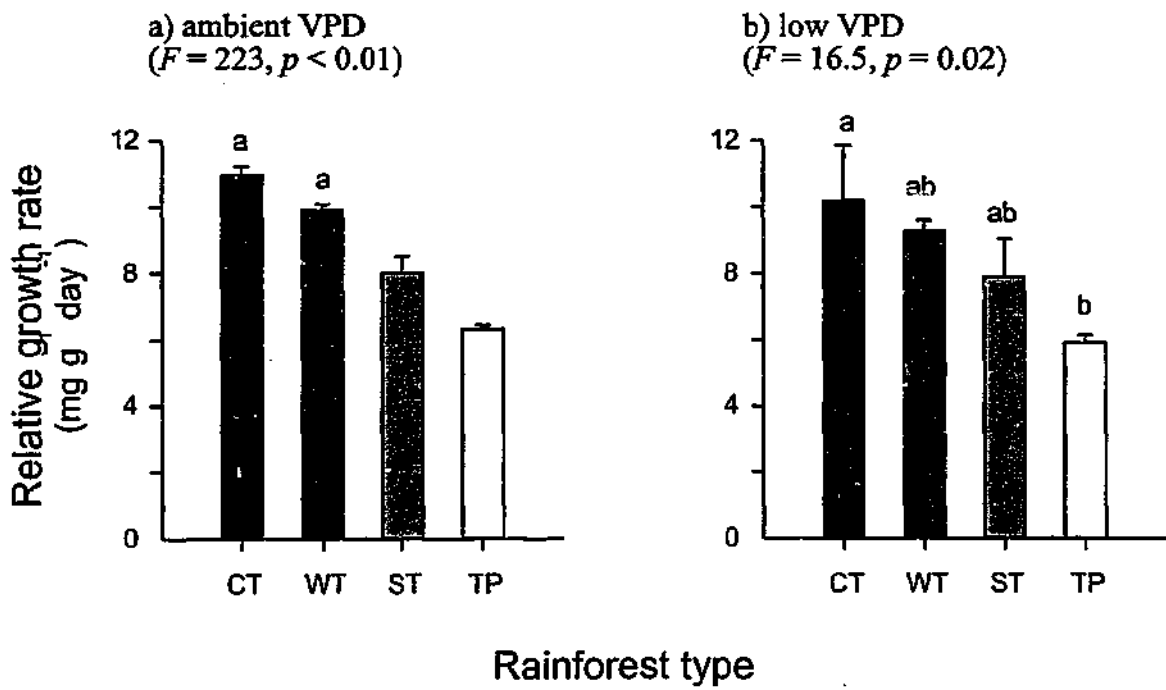


Figure 8.2 Relative growth rate of the rainforest types grown under ambient and low VPD. The rainforest types are labelled as follows: cool-temperate (CT), warm-temperate (WT), subtropical (ST) and tropical (TP). Values are means of two glasshouses with bars representing one standard error.

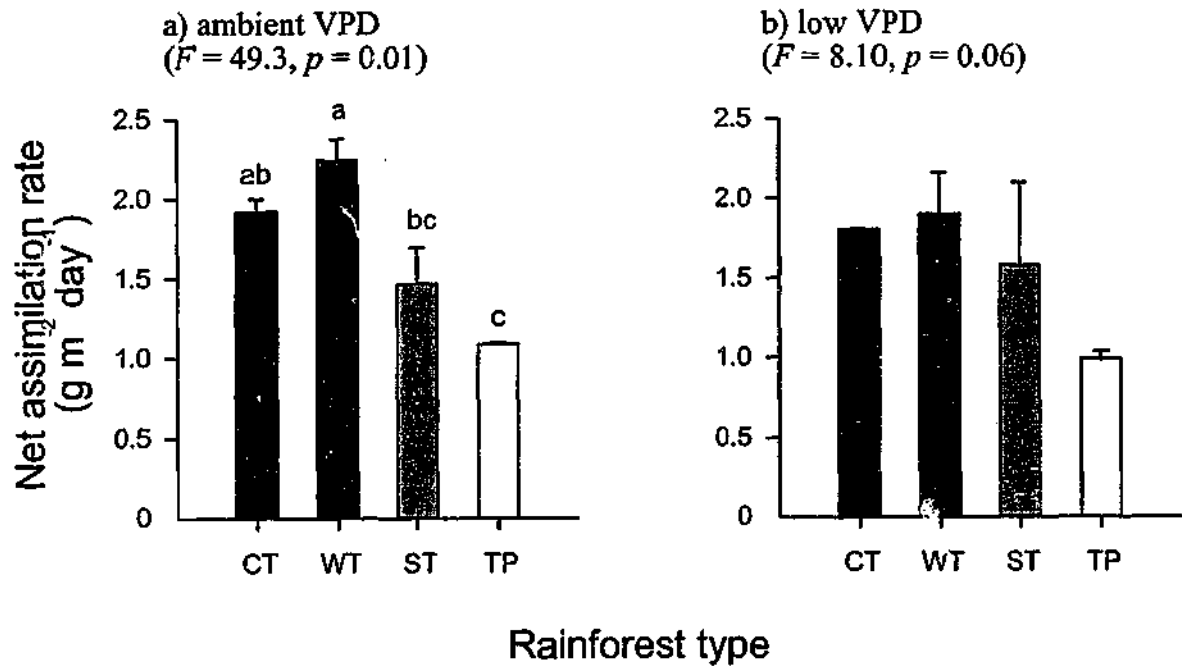


Figure 8.3 Net assimilation rate of the rainforest types grown under ambient and low VPD. The rainforest types are labelled as in Figure 8.2. Values are means of two glasshouses with bars representing one standard error.

Table 8.5 Net assimilation rate ($\text{g m}^{-2} \text{ day}^{-1}$) of the species grown under ambient and low VPD. Values are means of two glasshouses with standard errors in brackets. The results of the random complete block ANOVA within each treatment are given. Letters denote non-significant groupings of means.

		Growth VPD	
Species		ambient	low
<i>E. lucida</i>		1.89 (0.16) ^{abcd}	1.86 (0.25)
<i>N. cunninghamii</i>		1.96 (0.08) ^{abc}	1.74 (0.24)
<i>A. smithii</i>		2.08 (0.15) ^{ab}	1.61 (0.10)
<i>T. laurina</i>		2.41 (0.01) ^a	2.19 (0.18)
<i>S. woollsii</i>		1.56 (0.15) ^{bcd}	1.81 (0.49)
<i>H. trifoliolata</i>		1.37 (0.09) ^{bcd}	1.35 (0.08)
<i>C. australe</i>		0.85 (0.01) ^d	0.84 (0.08)
<i>A. scholaris</i>		1.33 (0.03) ^{cd}	1.13 (0.02)
species	<i>F</i>	23.0	3.98
	<i>p</i>	< 0.01	0.05
glasshouse	<i>F</i>	1.12	1.60
	<i>p</i>	0.32	0.25

The values of leaf area ratios (LAR) of the species ranged from 3.1 to 5.6 m² kg⁻¹ (Table 8.6). The values shown by both temperate and tropical species covered this range. Significant differences in LAR were only shown among the species when grown under ambient conditions due to a significant effect of glasshouse when grown under low VPD. The rainforest types showed an overall significant difference in LAR ($F = 5.98$, $p = 0.03$) but no significant differences were shown within either the ambient ($F = 4.26$, $p = 0.13$) or low VPD ($F = 3.41$, $p = 0.17$) treatments. Similarly, the climatic groups showed no overall significant difference in LAR ($F = 1.17$, $p = 0.39$).

Table 8.6 Leaf area ratio (m² kg⁻¹) of the species grown under ambient and low VPD. Values are means of two glasshouses with standard errors in brackets. The results of the random complete block ANOVA within each treatment are given. Letters denote non-significant groupings of means.

Species	Growth VPD	
	ambient	low
<i>E. lucida</i>	4.80 (0.40) ^{ab}	4.52 (0.22)
<i>N. cunninghamii</i>	5.21 (0.08) ^a	5.59 (0.29)
<i>A. smithii</i>	3.10 (0.28) ^b	4.37 (0.58)
<i>T. laurina</i>	4.63 (0.11) ^{ab}	4.94 (0.25)
<i>S. woollsii</i>	4.07 (0.17) ^{ab}	3.64 (0.60)
<i>H. trifoliolata</i>	5.35 (0.49) ^a	5.39 (0.07)
<i>C. australe</i>	3.79 (0.19) ^{ab}	3.59 (0.15)
<i>A. scholaris</i>	4.64 (0.24) ^{ab}	5.04 (0.20)
species	<i>F</i>	7.42
	<i>p</i>	0.01
glasshouse	<i>F</i>	1.03
	<i>p</i>	0.35

The size of leaves ranged from 1 to 9 cm² in the temperate species and 15 to 49 cm² in the tropical species (Table 8.4). Consequently, the tropical species had leaves of significantly larger size under both treatments. There were distinct differences in the size of leaves of the rainforest types: the tropical and subtropical groups having the largest leaves, the warm-temperate group having smaller leaves and the cool-temperate group having the smallest leaves (Figure 8.4). Therefore, the size of leaves of the tropical group were very significantly larger than those of the temperate group ($F = 1.6 \times 10^5$, $p < 0.01$).

The temperate and tropical species showed similar values of leaf weight ratio (LWR) ranging between 0.3 and 0.5 g g⁻¹ (Table 8.7). There were significant differences among the species within the treatments but the trends were not consistent between glasshouses. The tropical rainforest type showed a significantly lower LWR than the other rainforest types when grown under ambient conditions (Figure 8.5). In contrast, the LWR of the tropical rainforest type was only significantly lower than that of the warm-temperate rainforest type when grown under a low VPD. Similarly, the tropical group showed a significantly lower LWR under ambient conditions ($F = 1225$, $p = 0.02$) but not under low VPD ($F = 17.0$, $p = 0.15$).

Values of specific leaf area (SLA) ranged from 10 to 19 m² kg⁻¹ and there were several significant differences among species (Table 8.8). The tropical rainforest type showed the largest SLA but it was only significantly greater than the warm-temperate rainforest type (Figure 8.6). There was an overall significant difference between the SLA of the climatic groups ($F = 29.6$, $p = 0.03$) but not separately under ambient ($F = 16.8$, $p = 0.15$) or low VPD conditions ($F = 17.5$, $p = 0.15$).

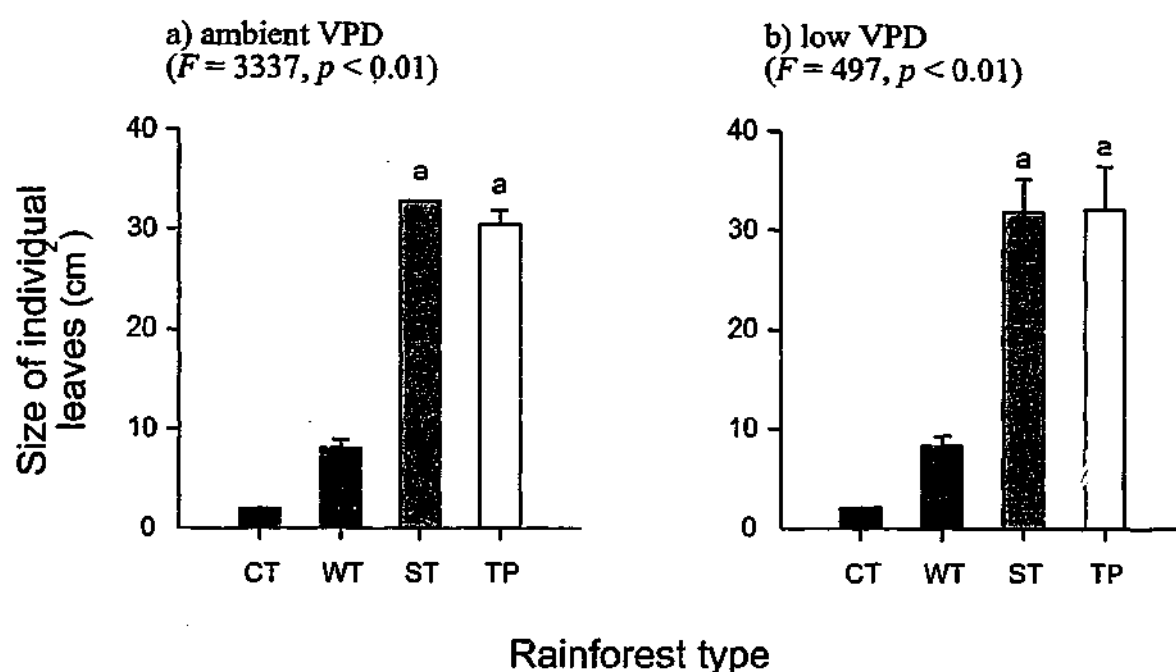


Figure 8.4 Leaf size of the rainforest types grown under ambient and low VPD. The rainforest types are labelled as in Figure 8.2. Values are means of two glasshouses with bars representing one standard error. Data were log-transformed for analysis whereas the data presented above are the raw values.

Table 8.7 Leaf weight ratio (g g^{-1}) of the species grown under ambient and low VPD. Values are means of two glasshouses with standard errors in brackets. The results of the random complete block ANOVA within each treatment are given.

Species		Growth VPD	
		ambient	low
<i>E. lucida</i>		0.39 (0.02)	0.38 (0.04)
<i>N. cunninghamii</i>		0.41 (0.02)	0.36 (0.03)
<i>A. smithii</i>		0.29 (0.03)	0.33 (0.02)
<i>T. laurina</i>		0.47 (0.02)	0.52 (0.00)
<i>S. woollsii</i>		0.31 (0.02)	0.29 (0.04)
<i>H. trifoliolata</i>		0.47 (0.02)	0.47 (0.00)
<i>C. australe</i>		0.31 (0.01)	0.29 (0.01)
<i>A. scholaris</i>		0.26 (0.01)	0.32 (0.00)
species	<i>F</i>	172.2	26.4
	<i>p</i>	< 0.01	< 0.01
glasshouse	<i>F</i>	60.0	10.2
	<i>p</i>	< 0.01	0.02

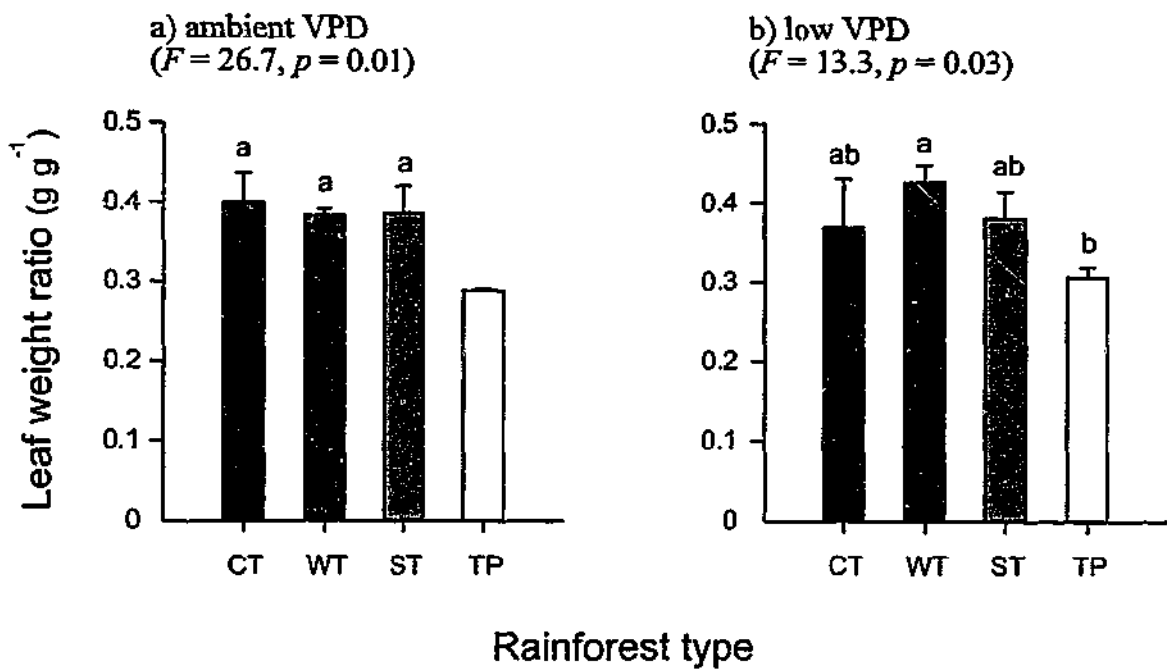


Figure 8.5 Leaf weight ratio of the rainforest types grown under ambient and low VPD. The rainforest types are labelled as in Figure 8.2. Values are means of two glasshouses with bars representing one standard error.

Table 8.8 Specific leaf area ($\text{m}^2 \text{kg}^{-1}$) of the species grown under ambient and low VPD. Values are means of two glasshouses with standard errors in brackets. The results of the random complete block ANOVA within each treatment are given. Letters denote non-significant groupings of means.

Species	Growth VPD	
	ambient	low
<i>E. lucida</i>	13.0 (0.5) ^b	13.1 (0.8) ^{abc}
<i>N. cunninghamii</i>	12.9 (0.9) ^b	15.4 (0.4) ^{ab}
<i>A. smithii</i>	10.9 (0.1) ^b	13.2 (0.6) ^{abc}
<i>T. laurina</i>	10.4 (0.1) ^b	10.0 (0.5) ^c
<i>S. woollsii</i>	14.4 (0.5) ^{ab}	13.5 (0.4) ^{abc}
<i>H. trifoliolata</i>	12.1 (0.7) ^b	12.1 (0.2) ^{bc}
<i>C. australe</i>	14.8 (0.3) ^{ab}	15.0 (0.0) ^{ab}
<i>A. scholaris</i>	18.7 (1.4) ^a	16.8 (0.8) ^a
species	<i>F</i>	13.2
	<i>p</i>	< 0.01
glasshouse	<i>F</i>	0.17
	<i>p</i>	0.69

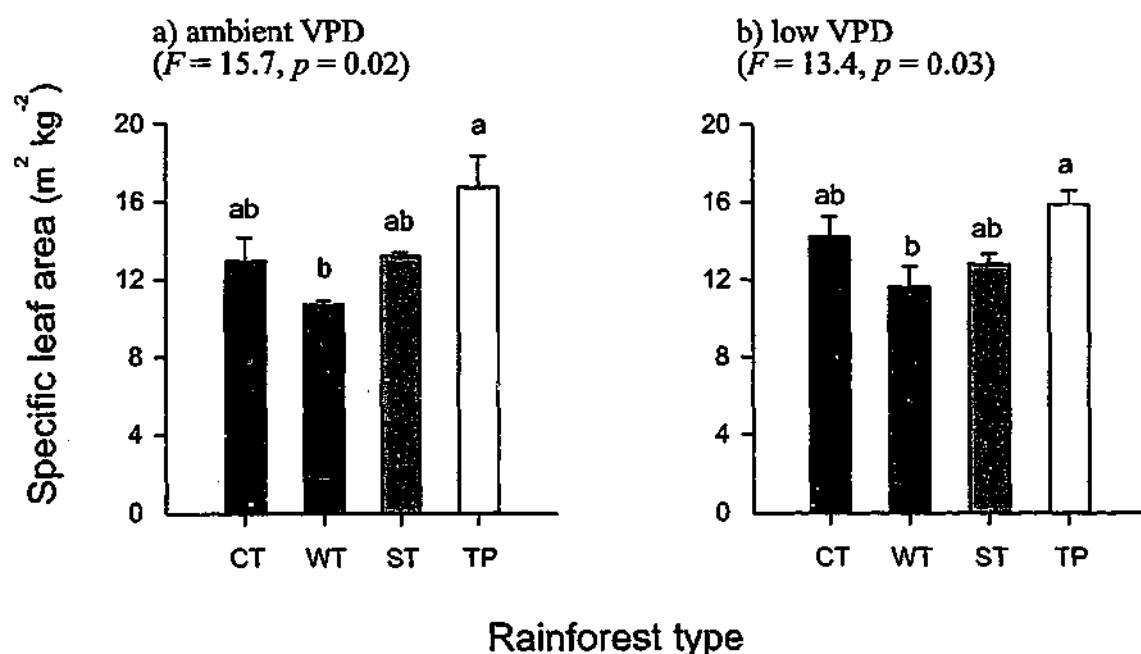


Figure 8.6 Specific leaf area of the rainforest types grown under ambient and low VPD. The rainforest types are labelled as in Figure 8.2. Values are means of two glasshouses with bars representing one standard error.

Root/shoot ratios ranged from 0.16 g g⁻¹ in *Eucryphia lucida* to 1.12 g g⁻¹ in *Acmena smithii* (Table 8.9). The temperate and tropical species showed a similar range of root/shoot ratios. The root/shoot ratio of cool-temperate rainforest type was significantly lower than the other rainforest types under ambient conditions but was only significantly lower than the subtropical rainforest type under low VPD (Figure 8.7). The temperate and tropical groups nearly had significantly different values of root/shoot ratio ($F = 19.5, p = 0.05$).

Values of leaf area per root mass ranged from 9 m² kg⁻¹ in *S. woollsii* to 39 m² kg⁻¹ in *E. lucida* (Table 8.10). There were only significant differences in leaf area/root mass among species under ambient conditions, as trends were not consistent between glasshouses under low VPD. The cool-temperate rainforest type showed the greatest leaf area/root mass ratio under both treatments (Figure 8.8). However, the leaf area/root mass ratio of the cool-temperate rainforest type was not significantly different from that of the warm-temperate rainforest type when grown under low VPD. The temperate group showed a significantly greater leaf area/root mass ratio than the tropical group under low VPD ($F = 678, p = 0.02$) but not under ambient conditions ($F = 53.7, p = 0.09$).

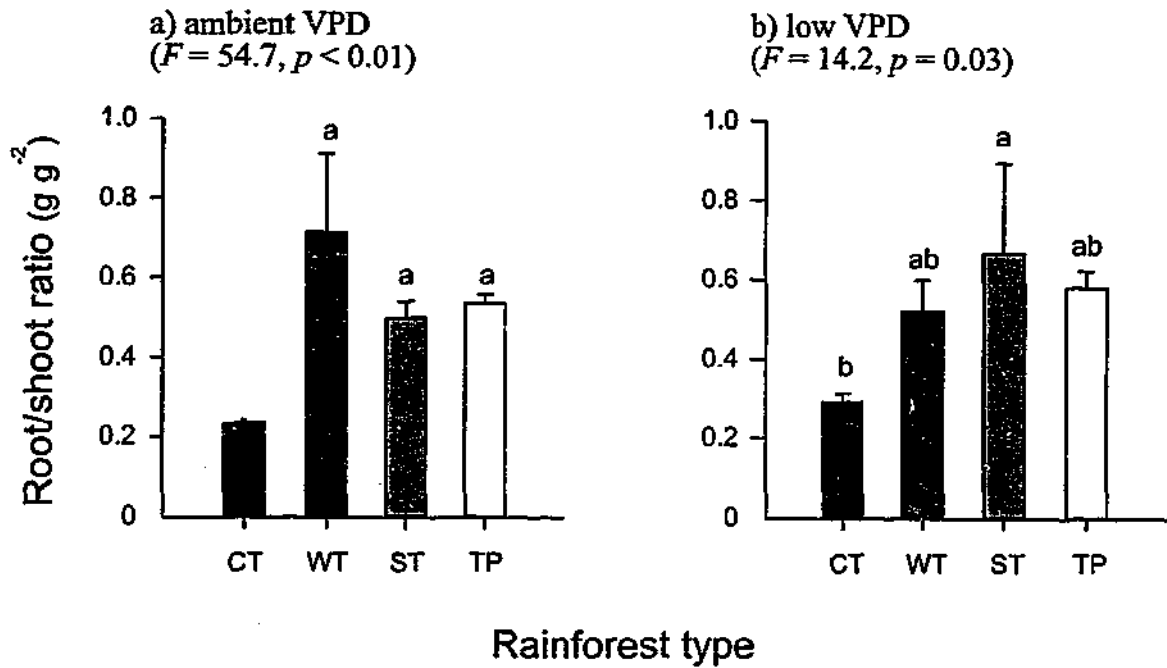


Figure 8.7 Root/shoot ratio of the rainforest types grown under ambient and low VPD. The rainforest types are labelled as in Figure 8.2. Values are means of two glasshouses with bars representing one standard error. The data were log-transformed for statistical analysis whereas the data are presented untransformed.

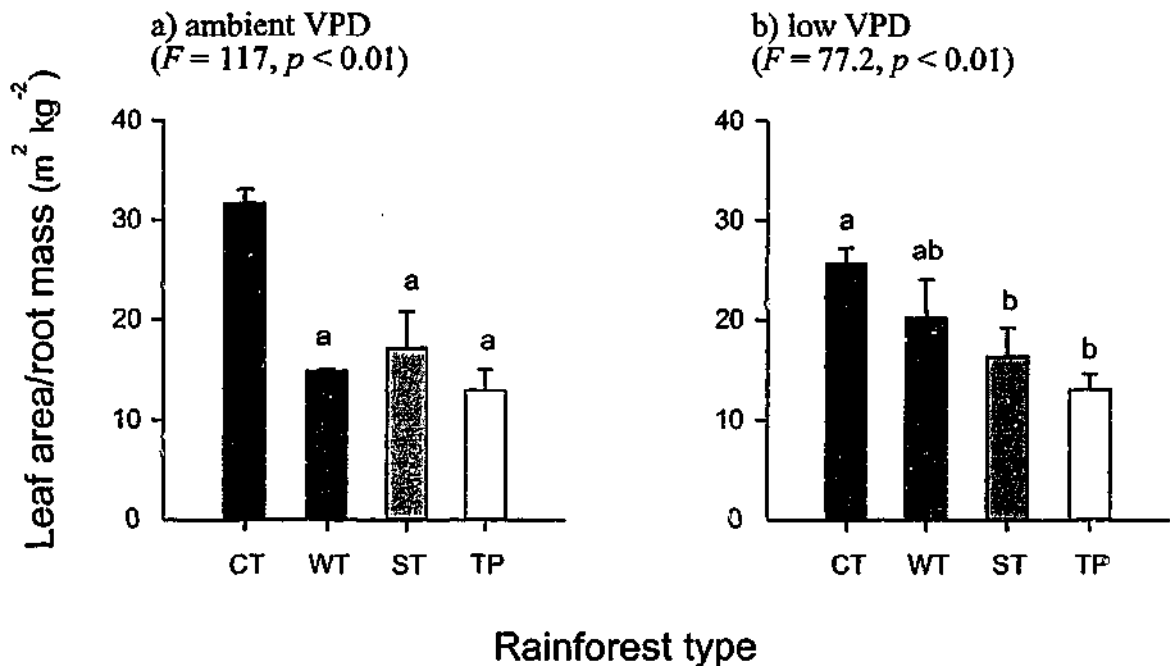


Figure 8.8 Leaf area/root mass of the rainforest types grown under ambient and low VPD. The rainforest types are labelled as in Figure 8.2. Values are means of two glasshouses with bars representing one standard error.

Table 8.9 Root/shoot ratio (g g^{-1}) of the species grown under ambient and low VPD. Values are means of two glasshouses with standard errors in brackets. The results of the random complete block ANOVA within each treatment are given. Letters denote non-significant groupings of means. The data were log-transformed for analysis whereas the data presented are untransformed.

Growth VPD		
Species	ambient	low
<i>E. lucida</i>	0.16 (0.03)	0.19 (0.02) ^e
<i>N. cunninghamii</i>	0.39 (0.00) ^c	0.31 (0.02) ^{bcd}
<i>A. smithii</i>	1.12 (0.24) ^a	0.79 (0.08) ^a
<i>T. laurina</i>	0.31 (0.02) ^c	0.25 (0.01) ^{de}
<i>S. woollsii</i>	0.69 (0.02) ^{ab}	1.01 (0.23) ^a
<i>H. trifoliolata</i>	0.31 (0.02) ^c	0.32 (0.02) ^{cde}
<i>C. australe</i>	0.55 (0.01) ^{abc}	0.65 (0.00) ^{ab}
<i>A. scholaris</i>	0.53 (0.01) ^{bc}	0.51 (0.05) ^{abc}
species	<i>F</i>	34.7
	<i>p</i>	< 0.01
glasshouse	<i>F</i>	2.08
	<i>p</i>	0.19

Table 8.10 Leaf area/root mass ($\text{m}^2 \text{kg}^{-1}$) of the species grown under ambient and low VPD. Values are means of two glasshouses with standard errors in brackets. The results of the random complete block ANOVA within each treatment are given. Letters denote non-significant groupings of means.

		Growth VPD	
Species		ambient	low
<i>E. lucida</i>		39.1 (2.0)	30.1 (1.0)
<i>N. cunninghamii</i>		24.3 (0.4) ^a	21.3 (0.8)
<i>A. smithii</i>		7.5 (1.4) ^b	13.7 (3.7)
<i>T. laurina</i>		22.2 (1.2) ^a	26.7 (0.5)
<i>S. woollsii</i>		10.3 (0.4) ^b	8.7 (1.8)
<i>H. trifoliolata</i>		24.0 (3.6) ^a	24.0 (1.3)
<i>C. australe</i>		11.4 (1.0) ^b	9.7 (0.2)
<i>A. scholaris</i>		14.4 (1.2) ^{ab}	16.5 (1.8)
species	<i>F</i>	49.4	45.3
	<i>p</i>	< 0.01	< 0.01
glasshouse	<i>F</i>	3.57	10.6
	<i>p</i>	0.10	0.01

There were several significant Pearson correlations between the various growth variables and the percentage reduction in net photosynthesis with increasing VPD (PRP, Table 8.11). The growth variables that showed significant Pearson correlations with PRP were those that differentiated the temperate and tropical species. That is, the higher RGR, NAR, and LA/root mass and the lower size of leaves and root/shoot ratio of temperate species compared with tropical species.

Table 8.11 Pearson correlation values of growth variables with Percentage change in net photosynthesis with increasing vapour pressure deficit (% 1kPa^{-1}) for species grown under a low or ambient vapour pressure deficit. Unadjusted probabilities are given in brackets and variables that were log-transformed to improve normality of the data are denoted \log_e .

Growth parameter	ambient	low
RGR	0.67 (0.07)	0.78 (0.02)
NAR	0.67 (0.07)	0.75 (0.03)
LAR	0.46 (0.25)	0.63 (0.10)
\log_e leaf size	-0.86 (0.21)	-0.51 (0.20)
LWR	0.66 (0.01)	0.68 (0.07)
\log_e SLA	-0.63 (0.08)	-0.53 (0.18)
\log_e root/shoot	-0.45 (0.27)	-0.71 (0.05)
LA/root mass	0.64 (0.09)	0.76 (0.03)

DISCUSSION

Effect of vapour pressure deficit on growth

There was no significant effect of VPD on any of the growth parameters measured (Table 8.2). All species showed non-significant increases in relative growth rate of less than 10% when grown under low VPD (Table 8.3). A survey of previously published studies on the effect of VPD on well-watered plants reveals two thirds of species show increases in growth at lower VPD but many of these increases are non-significant (Table 8.12). Acock (1974) suggested that low VPD has a short-term beneficial effect but a long-term detrimental effect on growth. However, this has not been tested as the length of most studies was less than two months. Furthermore, none of these studies investigated the effect of long-term versus short-term exposure to low VPD in the same species.

The majority of the above studies were of herbaceous crops, which are unlikely to respond the same way as canopy trees. A direct comparison of tree species found that the more mesic species *Picea mariana* showed no response to decreased VPD whereas the drought avoiding species *Pinus banksiana* showed a significant increase in growth (Darlington *et al.* 1997). However, these species are conifers, which possess different water conducting tissues to angiosperms, and are therefore likely to show different responses to VPD. In contrast, the tropical rainforest tree *Theobroma cacao* showed decreased growth under lower VPD (Sale 1970). The shrubs in which the response of growth to VPD has been studied include two species of mangroves (*Rhizophora apiculata* and *R. stylosa*), a desert shrub (*Atriplex spongiosa*) and a horticultural shrub (*Euphorbia pulcherrima*). Interestingly, the mangrove species showed the opposite trend to that of the conifers, with the species from the more humid environment showing a greater responsiveness to changes in VPD (Ball *et al.* 1997). It is not possible to make general conclusions about the growth response to VPD of woody species from different environments due to the diverse range and limited number of species in previous studies.

Table 8.12 The percentage increase in growth at low VPD recorded in previous studies. Growth measures included total biomass (TOT) and relative growth rate (RGR). ns = a statistically non-significant result.

Species	% increase in growth at low VPD	VPD range (kPa)	Growth measurement	Growth period (days)	Source
<u>Grasses</u>					
<i>Oryza sativa</i>	89	0.7 - 2.1	TOT	28	Kawamitsu <i>et al.</i> (1993)
<i>Panicum maximum</i>	54	0.7 - 2.1	TOT	28	Kawamitsu <i>et al.</i> (1993)
<i>Triticum aestivum</i>	- 7 ns	0.2 - 1.3	TOT	56	Ford & Thorne (1974)
<u>Herbaceous</u>					
<i>Begonia hiemalis</i>	47	0.2 - 0.9	TOT	60	Mortensen (1986)
<i>Beta vulgaris</i>	41 ns	0.2 - 1.3	TOT	56	Ford & Thorne (1974)
<i>Brassica oleracea</i>	55	0.2 - 1.3	TOT	56	Ford & Thorne (1974)
<i>Campanula isophylla</i>	0	0.2 - 0.9	TOT	70	Mortensen (1986)
<i>Chrysanthemum morifolium</i>	31	0.2 - 0.9	TOT	45	Mortensen (1986)
<i>Cirsium arvense</i>	68	0.1 - 1.4	TOT	60	Hunter <i>et al.</i> (1985)
<i>Cucumis sativus</i>	13	0.2 - 1.4	RGR	23	van de Sanden & Veen (1992)
<i>Dendranthema grandiflora</i>	0 - 14 ns	0.1 - 1.1	TOT	56	Hand <i>et al.</i> (1996)

Table 8.12 (continued).

Species	% increase in growth		Growth measurement	Growth period	
	at low VPD	VPD range (kPa)		(days)	Source
<i>Glycine max</i>	- 23	0.8 - 2.2	TOT	90	Woodward & Begg (1976)
<i>Helianthus annuus</i>	17 ns	0.3 - 2.2	RGR	11	Salim (1989)
<i>Ipomoea batatas</i>	24	0.6 - 1.9	RGR	120	Mortley <i>et al.</i> (1994)
<i>Lactuca sativa</i>	0	0.2 - 0.9	TOT	40	Mortensen (1986)
<i>Lycopersicon esculentum</i>	20	0.2 - 0.9	TOT	33	Mortensen (1986)
<i>Phaseolus vulgaris</i>	- 6 ns	0.3 - 2.2	RGR	11	Salim (1989)
<i>Rosa</i> spp.	0	0.2 - 0.9	TOT	50	Mortensen (1986)
<i>Saintpaula ionantha</i>	17 - 36	0.2 - 0.9	TOT	80	Mortensen (1986)
<i>Solanum tuberosum</i>	4 ns	0.4 - 1.2	TOT	56	Wheeler <i>et al.</i> (1989)
<i>Soleirolia soleirolia</i>	- 19	0.2 - 0.9	TOT	53	Mortensen (1986)
<i>Vigna radiata</i>	6 ns	0.3 - 2.2	RGR	11	Salim (1989)

Table 8.12 (continued).

Species	% increase	VPD range (kPa)	Growth measurement	Growth period	Source
	in growth			(days)	
Ferns					
<i>Nephrolepis exaltata</i>	75	0.4 - 2.2	TOT	40	Dawson <i>et al.</i> (1991)
<i>Nephrolepis cordifolia</i>	113	0.4 - 2.2	TOT	40	Dawson <i>et al.</i> (1991)
Trees and shrubs					
<i>Atriplex spongiosa</i>	47 ns	0.3 - 2.2	RGR	11	Salim (1989)
<i>Euphorbia pulcherrima</i>	31	0.2 - 0.9	TOT	67	Mortensen (1986)
<i>Picea mariana</i>	14 ns	0.6 - 2.3	RGR	28	Darlington <i>et al.</i> (1997)
<i>Pinus banksiana</i>	108	0.6 - 2.3	RGR	28	Darlington <i>et al.</i> (1997)
<i>Rhizophora apiculata</i>	30	0.6 - 2.4	RGR	98	Ball <i>et al.</i> (1997)
<i>Rhizophora stylosa</i>	- 30 ns	0.6 - 2.4	RGR	98	Ball <i>et al.</i> (1997)
<i>Theobroma cacao</i>	- 34	0.3 - 1.6	TOT	378	Sale (1970)

The lack of significant increase in growth of the rainforest species under low VPD could reflect the difference in VPD between the treatments not being large enough. The mean and maximum daytime VPD in the low VPD treatment remained at 0.4 kPa and 0.7 kPa respectively throughout the year (Figure 8.1). In contrast, the ambient treatment had a mean daytime VPD that ranged from 0.3 to 1.2 kPa and a maximum daytime VPD that ranged from 0.6 to 2.1 kPa between winter and summer. Consequently, large differences in VPD between the treatments only occurred during the warmer two-thirds of the year. However, as the majority of growth occurs during the warmer months a difference in growth between the treatments would have been expected if the ambient VPD of a temperate climate significantly affected growth.

The reductions in net photosynthesis with increasing VPD recorded in the previous chapter may not have been large enough to affect the overall growth rate. The mean net photosynthetic rate of plants in both treatments during summer was estimated from the photosynthetic rates shown by plants at instantaneous VPD equal to the mean daytime VPD of the treatments during summer (Table 8.13). That is, the net photosynthetic rate of plants from the ambient and low VPD treatments were estimated from the rate they showed at a VPD of 1.2 kPa and 0.5 kPa respectively. No species showed a significant decrease in the estimated rate of net photosynthesis when grown under ambient conditions compared with a low VPD. *Castanospermum australe* and *Eucryphia lucida* were estimated to show a significant decrease of 12 and 14% in net photosynthesis respectively under ambient summer conditions, which could have caused a significant decrease in growth. In contrast, the two subtropical species were estimated to show a 25% increase in net photosynthesis during summer under ambient conditions compared with low VPD. Therefore, for most species a similarity in the estimated rate of net photosynthesis may explain the similarity of growth rates between the treatments.

Table 8.13 Net photosynthetic rates of species shown at instantaneous VPD equal to mean daytime VPD recorded during summer the two treatments. Net photosynthesis at 0.5 kPa and 1.2 kPa are shown respectively for the plant growing under low and ambient VPD. Values are means of two glasshouses with a standard error given in brackets.

Species	Growth VPD		<i>F</i>	<i>p</i>	% change in net photosynthesis in plants grown under ambient VPD compared with low VPD
	low	ambient			
<i>E. lucida</i>	10.89 (0.40)	9.59 (0.40)	5.27	0.15	- 12.0
<i>N. cunninghamii</i>	7.63 (0.37)	8.03 (0.14)	0.97	0.43	5.2
<i>A. smithii</i>	6.22 (0.25)	6.74 (0.45)	1.02	0.42	4.0
<i>T. laurina</i>	11.85 (0.57)	11.29 (0.33)	0.71	0.49	- 4.7
<i>S. woollsii</i>	3.57 (0.05)	4.49 (0.34)	7.41	0.11	25.8
<i>H. trifoliolata</i>	5.29 (0.09)	7.14 (0.06)	300	<0.01	35.0
<i>C. australe</i>	3.55 (0.53)	3.06 (0.05)	0.12	0.74	- 13.8
<i>A. scholaris</i>	7.94 (0.15)	8.07 (0.20)	0.27	0.66	1.6

An important difference between the two treatments was the amount of water received by plants. During summer, plants in the ambient treatment had to be watered twice as often to maintain the same soil moisture as those in the low VPD treatment. This greater water usage of the plants under the ambient treatment during the summer months suggests a greater transpiration rate. This is not surprising as transpiration rate of leaves increases with increasing VPD (Löscher 1979; Schulze & Hall 1982). The fact that the soil was not allowed to dry out may mean that the water status of the leaves did not fall below the critical level need for expansion to continue. Furthermore, increases in leaf expansion rate due to decreased VPD have been shown to only last for 10-20 minutes (Stirzaker *et al.* 1997; Clifton-Brown & Jones 1999). Therefore, the difference in VPD between the treatments in summer is unlikely to have affected the daily rate of leaf expansion.

The greater water usage of plants in the ambient treatment during summer suggests a higher rate of nutrient uptake. This is supported by previous findings that plants grown under low VPD (<0.5 kPa) often show calcium deficiency (Bakker 1984; Holder & Cockshull 1990). A study of five horticultural plants found that plants grown at a VPD of 0.2 kPa had significantly lower concentrations of nutrients in their leaves than plants grown at a VPD of 1.0 kPa (Gisleröd *et al.* 1987). Therefore, previous studies have found nutrient deficiencies in plants grown at comparable values of VPD to the low VPD treatment (0.4 kPa). The potentially greater uptake of nutrients under ambient conditions may have lead to an improved growth rate of these plants.

In summary, the lack of a significant effect of lowering VPD on the growth of the tropical rainforest species when well-watered has several potential causes. Firstly, the reduction in net photosynthesis was too small to affect the overall growth. Secondly, the cost of a reduced uptake of nutrients in plants grown under low VPD outweighs the benefits of an increased water status of leaves. Thirdly, the lack of a significant increase in the growth of the tropical species with lowered VPD may reflect an inability to improve growth rates at the lower temperatures in the glasshouses relative to a tropical climate. Under temperatures representative of a tropical summer the tropical species may show improved growth with a lowering of the ambient VPD.

In addition to the lack of significant change in growth rate, there were also no significant changes in allocation of biomass under low VPD compared with ambient VPD (Table 8.2). The only trend shown was an increase in the size of individual leaves under low VPD (Table 8.4). Increases in the size of individual leaves with decreasing VPD have been shown in many horticultural species (Ford & Thorne 1974; Hoffman 1979; Mortensen 1986; van de Sanden & Veen 1992). Similarly, the tropical rainforest understorey shrub *Psychotria horizontalis* showed a 35% increase in the size of individual leaves when grown at a site with lower VPD (Hogan *et al.* 1994). In contrast, the tropical rainforest tree *Theobroma cacao* showed a 32% decrease in the size of individual leaves when grown under a lower VPD (Sale 1970). The development of smaller leaves is a common response of plants to reduce water loss under conditions of water stress (Ludlow 1989).

Another response of plants to water stress is to increase the root/shoot ratio by reducing leaf area while increasing root mass (Ludlow 1989). There was no consistent trend in the response of root/shoot ratio to increasing VPD among the rainforest species (Table 8.10). Interestingly, the species with the largest root/shoot ratio under ambient conditions, *Acmena smithii*, also showed the largest change with growth VPD. The few woody plants that have been studied show increases (Marsden *et al.* 1996; Hogan *et al.* 1994), a decrease (Darlington *et al.* 1997) and no response (Salim 1989) of root/shoot ratio to increasing VPD.

Differences in growth parameters among the taxa

An important result of this experiment was that the temperate rainforest types had a higher growth rate than the tropical rainforest types under the ambient conditions of a temperate climate (Figure 8.2). The temperate species showed higher growth rates under both the ambient and the low VPD treatments. This shows clearly that temperate species have higher growth rates than tropical species when grown at the lower temperatures of a temperate climate. In contrast, the results of the growth cabinet experiment were not as clear, with only the warm-temperate rainforest type showing a higher growth rate than the tropical rainforest types at low growth temperatures (Table 5.4). Temperatures in the glasshouses used in this experiment were not lower than those used in the growth cabinets, as heating ensured night temperatures did not fall

below 8°C. Therefore, the cool-temperate species may only show a greater growth rate under low temperatures than the tropical species when grown under the fluctuating temperatures of the field. This greater growth of the temperate species at the low temperatures of a temperate climate can be attributed to the lower growth temperatures for maximum net photosynthesis and the greater temperature acclimation potential of net photosynthesis in the temperate species than the tropical species shown in Chapters 4 and 6. The greater net assimilation rates of the temperate rainforest types compared with other rainforest types reflect their greater photosynthetic capacity under temperate conditions (Figure 8.3).

There are several important differences in the allocation patterns of the temperate and tropical species that support the success of the temperate species under the drier summer conditions of southern Australia. The tropical rainforest type, which comes from an area of wet summers, had the largest leaves and the highest specific leaf areas (Figures 8.4 & 8.6). A similar trend has been found in *Eucalyptus* and *Quercus*, with species found in less arid environments having larger leaves and higher specific leaf areas (Mooney *et al.* 1978b; Abrams 1990; Abrams *et al.* 1994). This reduction in leaf size from mesic to arid environments has been explained by optimal water-use efficiency, avoidance of extreme leaf temperatures or maximization of plant productivity (Parkhurst & Loucks 1972; Taylor 1975; Givnish 1979). This is because under the same conditions large leaves tend to have a higher temperature than small leaves. However, plants with large leaves can reduce their temperature through evaporative cooling. This is a feasible adaptation in environments, such as tropical rainforests, where the availability of water is high during summer (Medina 1983). In contrast, reduction in leaf size is likely to be a better adaptation in environments with summer drought. Mooney *et al.* (1978b) suggested the lower SLA in the more arid species of *Eucalyptus* would lead to a greater water-use efficiency due to a greater stacking of photosynthetic tissue in the smaller leaves.

A common adaptation of plants to more arid environments is a greater allocation to roots (i.e. a higher root/shoot ratio). The rainforest species in this study showed a trend (although weak) of increasing root/shoot ratio under ambient conditions with decreasing annual precipitation (Figure 8.10). In contrast, there was no such relationship between root/shoot ratio and summer precipitation among the species. The warm-temperate

rainforest type showed one the highest root/shoot ratios (Figure 8.7) as it did in the temperature experiment (Table 8.14). In particular, the high root/shoot ratio of *Acmena smithii* is consistent with its growth outside rainforests across a wide range of precipitation and soil types. In contrast, the cool-temperate rainforest type showed the lowest root/shoot ratio (Figure 8.7), and the highest leaf area/ root mass ratio (Figure 8.8). Furthermore, the tropical rainforest type showed the lowest leaf weight ratio of all the rainforest types (Figure 8.5). Therefore, the results do not support the hypothesis that the temperate species would allocate more biomass to roots than tropical species.

Interestingly, the cool-temperate rainforest type showed a much lower root/shoot ratios in this experiment compared with the temperature experiment (Table 8.14). In these experiments, the age of plants differed, with plants at harvest being 16 and 20 months-old in the temperature growth experiment and 24 months-old in this experiment. In addition, the plants were of quite different sizes at the time of harvest as can be seen from the total weights at harvest (Table 8.15). Generally, tree seedlings show an increase in root/shoot ratio during the first year of growth followed by a consistent decline (Hermann 1977). Therefore, the lower root/shoot ratio of cool-temperate species in the present experiment compared to previous experiment may be an ontogenetic change. The plants in both these experiments were well-watered and therefore a large root mass may not have been necessary to maintain water status. Increases in root/shoot ratio are usually associated with the stress of low temperatures or low moisture (Klepper 1991). Therefore, the cool-temperate species may allocate more biomass to roots when exposed to lower soil moisture.

Table 8.14 Comparison of the range of root/shoot ratios of the rainforest types shown in the two growth experiments.

Rainforest type	VPD experiment	Temperature experiment
Cool - temperate	0.23 - 0.29	0.50 - 0.62
Warm - temperate	0.52 - 0.71	0.62 - 0.75
Subtropical	0.50 - 0.67	0.48 - 0.68
Tropical	0.54 - 0.58	0.37 - 0.69

Table 8.15 Comparison of total weights of cool - temperate species at harvest in the various experiments. Values are means of five replicates in the temperature experiment, and ten and twenty replicates for *E. lucida* and *N. cunninghamii* respectively in the VPD experiment, with standard errors given in brackets.

species	Temperature experiment			
	22°C/14°C cabinet		VPD experiment	
	Run 1	Run 2	ambient	low
<i>E. lucida</i>	0.79 (0.11)	0.77 (0.14)	9.51 (0.76)	8.05 (1.20)
<i>N. cunninghamii</i>	1.30 (0.09)	2.11 (0.28)	7.33 (0.65)	5.58 (0.60)

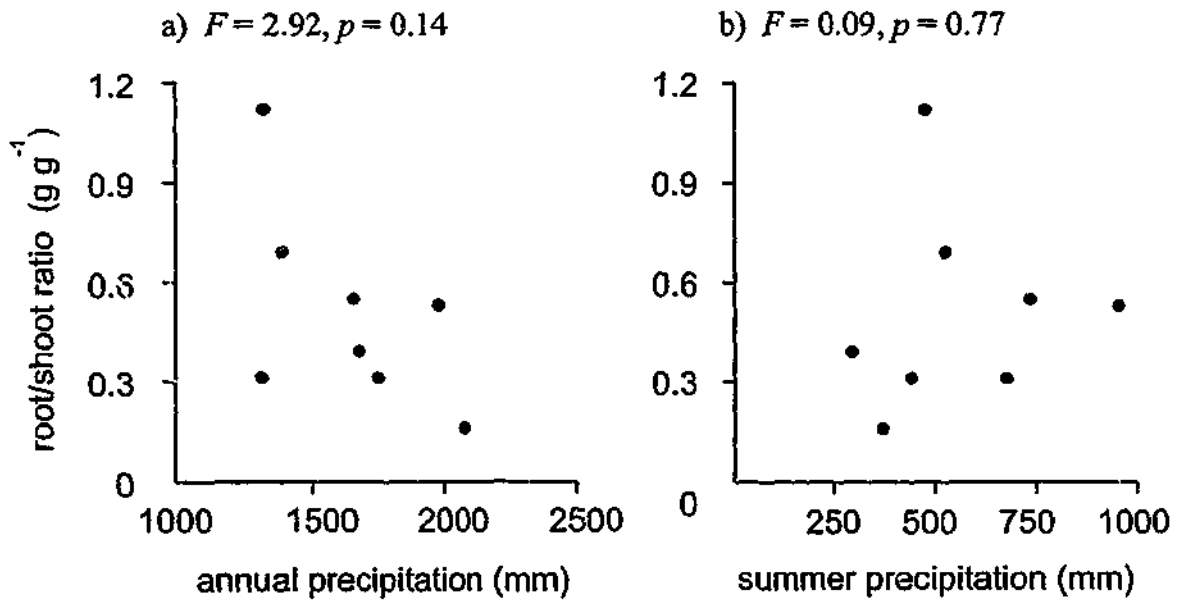


Figure 8.10 Relationship between the mean root/shoot ratio shown when grown under ambient conditions and the a) annual precipitation b) summer precipitation of species.

In conclusion to the specific hypotheses:

1. The growth rate of both tropical and temperate species was unaffected by VPD.
2. Temperate species did not allocate more biomass to roots than tropical species.

In the field, unlike in this experiment, the higher values of VPD in summer would be associated with a limited water supply in temperate climates. Therefore, the difference between temperate and tropical rainforest species may lie in the ability of temperate species to maintain photosynthesis and growth for a longer time under low soil moisture. Firstly, tropical rainforest species are known to produce shallow root systems, especially in high precipitation areas where the soil may remain wet for almost the whole year (Doley 1981). Trees with extensive root systems are known to survive drought better than those with shallow root systems due to greater access to water (Kozłowski & Pallardy 1997a). Therefore, temperate rainforest trees may produce deeper roots systems than tropical rainforest trees. Secondly, a variety of temperate trees and shrubs have been shown to tolerate water deficits through osmotic adjustments of leaves (Kozłowski & Pallardy 1997a). In contrast, osmotic adjustments tend to be shown by tropical trees from dry forests (Mulkey & Wright 1996). Thirdly, tropical trees from warm, wet environments tend to have larger vessels than trees from drier or cooler environments (Tyree *et al.* 1994). There is a trend for species with larger vessel diameters, and hence higher hydraulic conductivity, to be more vulnerable to cavitation and embolism (Tyree & Ewers 1996). Therefore, temperate rainforest species may be less susceptible to cavitation during periods of low soil moisture.

CHAPTER 9

General Discussion

This study aimed to investigate physiological differences between temperate and tropical rainforest canopy trees in Australia. In the previous chapters, results of experiments have shown several physiological differences between the temperate and tropical rainforest trees of eastern Australia (Table 9.1). The important findings in relation to the main questions of this study were:

- 1) Do temperate and tropical species have different temperatures for maximum growth and photosynthesis?
 - (i) The temperate species showed maximum net photosynthesis at lower growth temperatures than the tropical species.
 - (ii) The temperate species showed maximum growth at lower temperatures than the tropical species
- 2) Do temperate species maintain maximum growth and photosynthesis over a wider range of temperatures than tropical species?
 - (i) The temperate species showed close to maximum net photosynthesis over a wider range of growth temperatures than the tropical species.
 - (ii) The temperate species showed an ability to acclimate to a greater span of temperatures than the tropical species
 - (iii) Although growth rates changed with temperature, there was little difference between the growth rates of tropical and temperate species across the range of temperatures used.

3) Do tropical species show a greater sensitivity of growth and photosynthesis to high vapour pressure deficits than temperate species?

- (i) The tropical species showed greater reductions in net photosynthesis with increasing VPD than the temperate species.
- (ii) The growth rate of temperate and tropical species was not affected by vapour pressure deficit over the range examined.

Although these findings were determined from a limited number of species, they may reflect broad trends in the physiology of temperate and tropical rainforest trees of Australia. In this chapter, these differences will be discussed in several ways. Firstly, this chapter explores what the present results and those of other studies suggest about differences in the strategies of temperate and tropical rainforest species of Australia to compete under their climates. Secondly, the discussion focuses on the possible role of past climates in shaping these strategies. Thirdly, the findings of the present study are discussed in the context of differences between temperate and tropical trees of the world. Finally, the discussion examines the implications of the differences in physiology between the temperate and tropical rainforest species to vegetation-climate models.

Table 9.1 Differences in the response of net photosynthesis and growth found between the temperate and tropical species. The range of values shown by the individual species is shown. In the case of reductions in net photosynthesis with increasing VPD, positive values indicate an increase and negative values indicate a decrease.

Physiological parameter	Temperate	Tropical	Data reference
Net photosynthesis			
a) growth temperature			
temperature for maximum net photosynthesis (°C)	19 - 25	24 - 27	Table 4.4
temperature span for maximum net photosynthesis (°C)	12 - 16	9 - 11	Table 4.4
b) acclimation temperature			
temperature for maximum net photosynthesis (°C)	23 - 26	26 - 27	Table 6.11
temperature span for maximum net photosynthesis (°C)	16 - 18	7 - 13	Table 6.13
c) vapour pressure deficit			
reduction in maximum net photosynthesis (% 1kPa^{-1})	+7 to -5	-3 to -18	Table 7.5
Growth			
a) constant temperature regimes			
temperature for maximum growth (°C)	26 - 30 ⁺	30 ⁺	Table 5.2
growth rate at 14°C ($\text{mg g}^{-1} \text{day}^{-1}$)	12 - 17	12 - 14	Table 5.4
growth rate at 30°C ($\text{mg g}^{-1} \text{day}^{-1}$)	20 - 23	19 - 26	Table 5.4
b) temperate climate			
growth rate ($\text{mg g}^{-1} \text{day}^{-1}$)	7 - 11	4 - 8	Table 8.3

Strategies of Australia rainforest species to compete under temperate and tropical climates

In this study, the temperate rainforest species showed maximum net photosynthesis under lower growth temperatures and acclimation temperatures than the tropical rainforest species (Chapter 4 & 6). Similarly, Hill *et al.* (1988) found that high latitude species of temperate rainforests showed maximum net photosynthesis at lower acclimation temperatures than lower latitude species. In contrast, the temperate and tropical species of *Nothofagus* showed maximum net photosynthesis over a similar range of acclimation temperatures (Read 1990). However, this may reflect genetic constraints of the genus. Furthermore, these species are found in climates with similar summer temperatures due to the tropical species of *Nothofagus* coming from higher altitudes than the temperate species. All these studies suggest rainforest species from warmer climates in Australia show maximum net photosynthesis at higher temperatures than rainforest species from cooler climates.

The temperate species in this study showed maximum net photosynthesis over a greater span of growth temperatures, acclimation temperatures and instantaneous temperatures than the tropical species (Chapters 4 & 6). In Australia, other temperate rainforest species have shown maximum net photosynthesis over a greater span of acclimation temperatures and instantaneous temperatures than tropical species (Hill *et al.* 1988; Read 1990; Read & Busby 1990; Swanborough *et al.* 1998). However, tropical rainforest species occurring at high altitudes, which experience large diurnal temperature ranges, also show maximum net photosynthesis over a large span of instantaneous temperatures (Pearcy 1987). Therefore, temperate rainforest species in Australia show a greater ability to adjust photosynthesis to changes in growth and acclimation temperature, but not necessarily instantaneous temperature, than tropical rainforest species.

In comparison to photosynthetic responses, differences in growth responses to temperature between the temperate and tropical rainforest species were less distinct (Chapter 5). The temperate and tropical rainforest species showed considerable overlap in their absolute growth rates across the range of temperatures used. The majority of the rainforest species studied showed their highest growth rate under the highest

temperature of 30°C. The higher growth rate of the tropical rainforest type than the cool-temperate rainforest type at 30°C, was the only difference consistent with the distributions of the rainforest types. However, regressions indicated that the temperate rainforest species showed maximum growth at lower temperatures than the tropical rainforest species. Furthermore, the growth rate of the temperate rainforest species was significantly higher than the tropical rainforest species when grown under the low and fluctuating temperatures of a temperate climate (Chapter 8). Therefore, although the temperate rainforest species showed maximum growth at lower constant temperatures than tropical rainforest species, differences in the growth rates were only clear when grown under a temperate climate. The only published study to investigate growth responses of Australian rainforest trees to temperature compared an evergreen tropical species with a deciduous tropical species (Herwitz 1993). The differences between these species reflected their phenology more than any differences in their climates.

The temperate and tropical rainforest species of this study differed in their photosynthetic responses to vapour pressure deficit (VPD, Chapter 7). In well-watered plants, the tropical species showed greater reductions in net photosynthesis with increasing VPD than the temperate species. In contrast, growing the rainforest species under contrasting VPD had little influence on the maximum rate of net photosynthesis. The greater reductions in photosynthesis with increasing VPD of the tropical rainforest species suggest a greater stomatal sensitivity to VPD. Tropical rainforest species of Australia have been shown to have a greater stomatal sensitivity than temperate deciduous species from the Northern Hemisphere (Franks & Farquhar 1999). The greater long-term water-use efficiency shown by tropical species of *Nothofagus* compared with temperate species also implies a greater stomatal sensitivity of tropical rainforest species (Read & Farquhar 1991). This is further supported by the ability of the temperate species *Nothofagus cunninghamii* to keep its stomata open and make osmotic adjustments under mild water stress (Read 1998). Read and Farquhar (1991) proposed that in order to avoid desiccation the temperate species of *Nothofagus* may maintain water uptake with a high root/shoot ratio or osmotic adjustment. Therefore, it appears that temperate rainforest species tend to be 'optimistic' species maintaining high net photosynthesis and stomatal conductance while soil moisture is adequate. In contrast, tropical rainforest species show a 'pessimistic' strategy with stomatal closure at mild VPD when soil moisture is high.

Although there were differences in the stomatal sensitivity of the temperate and tropical rainforest species studied, the growth of well-watered plants was unresponsive to a lower VPD (Chapter 8). However, the growth of both temperate and tropical species is likely to be responsive to water stress. Several temperate rainforest species have shown a degree of resistance to water stress (Melick 1990b; Barrett & Ash 1992; Read 1998). By comparison, the temperate rainforest species *N. cunninghamii* uses osmotic adjustments to maintain water uptake but plants do not survive below a critical relative water content of 70%, which is high relative to many other tree species (Read & Brown 1996). Field measurements of tropical rainforest species have shown both a lack of control and tight control of water loss during the dry season (Doley *et al.* 1987; Yates *et al.* 1988). Osmotic adjustments in response to water stress have been shown by the tropical rainforest species *Castanospermum australe* (Myers *et al.* 1987). From the above results, it appears that both temperate and tropical rainforest species of Australia show varying degrees of drought resistance.

These physiological differences between temperate and tropical rainforest trees of eastern Australia suggest strategies to compete under their contrasting climates. Firstly, the lower temperatures for maximum net photosynthesis and growth in the temperate rainforest species compared with the tropical rainforest species are consistent with the lower temperatures throughout the year in the temperate compared with the tropical climate. Secondly, temperate rainforest species are exposed to greater seasonal and day-to-day fluctuations in temperature than tropical species. In addition, temperate rainforest species produce leaves predominantly in a single flush during spring (Specht 1981). The ability of temperate rainforest species to maintain maximum net photosynthesis in leaves developed under a wide range of temperatures may also enable them to maintain high photosynthetic rates in leaves developed under fluctuating conditions. Furthermore, the ability of temperate rainforest species to acclimate to a wider range of temperatures than tropical species would better enable them to maintain maximum net photosynthesis in these leaves during the seasonal fluctuations of a temperate climate. In tropical rainforest species, such adaptations are less important as leaves are produced more continuously during the wet season from late spring to early autumn (Frith & Frith 1985; Hopkins & Graham 1989) and are exposed to smaller temperature fluctuations throughout the year. In addition, during the cooler months

photosynthesis may be more restricted by the water stress of the dry season than by temperature. For example, a species in the wet tropics of northeast Queensland, *Argyrodendron peratalum*, showed no net photosynthesis three days after rain in the dry season (Doley *et al.* 1987). Finally, differences in the seasonality of climate mean that the warm growing season for the temperate species is the dry season whereas the growing season for the tropical species is the wet season. Stomatal control is a cost-effective adaptation for the tropical rainforest species, which have a long warm growing season and rarely experience water stress during summer. In contrast, temperate species must use other adaptations, such as high root/shoot ratio or osmotic adjustment, if they are to be productive in their relatively drier, summer climate.

These findings present some possible explanations for the latitudinal restriction of rainforest canopy trees in Australia. The photosynthetic responses of temperate and tropical rainforest species suggest adaptations to their respective climates. In contrast, differences in growth rates under constant temperature regimes were less clear.

Although temperate rainforest species showed maximum growth at lower temperatures than tropical rainforest species, differences in growth rates were only clear when grown under a fluctuating temperate climate. These results provide evidence for the exclusion of tropical rainforest species from temperate climates due to higher growth rates but not for the reverse - that is, temperate rainforest species are able to maintain similar growth rates to tropical rainforest species under tropical temperatures.

Explanations for the exclusion of temperate rainforest species from tropical rainforests may be found in their different growth patterns. Firstly, tropical rainforest species may be able to maintain growth for a longer a period throughout the year under tropical conditions than temperate species. Leaf growth of many tropical rainforest species is continuous whereas many temperate rainforest species, such as *N. cunninghamii*, show determinate growth. In the long term, temperate species may not be able to meet the respiratory costs of growing for long periods at warm temperatures. For example, the growth of many temperate trees is reduced by warm night temperatures, presumably due to excessive respiration (eg. Brix 1971; Hellmers & Rook 1973; Hawkins & Sweet 1989). Secondly, tropical rainforest species may have allocation patterns that allow them to rapidly overtop other species. Many tropical rainforest species show rapid height growth (Vázquez-Yanes 1974; Swaine & Hall 1983). The higher specific leaf

area of the tropical rainforest species compared with the temperate rainforest species found in this study means that for the same amount of biomass, the tropical rainforest species will produce more cover than the temperate rainforest species. Therefore, temperate rainforest species may be quickly shaded out by tropical rainforest species in a tropical climate due to the longer growth period, more rapid height growth and the reduced cost of leaf production of tropical rainforest species.

Role of past climates

The present climate is only one of numerous climates that have shaped the rainforests of Australia (Table 9.2). At the beginning of the Tertiary (66 Ma), the climate was warmer and wetter than the present climate (Kemp 1981). Rainforests composed of predominantly gymnosperms but also containing a diverse angiosperm flora (including *Nothofagus*) covered Australia at this time (Truswell 1993). The Eocene (55-38 Ma) saw the dominance of tropical rainforests in coastal and lowland areas, with subtropical forest inland and *Nothofagus* forest restricted to the highlands of southeast Australia (Macphail *et al.* 1994). In the middle to late Eocene tropical forest began to decline and subtropical forest containing *Nothofagus* reached its highest dominance (Macphail *et al.* 1994). Although fossil records show a mixed subtropical forest, it has been proposed that temperate species were restricted to the drier margins of these forests (Read *et al.* 1990; Truswell 1990). Read and Farquhar (1991) proposed that it was under these conditions that temperate species evolved adaptations to maintain productivity under high VPD. This may have included the reduced sensitivity of net photosynthesis to increasing VPD shown by the temperate rainforest species compared with the tropical rainforest species in this study. The Oligocene (37-24 Ma) was a period of continued wet conditions but substantial cooling with an increased latitudinal gradient of temperature (Truswell 1993). These climate conditions led to the expansion of temperate rainforests, and the evolution of cool-temperate and Araucarian dry rainforest types (Macphail *et al.* 1994). Differences in the temperature for maximum growth and photosynthesis, like those shown among the study species, may have first arisen during this period. The present rainforest types can be viewed as the result of climatic sifting of the rainforests present during the Oligocene (Truswell 1993).

Table 9.2 Summary of past climates and rainforests of eastern Australia. The geological timescale follows that of Berggren *et al.* (1985).

Epoch	Timescale (Ma)	Climate	Vegetation trend
Paleocene	66 - 58	warm and wet	gymnosperm-angiosperm rainforest widespread
Eocene	58 - 37	warm and wet	tropical angiosperm rainforest dominants
Oligocene	37 - 24	coolest epoch but still wet	expansion of temperate rainforest
early Miocene	24 - 17	period of warming	mixed subtropical- <i>Nothofagus</i> rainforest expands
middle to late Miocene	17 - 5	increasing aridity and increasing seasonality of temperature and precipitation	rainforests decline with dry rainforest more widespread
early Pliocene	5 - 3	current climate zones established	brief resurgence of <i>Nothofagus</i> and dry rainforest
late Pliocene	3 - 2	cooler and drier	further reduction of rainforests
Pleistocene	2 - 0.1	oscillations between glacial and interglacial periods	rainforests continue to decline

The early Miocene (24-17 Ma) was a period of climatic amelioration with warm temperatures and summer precipitation but low seasonality, which allowed subtropical-*Nothofagus* rainforests to become widespread (Macphail *et al.* 1994). In contrast, the period of middle to late Miocene (16-5 Ma) was one of increasing aridity, decreasing temperature and increasing seasonality (Bowler 1982; Nix 1982). The wider temperature range for maximum net photosynthesis showed in this study by the temperate species compared with the tropical species may have arisen during this period. In response to the increasing aridity, the wet rainforests declined while the Araucarian dry rainforests became more widespread (Kershaw 1988). The Pliocene (5-2 Ma) saw the establishment of the present climatic zonation, with southern Australia coming under the influence of cool winter rains for the first time (Bowler 1982). During the early Pliocene there was a brief resurgence of *Nothofagus* rainforest and dry rainforest but not to the exclusion of the Myrtaceae (Martin 1987). During the remainder of the Pliocene, the climate became progressively cooler and drier resulting in the further retraction of rainforest to the Eastern Highlands and the expansion of more open vegetation (Truswell 1990). The general retraction of rainforest with increasing aridity is consistent with the apparent lack of any overall difference in the drought resistance of temperate and tropical species.

The Quaternary was a period of repeated climatic oscillation between glacial and interglacial periods (Hope 1994). This is believed to have accelerated the contraction of rainforest with expansion during warmer periods not reaching its former range (Kershaw 1981). The greater climatic tolerance of the temperate species would have made them more adaptable to the climatic oscillations of the Quaternary than the tropical species. The presence of many temperate species at high altitudes supports their ability to tolerate colder climates. How tropical species would have endured glacial periods is uncertain. Both temperate and tropical rainforest species show maximum growth at temperatures greater than 25°C, even though only 10% of the Quaternary, a period of 100 000 years, has been as warm or warmer than the present climate. This retention of growth rhythms suitable in the early Tertiary may reflect molecular constraints of enzymes and not a lack of selection pressure as suggested by Hawkins and Sweet (1989).

Physiological differences between temperate and tropical trees

The predominant changes in climate from temperate to tropical forests are the increase in temperature, the reduction in seasonality of temperatures and the shift from winter-dominant to summer-dominant precipitation (Archibold 1995). These climate differences are reflected in the phenology of these forests, with growth cycles in temperate forests associated with temperature, whereas growth cycles tend to be associated with precipitation in tropical forests (Lechowicz 1995; Reich 1995). Consequently, research on the physiology of tropical trees has often concentrated on water relations (eg. Medina 1983; Robichaux *et al.* 1984; Fetcher *et al.* 1994; Mulkey *et al.* 1996). There is a lack of direct physiological comparisons between temperate and tropical trees. In addition, many of these studies are complicated by the comparison of different growth forms (eg. Schreiber & Riederer 1996; Franks & Farquhar 1999). The many studies of cold tolerance in trees have shown that temperate species are more tolerant of chilling and freezing temperatures than tropical species (Berry & Björkman 1980; Graham & Patterson 1982; Sakai & Larcher 1987). However, in regions with episodic frosts the entire population of a species is seldom destroyed by a frost (Larcher & Bauer 1981). Therefore, physiological responses at moderate temperatures may be more important than cold tolerance to the limits of temperate and tropical tree species.

Photosynthetic responses of the rainforest species in this study suggest that temperate species maintain maximum net photosynthesis over a broader range of temperatures than tropical species. The few studies of acclimation potential in lowland tropical species support their reduced temperature range compared with temperate species (Downes & Connor 1973; Read 1990). In contrast, tropical treeline species show an ability to maintain maximum net photosynthesis over a wide range of acclimation temperatures (Goldstein *et al.* 1994). With respect to instantaneous temperatures, there is no consistent trend, with both tropical lowland and alpine species showing maximum net photosynthesis over similar spans to the temperate species in this study (Pearcy 1987; Mori *et al.* 1990; Goldstein *et al.* 1994). The present study appears to be the only investigation of the photosynthetic response of leaves developed under different temperature regimes in tropical species. The findings of this study suggest that the reduced acclimation potential of lowland tropical species should translate into a narrow response to growth temperature.

Globally, temperate tree species have maximum growth over the temperature range of 15°C to 25°C (Brix 1971; Hellmers & Rook 1973; Paton 1980; Schaffer & Andersen 1994a), whereas tropical species tend to have maximum growth at temperatures between 25°C and 35°C (Opeke 1982; Schaffer & Andersen 1994b). However, the temperate rainforest species in this study and others from the Southern Hemisphere (Hawkins & Sweet 1989) have shown maximum growth at temperatures in the same range (27-30°C) as those of tropical species. Therefore, differences in the temperature for maximum growth between temperate and tropical species are not as distinct as previously thought.

Tropical and temperate forests grow across a wide range of precipitation (500-4000 mm per year) and both can experience a distinct dry season (Archibold 1995; Mulkey & Wright 1996). Therefore, it is not surprising that tropical and temperate tree species both show adaptations to water stress such as osmotic adjustments and deep root systems (Medina 1983; Sobrado 1986; Kozlowski & Pallardy 1997b). The consistently warm temperatures of the tropical climate mean that tropical species can be highly productive during the wet season and need only survive the dry season. This is supported by the number of tropical trees that show some degree of drought deciduousness and the evergreen species that show limited carbon gain, or even loss, during the dry season (Doley *et al.* 1987; Mulkey & Wright 1996). The seasonality of temperate climates means that the wet season is also the coldest, so temperate species need adaptations to maintain productivity during the dry season. In the case of wet forests, the present findings and those of others suggest that temperate species have adaptations that allow the maintenance of high gas exchange rates under higher vapour pressure deficits than tropical species (Read & Farquhar 1991; Read 1998). This is supported by the regular midday stomatal closure of tropical species in the field (Meinzer 1993; Zotz & Winter 1996).

Significance of findings to vegetation-climate models

Present vegetation-climate models use various physiological assumptions to explain the distribution of vegetation. Many models assume that photosynthetic responses of leaves to temperature translate into growth responses of whole plants. In addition, some models assume that the latitudinal zonation of tree species reflects differences in the maximum temperature for growth. Finally, many models state that the latitudinal limits of vegetation types are set by cold tolerance at high latitudes and by competitive exclusion at low latitudes. These assumptions will be discussed in the light of the present findings and the findings of others.

Forest growth models such as that of Botkin (1993) assume that the growth response to temperature of trees can be determined from photosynthetic measurements. However, there is often not a strong correlation between the photosynthetic response to temperature and growth in plants (Körner 1991; Pereira 1994). Several studies, including the present study, have showed higher temperatures for growth than for maximum net photosynthesis (eg. Teskey & Will 1999; Xiong *et al.* 2000). Furthermore, Botkin (1993) states that the study of Ledig and Korbobo (1983), which only measured photosynthetic responses to instantaneous temperatures of seedlings grown under a common environment, was the preferred method for determining the temperature limits for growth. Even if photosynthesis and growth were directly correlated, this method would not measure the ability of plants to acclimate photosynthesis to changing temperature. There is now strong evidence that photosynthetic responses to temperature can not be used as a surrogate for actual growth measurements.

Specht (1981) and Nix (1982) proposed similar vegetation-climate models for Australia based on the existence of different thermal response groups among tree species (Figure 9.1). The prediction of these models is that the temperature for maximum growth of the dominant species of a community decreases with increasing latitude. In particular, Nix (1991) predicted that the rainforest types of Australia would be dominated by different thermal response groups, each with different temperatures for maximum growth (Figure 9.1a). The photosynthetic responses to growth temperature of the rainforest types found in this study showed such a pattern (Figure 9.2a). By comparison, the growth responses

to temperature were quite different (Figure 9.2b). Although the results do predict that temperate species show maximum growth at lower temperatures than tropical species, temperatures for maximum growth were considerably higher than those for maximum net photosynthesis. Furthermore, the temperatures for maximum growth of the rainforest species ($>25^{\circ}\text{C}$) in this study were considerably higher than the range for maximum growth ($10\text{--}25^{\circ}\text{C}$) predicted by the above models. Therefore, the curves presented by Nix (1982) and Specht (1981) may not be representative of the species within the different rainforest types. The curves of Nix (1982) are representative of the mean daily temperatures at which the rainforest types are dominant. Therefore, as the growth curves for the rainforest species did not follow this trend, the dominance of rainforest types may not be due to differences in the temperature for maximum growth.

Woodward (1987) proposed a vegetation-climate model based on physiological assumptions, which have been incorporated into many subsequent models (eg. Prentice *et al.* 1992). This model makes two general conclusions about the distribution of vegetation types:

- (1) "the poleward spread of a particular physiognomic type of vegetation will be strongly controlled by minimum temperature and the physiological ability to survive low temperature." (Woodward 1987, p.80)
- (2) "this poleward spread will be at the expense of equatorial spread because of the reduced competitive ability due, at least in part, to the extensive biochemical changes involved in winter hardiness." (Woodward 1987, p.83)

The competitive ability of canopy dominants is likely to be determined by their relative growth rates. Individuals that have faster growth rates are more likely to dominate use of available resources and overshadow slower growing competitors (Lambers & Dijkstra 1987; Firbank & Watkinson 1990). The temperate and tropical rainforest tree species of this study showed similar absolute growth rates under a constant low temperature regime. However, when grown for a year under the fluctuating conditions of a temperate climate, the temperate species showed higher growth rates than the tropical species. Therefore, although tropical species can tolerate temperate conditions,

they are likely to be outcompeted by temperate species due to their slower growth rate. This suggests that it may not be necessary to invoke differences in cold tolerance to explain the cold limit of tropical rainforest.

The warm limit of temperate forests may also be the result of slower growth rates of temperate species compared with tropical species under tropical conditions. However, under the warmest temperature regime used in this study, there was considerable overlap in absolute growth rates among the temperate and tropical rainforest species. Therefore, based on growth rates, it could not be concluded that the temperate rainforest species would be excluded from tropical rainforests. However, under tropical field conditions, the tropical rainforest species may show growth rates similar to those recorded in the field for other tropical rainforest species (eg. Kitajima 1996), which are higher than the temperate species. In addition, the greater competitive ability of tropical rainforest species in the tropics may due to their faster height growth rate and their ability to grow for longer periods than temperate species. These possible differences between temperate and tropical species could be tested in common garden experiments in a tropical climate.

General conclusion

The findings of this study show a clear difference between temperate and tropical rainforest trees of Australia in the response of net photosynthesis to the climatic variables of temperature and vapour pressure deficit. By comparison, although the temperate rainforest species showed maximum growth at lower temperatures than the tropical rainforest species, they showed similar relative growth rates across the temperature range used. The temperate rainforest species only showed a distinctly higher growth rate than the tropical rainforest species when grown under the ambient conditions of a temperate climate. Therefore, based on growth rates, these findings only provide evidence for the competitive exclusion of tropical rainforest species from the temperate region and not the exclusion of temperate rainforest species from the tropics.

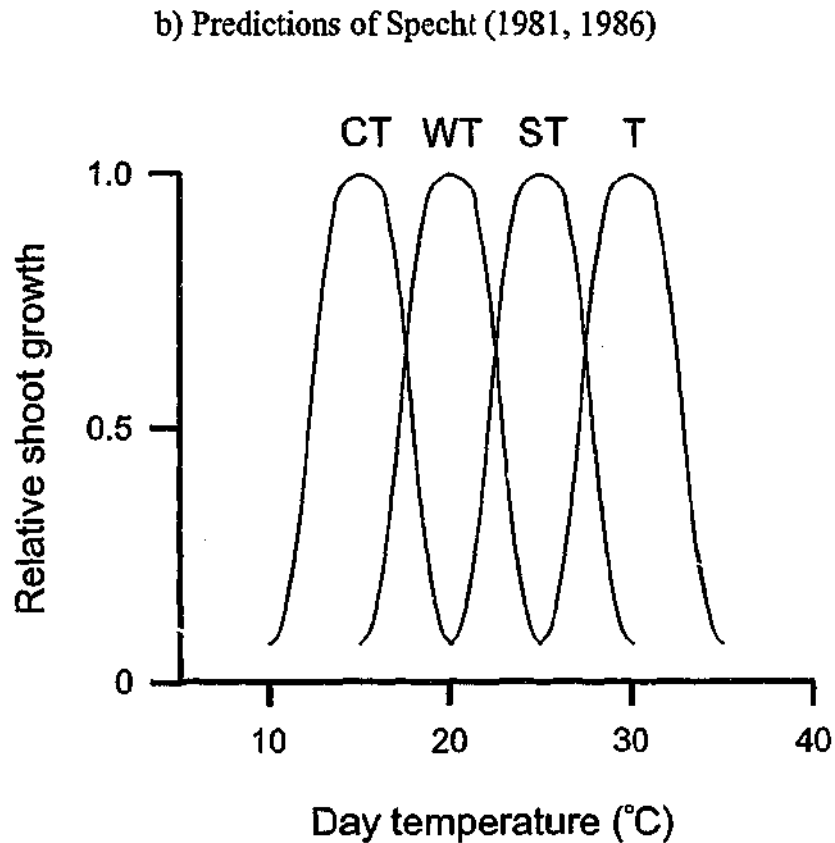
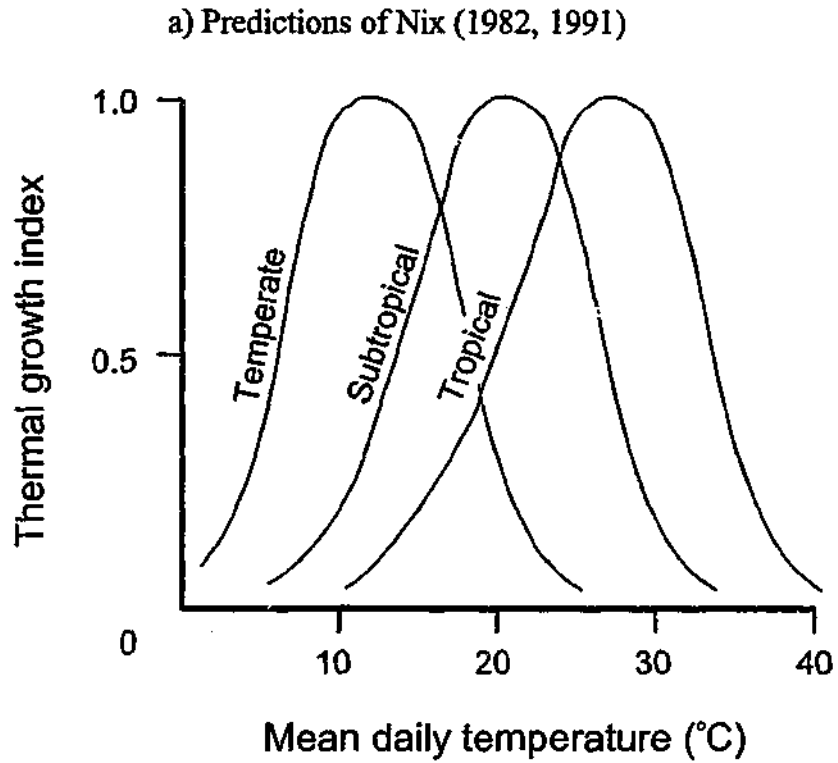


Figure 9.1 The relationships between growth and temperature predicted by Nix (1982, 1991) and Specht (1981, 1986) for the rainforest types of Australia. The thermal groups of Specht are indicated as follows: cool-temperate (CT), warm-temperate (WT), subtropical (ST) and tropical (T).

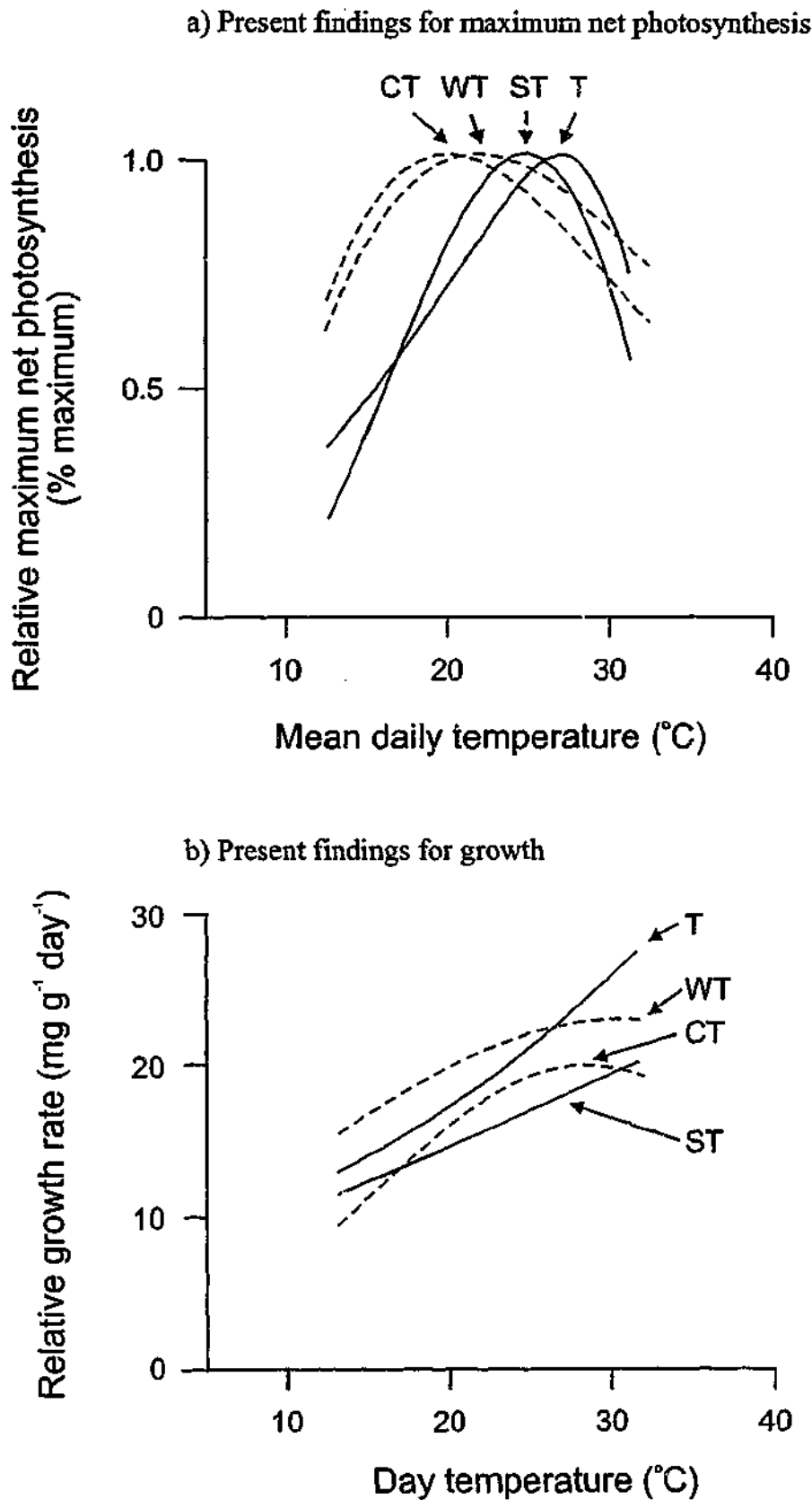


Figure 9.2 Photosynthetic and growth responses to temperature found in rainforest species of Australia. The rainforest types are indicated as follows: cool-temperate (CT), warm-temperate (WT), subtropical (ST) and tropical (T).

References

- Abrams, M.D. (1990) Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiology*, **7**, 227-238.
- Abrams, M.D., Kubiske, M.E., & Mostoller, S.A. (1994) Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. *Ecology*, **75**, 123-133.
- Abu-Zeyad, R., Khan, A.G., & Khoo, C. (1999) Occurrence of arbuscular mycorrhiza in *Castanospermum australe* A. Cunn. & C. Fraser and effects on growth and production of castanospermine. *Mycorrhiza*, **9**, 111-117.
- Acock, B. (1974) The design and use of growth chambers for investigating the effects of environmental factors on plant growth. *Acta Horticulturae*, **39**, 15-38.
- Adam, P. (1992) Australian Rainforests. Oxford University Press, Oxford.
- Ågren, G.I. & Ingestad, T. (1987) Root:shoot ratio as a balance between nitrogen productivity and photosynthesis. *Plant Cell and Environment*, **10**, 579-586.
- Amthor, J.S. (1989) Respiration and Crop Productivity. Springer-Verlag, New York.
- Archibold, O.W. (1995) Ecology of World Vegetation. Chapman and Hall, London.
- Ashton, D.H. & Frankenberg, J. (1976) Ecological studies of *Acmena smithii* (Poir.) Merrill & Perry with special reference to Wilson's Promontory. *Australian Journal of Botany*, **24**, 453-487.
- Attiwill, P.M. & Leeper, G.W. (1987) Forest Soils and Nutrient Cycles. Melbourne University Press, Melbourne.
- Atwell, B., Kriedemann, P., & Turnbull, C. (1999) Plants In Action. Adaptation in Nature, Performance in Cultivation. MacMillan Education, Melbourne.
- Austin, M.P., Cunningham, R.B., & Fleming, P.M. (1984) New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. *Vegetatio*, **55**, 11-27.
- Austin, M.P., Nicholls, A.O., & Margules, C.R. (1990) Measurement of the realized niche: environmental niches of five *Eucalyptus* species. *Ecological Monographs*, **60**, 161-177.
- Badger, M.R., Björkman, O., & Ammond, P.A. (1982) An analysis of photosynthetic response and adaptation to temperature in higher plants: temperature acclimation in the desert evergreen *Nerium oleander* L. *Plant, Cell and Environment*, **5**, 85-99.
- Bahari, Z.A., Pallardy, S.G., & Parker, W.C. (1985) Photosynthesis, water relations and drought adaptation in six woody species of oak-hickory forests in central Missouri. *Forest Science*, **31**, 557-569.
- Bakker, J.C. (1984) Physiological disorders in cucumber under high humidity conditions and low ventilation rates in greenhouses. *Acta Horticulturae*, **156**, 252-264.

- Bakker, J.C. (1985) Physiological disorders in cucumber under high humidity conditions and low ventilation rates in greenhouses. *Acta Horticulturae*, **156**, 257-264.
- Ball, M.C., Cochrane, M.J., & Rawson, H.M. (1997) Growth and water use of the mangroves *Rhizophora apiculata* and *R. stylosa* in response to salinity and humidity under ambient and elevated concentrations of atmospheric CO₂. *Plant, Cell and Environment*, **20**, 1158-1166.
- Baly, E.C.C. (1935) The kinetics of photosynthesis. *Proceedings of the Royal Society of London. Series B*, **117**, 218-239.
- Bannister, T.T. (1979) Quantitative description of steady state, nutrient-saturated algal growth, including adaptation. *Limnology and Oceanography*, **24**, 76-96.
- Barrett, D.J. & Ash, J.E. (1992) Growth and carbon partitioning in rainforest and eucalypt forest species of south coast New South Wales, Australia. *Australian Journal of Botany*, **40**, 13-25.
- Baruch, Z. (1979) Elevational differentiation in *Espeletia schultzei* (Compositae), a giant rosette plant of the Venezuelan paramos. *Ecology*, **60**, 85-98.
- Basset, Y. (1991) Leaf production of an overstorey rainforest tree and its effects on the temporal distribution of associated insect herbivores. *Oecologia*, **88**, 211-219.
- Battaglia, M., Beadle, C., & Loughhead, S. (1996) Photosynthetic temperature responses of *Eucalyptus globulus* and *Eucalyptus nitens*. *Tree Physiology*, **16**, 81-89.
- Bauer, H., Larcher, W., & Walker, R.B. (1975). Influence of temperature stress on CO₂ gas exchange. In *Photosynthesis and Productivity in Different Environments* (ed J.P. Cooper), pp. 557-586. Cambridge University Press, Melbourne.
- Bazzaz, F.A. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, **10**, 351-371.
- Bazzaz, F.A. & Carlson, R.W. (1982) Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia*, **54**, 313-316.
- Bazzaz, F.A. & Pickett, S.T.A. (1980) Physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics*, **11**, 287-310.
- Beardsell, M.F., Mitchell, K.J., & Thomas, R.G. (1973) Transpiration and photosynthesis in soybean. *Journal of Experimental Botany*, **24**, 587-595.
- Ben Haj Salah, H. & Tardieu, F. (1996) Quantitative analysis of the combined effects of temperature, evaporative demand and light on leaf elongation rate in well-watered field and laboratory-grown maize plants. *Journal of Experimental Botany*, **47**, 1689-1698.
- Berggren, W.A., Kent, D.V., Flynn, J.J., & van Couvering, J.A. (1985) Cenozoic geochronology. *Geological Society of America Bulletin*, **96**, 1406-1418.
- Berry, J.A. & Björkman, O. (1980) Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology*, **31**, 491-543.
- Berry, J.A. & Raison, J.K. (1981). Responses of macrophytes to temperature. In *Physiological Plant Ecology I. Responses to the Physical Environment* (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler), pp. 277-338. Springer-Verlag, Berlin.

- Billings, W.D., Godfrey, P.J., Chabot, B.F., & Bourque, D.P. (1971) Metabolic acclimation to temperature in arctic and alpine ecotypes of *Oxyria digyna*. *Arctic and Alpine Research*, 3, 277-289.
- Billings, W.D. & Mooney, H.A. (1968) The ecology of arctic and alpine plants. *Biological Reviews* 43, 481-529.
- Björkman, O. (1971). Comparative photosynthetic CO₂ exchange in higher plants. In *Photosynthesis and Photorespiration* (eds M.D. Hatch, C.B. Osmond & R.O. Slatyer), pp. 18-32. Wiley Interscience, Sydney.
- Björkman, O. (1973). Comparative studies on photosynthesis in higher plants. In *Photophysiology. Current Topics in Photobiology and Photochemistry*. (ed A.C. Giese), Vol. VIII, pp. 1-63. Academic Press, London.
- Björkman, O. (1981a). The responses of photosynthesis to temperature. In *Plants and their Atmospheric Environment* (eds J. Grace, E.D. Ford & P.G. Jarvis), pp. 273-301. Blackwell Scientific Publications, Melbourne.
- Björkman, O. (1981b). Responses to different quantum flux densities. In *Encyclopedia of Plant Physiology. Physiological Plant Ecology. Vol. 12A. Responses to the Physical Environment*. (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler), pp. 57-107. Springer-Verlag, Berlin.
- Björkman, O., Badger, M., & Armond, P.A. (1978) Thermal acclimation of photosynthesis: effect of growth temperature on photosynthetic characteristics and components of the photosynthetic apparatus in *Nerium oleander*. *Carnegie Institution of Washington Yearbook*, 78, 262-276.
- Björkman, O., Badger, M.R., & Armond, P.A. (1980). Responses and adaptation of photosynthesis to high temperatures. In *Adaptations of Plants to Water and High temperature Stress* (eds N.C. Turner & P.J. Kramer), pp. 233-249. Wiley Interscience, New York.
- Björkman, O., Downton, W.J.S., & Mooney, H.A. (1980b) Response and adaptation to water stress in *Nerium oleander*. *Carnegie Institution of Washington Yearbook*, 79, 150-157.
- Björkman, O., Mooney, H.A., & Ehleringer, J. (1975) Photosynthetic responses of plants from habitats with contrasting thermal environments: comparison of photosynthetic characteristics of intact plants. *Carnegie Institution of Washington Yearbook*, 74, 743-748.
- Bloom, A.J. (1985) Resource limitation in plants - an economic analogy. *Annual Review of Ecology and Systematics*, 16, 363-392.
- Boardman, N.K. (1977) Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology*, 28, 355-377.
- Boland, D.J., Brooker, M.I.H., Chippendale, G.M., Hall, N., Hyland, B.P.M., Johnston, R.D., Kleinig, D.A., & Turner, J.D. (1994) *Forest Trees of Australia*. CSIRO Publications, Melbourne.
- Bonan, G.B. & Sirois, L. (1992) Air temperature, tree growth, and the northern and southern range limits to *Picea mariana*. *Journal of Vegetation Science*, 3, 495-506.
- Botkin, D.B. (1993) *Forest Dynamics. An ecological model*. Oxford University Press, Oxford.

- Bowen, G.D. (1991). Soil temperature, root growth, and plant function. In *Plant Roots. The Hidden Half* (eds Y. Waisel, A. Eshel & U. Kafkafi), pp. 309-330. Marcel Dekker, Inc., New York.
- Bowler, J.M. (1982). Aridity in the late Tertiary and Quaternary of Australia. In *Evolution of the Flora and Fauna of Arid Australia* (eds W.R. Barker & P.J.M. Greensdale), pp. 35-45. Peacock Publications, Frewville, SA.
- Bowman, D.M.J.S. (2000) Australian rainforests: islands of green in a land of fire. Cambridge University Press, Cambridge.
- Bowman, W.D. & Turner, L. (1993) Photosynthetic sensitivity to temperature in populations of two *C₄ Bouteloua* (Poaceae) species native to different altitudes. *American Journal of Botany*, **80**, 369-374.
- Box, E.O. (1981) Macroclimate and Plant forms: an introduction to predictive modelling in phytogeography. Dr. W. Junk Publishers, The Hague.
- Box, E.O. (1995) Factors determining distributions of tree species and plant functional types. *Vegetatio*, **121**, 101-116.
- Bradford, K.J. & Hsiao, T.C. (1982). Physiological responses to moderate water stress. In *Encyclopedia of Plant Physiology. Physiological Plant Ecology. Vol. 12B. Water Relations and Carbon Assimilation* (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler), pp. 263-324. Springer-Verlag, Berlin.
- Breeze, V. & Elston, J. (1983) Examination of a model and data describing the effect of temperature on the respiration rate of crop plants. *Annals of Botany*, **51**, 611-616.
- Brix, H. (1971) Growth response of western hemlock and Douglas-fir seedlings to temperature regimes during day and night. *Canadian Journal of Botany*, **49**, 289-294.
- Brooker, I. & Kleinig, D. (1996) Eucalyptus. An Illustrated Guide to Identification. Reed Books, Melbourne.
- Brouwer, R. (1983) Functional equilibrium: sense or nonsense. *Netherlands Journal of Agricultural Science*, **31**, 335-348.
- Brzeziecki, B., Kienast, F., & Wildi, O. (1995) Modelling potential impacts of climate change on the spatial distribution of zonal forest communities in Switzerland. *Journal of Vegetation Science*, **6**, 257-268.
- Buckley, R.C., Corlett, R.T., & Grubb, P.J. (1980) Are the xeromorphic trees of tropical upper montane rain forests drought-resistant? *Biotropica*, **12**, 124-136.
- Bunce, J.A. (1981) Comparative responses of leaf conductance to humidity in single attached leaves. *Journal of Experimental Botany*, **32**, 629-634.
- Bunce, J.A. (1986) Responses of gas exchange to humidity in populations of three herbs from environments differing in atmospheric water. *Oecologia*, **71**, 117-120.
- Bunce, J.A., Miller, L.N., & Chabot, B.F. (1977) Competitive exploitation of soil water by five eastern North American tree species. *Botanical Gazette*, **138**.
- Bureau of Meteorology (1989) Climate of Australia. Australian Government Publishing Service, Canberra.
- Busby, J.R. (1986) A biogeoclimatic analysis of *Nothofagus cunninghamii* (Hook.) Oerst. in southeastern Australia. *Australian Journal of Ecology*, **11**, 1-7.

- Cain, S.A. (1944) Foundations of Plant Geography. Harper, New York.
- Calder, D.M. (1973). The effect of temperature on growth and dry weight distribution of populations of *Poa annua* L. In *Plant Response to Climatic Factors. Proceedings of the Uppsala Symposium* (ed R.O. Slatyer), pp. 145-152. United Nations Educational, Scientific and Cultural Organization, Paris.
- Cao, K.-F., Peters, R., & Oldeman Roelof, A.A. (1995) Climatic range and distribution of Chinese *Fagus* species. *Journal of Vegetation Science*, 6, 316-324.
- Carey, P.D., Watkinson, A.R., & Gerard, F.F.O. (1995) The determinants of the distribution and abundance of the winter annual grass *Vulpia ciliata* ssp. *ambigua*. *Journal of Ecology*, 83, 177-187.
- Chabot, B.F. & Lewis, A.R. (1976) Thermal acclimation of photosynthesis in Northern Red Oak. *Photosynthetica*, 10, 130-135.
- Chapin, F.S., III (1983) Direct and indirect effects of temperature on Arctic plants. *Polar Biology*, 2, 47-52.
- Chapin, I., F. S. (1974) Phosphate absorption capacity and acclimation potential in plants along a latitudinal gradient. *Science*, 183, 521-523.
- Clarke, K.R. (1988). Detecting changes in benthic community structure. In *Proceedings of the XIVth International Biometric Conference, Namur: Invited Papers*, pp. 131-142. Societe Adolphe Quetelet, Gembloux, Belgium.
- Clarke, K.R. & Ainsworth, M. (1993) A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*, 92.
- Clarke, K.R. & Warwick, R.M. (1994) Change in Marine Communities: an Approach to Statistical Analysis and Interpretation. Plymouth Marine Laboratory, Plymouth, U.K.
- Clements, F.E. (1916) Plant Succession. Carnegie Institute, Washington, D. C.
- Clifton-Brown, J.C. & Jones, M.B. (1999) Alteration of transpiration rate, by changing air vapour pressure deficit, influences leaf extension rate transiently in *Miscanthus*. *Journal of Experimental Botany*, 50, 1393-1401.
- Connell, J.H. & Lowman, M.D. (1989) Low-diversity tropical rain forests: some possible mechanisms for their existence. *American Naturalist*, 134, 88-119.
- Cooper, J.P. (1964) Climatic variation in forage grasses. I. Leaf development in climatic races of *Lolium* and *Dactylis*. *Journal of Applied Ecology*, 1, 45-61.
- Cosgrove, D.J. (1986) Biophysical control of plant growth. *Annual Review of Plant Physiology*, 37, 377-405.
- Cowan, I.R. (1977) Stomatal behaviour and environment. *Advances in Botanical Research*, 4, 117-228.
- Cremer, K.W. (1975) Temperature and other climatic influences on shoot development and growth of *Eucalyptus regnans*. *Australian Journal of Botany*, 26, 27-44.
- Dai, Z., Edwards, G.E., & Ku, M.S.B. (1992) Control of photosynthesis and stomatal conductance in *Ricinus communis* L. (Castor Bean) by leaf to air vapour pressure deficit. *Plant Physiology*, 99.
- Dargie, T.C.D. (1984) On the integrated interpretation of indirect site ordinations: a case study using semi-arid vegetation in southeastern Spain. *Vegetation*, 55, 37-55.

- Darlington, A.B., Halinska, A., Dat, J.F., & Blake, T.J. (1997) Effects of increasing saturation vapour pressure deficit on growth and ABA levels in black spruce and jack pine. *Trees*, 223-228.
- Davidson, R.L. (1969) Effect of root/leaf temperature differentials on root/shoot ratios in some grasses and clover. *Annals of Botany*, 33, 561-569.
- Davies, S.J. (1998) Photosynthesis of nine pioneer *Macaranga* species from Borneo in relation to life history. *Ecology*, 79, 2292-2308.
- Davies, W.J. & Kozlowski, T.T. (1977) Variations among woody plants in stomatal conductance and photosynthesis during and after drought. *Plant Soil*, 46, 435-444.
- Dawson, I.A., King, R.W., & van der Staay, R. (1991) Optimizing conditions for growth of *Nephrolepis* ferns. *Scientia Horticulturae*, 45, 303-314.
- de Candolle, A.I. (1855) *Geographie Botanique Raisonnee*. Masson, Paris.
- De Puit, E.J. & Caldwell, M.M. (1973) Seasonal pattern of net photosynthesis of *Artemisia tridentata*. *American Journal of Botany*, 60, 426-435.
- Debski, I., Burslem, D.F.R.P., & Lamb, D. (2000) Ecological processes maintaining differential tree species distributions in an Australian subtropical rain forest: Implications for models of species coexistence. *Journal of Tropical Ecology*, 16, 387-415.
- Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist*, 38, 209-211.
- Doley, D. (1981). Tropical and subtropical forests and woodlands. In *Water Deficits and Plant Growth Vol. 6 Woody Plant Communities* (ed T.T. Kozlowski). Academic Press, Sydney.
- Doley, D. & Yates, D.J. (1976) Gas exchange of Mitchell Grass (*Astrebla lappacea* (Lindl.) Domin) in relation to irradiance, carbon dioxide supply, leaf temperature and temperature history. *Australian Journal of Plant Physiology*, 3, 471-487.
- Doley, D., Yates, D.J., & Unwin, G.L. (1987) Photosynthesis in an Australian rainforest tree, *Argyrodendron peralatum*, during the rapid development and relief of water deficits in the dry season. *Oecologia*, 74, 441-449.
- Doran, J.C. & Turnbull, J.W. (1997) Australian trees and shrubs: species for land rehabilitation and farm planting in the tropics. Australian Centre for International Agricultural Research, Canberra.
- Downes, R.W. & Connor, D.J. (1973) Effect of growth environment on gas exchange characteristics of brigalow (*Acacia harpophylla* F. Muell.). *Photosynthetica*, 7, 34-40.
- Downton, J. & Slatyer, R.O. (1972) Temperature dependence of photosynthesis in cotton. *Plant Physiology*, 50, 518-522.
- Drew, A.P. & Ledig, F.T. (1981) Seasonal patterns of CO₂ exchange in the shoot and root of loblolly pine seedlings. *Botanical Gazette*, 142, 200-205.
- Dufrene, E. & Saugier, B. (1993) Gas exchange of oil palm in relation to light, vapour pressure deficit, temperature and leaf age. *Functional Ecology*, 7, 97-104.
- Eamus, D. & Cole, S. (1997) Diurnal and seasonal comparisons of assimilation, phyllode conductance and water potential of three *Acacia* and one *Eucalyptus* species in the wet-dry tropics of Australia. *Australian Journal of Botany*, 45, 275-290.

- Eldridge, K.G. (1969) Altitudinal Variation in *Eucalyptus regnans*. Ph.D. Thesis. Australian National University, Canberra.
- Ellis, A.R., Hubbell, S.P., & Potvin, C. (2000) *In situ* field measurements of photosynthetic rates of tropical tree species: a test of the functional group hypothesis. *Canadian Journal of Botany*, **78**, 1336-1347.
- El-Sharkawy, M.A. & Cock, J.H. (1984) Water use efficiency of cassava (*Manihot esculenta*). I. Effects of air humidity and water stress on stomatal conductance and gas exchange. *Crop Science*, **24**, 497-502.
- El-Sharkawy, M.A. & Cock, J.H. (1986). The humidity factor in stomatal control and its effect on crop productivity. In *Biological Control of Photosynthesis* (eds R. Marcelle, H. Clijsters & M. van Poucke), pp. 187-200. Martinus Nijhoff Publishers, Dordrecht.
- Evans, J.R. (1996). Developmental constraints on photosynthesis: effects of light and nutrition. In *Photosynthesis and the Environment* (ed N.R. Baker), pp. 281-304. Kluwer Academic Publishers, Netherlands.
- Evans, L.T. (1963). Extrapolation from controlled environments to the field. In *Environmental Control of Plant Growth* (ed L.T. Evans), pp. 421-437. Academic Press, New York.
- Evans, L.T., Wardlaw, I.F., & King, R.W. (1985) Plants and Environment: two decades of research at the Canberra phytotron. *The Botanical Review*, **51**, 203-272.
- Falk, S., Maxwell, D.P., Laudenbach, D.E., & Huner, N.P.A. (1996). Photosynthetic adjustment to temperature. In *Photosynthesis and the Environment* (ed N.R. Baker), pp. 367-385. Kluwer Academic Publishers, Netherlands.
- Fang, J.Y. & Yoda, K. (1989) Climate and vegetation in China. II. Distribution of main vegetation types and thermal climate. *Ecological Research*, **4**, 71-84.
- Fang, J.Y. & Yoda, K. (1990a) Climate and vegetation in China. III. Water balance and distribution of vegetation. *Ecological Research*, **5**, 9-24.
- Fang, J.Y. & Yoda, K. (1990b) Climate and vegetation in China. IV. distribution of tree species along the thermal gradient. *Ecological Research*, **5**, 291-302.
- Fang, J.Y. & Yoda, K. (1991) Climate and vegetation in China. V. effect of climatic factors on the upper limit of distribution of evergreen broadleaf forest. *Ecological Research*, **6**, 113-125.
- Ferrar, P.J., Slatyer, R.O., & Vranjic, J.A. (1989) Photosynthetic temperature acclimation in *Eucalyptus* species from diverse habitats, and a comparison with *Nerium oleander*. *Australian Journal of Plant Physiology*, **16**, 199-217.
- Fetcher, N., Oberbauer, S.F., & Chazdon, R.L. (1994). Physiological Ecology of Plants. In *La Selva. Ecology and natural history of a neotropical rain forest* (eds L. MacDade, K. Bawa, H. Hespeneide & G. Hartshorn), pp. 128-141. The University of Chicago Press, Chicago.
- Firbank, L.G. & Watkinson, A.R. (1990). On the effects of competition: From monocultures to mixtures. In *Perspectives On Plant Competition* (eds J. Grace & D. Tilman), pp. 165-192. Academic Press Inc., San Diego.
- Fitzpatrick, E.A. & Nix, H.A. (1970). The climatic factor in Australian grassland ecology. In *Australian Grasslands* (ed R.M. Moore), pp. 3-26. ANU Press, Canberra.

- Floyd, A.G. (1989) Rainforest Trees of Mainland and South-east Australia. Inkata Press, Melbourne.
- Floyd, A.G. (1990) Australian rainforests in New South Wales. Surrey Beatty & Sons, Chipping Norton, N.S.W.
- Ford, M.A. & Thorne, G.N. (1974) Effects of atmospheric humidity on plant growth. *Annals of Botany*, **38**, 441-452.
- Forseth, I.N. & Ehleringer, J.R. (1982) Ecophysiology of two solar-tracking desert winter annuals. I Photosynthetic acclimation to growth temperature. *Australian Journal of Plant Physiology*, **9**, 321-332.
- Forster, P.I. (1992) A taxonomic revision of *Alstonia* (Apocynaceae) in Australia. *Australian Systematic Botany*, **5**, 745-760.
- Francis, W.D. (1981) Australian Rain-Forest Trees. Australian Government Publishing Service, Canberra.
- Franklin, J. (1998) Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. *Journal of Vegetation Science*, **9**, 733-748.
- Franks, P.J. & Farquhar, G.D. (1999) A relationship between humidity response, growth form and photosynthetic operating point in C3 plants. *Plant, Cell & Environment*, **22**, 1337-1349.
- Frensch, J. & E.-D., S. (1988) The effect of humidity and light on cellular water relations and diffusion conductance of leaves of *Tradescantia virginiana* L. *Planta*, **173**, 554-562.
- Frith, C.B. & Frith, D.W. (1985) Seasonality of insect abundance in an Australian upland tropical rainforest. *Australian Journal of Ecology*, **10**, 237-248.
- Gates, D.M. (1980) Biophysical Ecology. Springer-Verlag, Berlin.
- Gavilán, R. & Fernández-González, F. (1997) Climatic discrimination of Mediterranean broad-leaved sclerophyllous and deciduous forests in central Spain. *Journal of Vegetation Science*, **8**, 377-386.
- Gifford, R.M., Thorne, J.H., Hitz, W.D., & Giaquinta, R.T. (1984) Crop productivity and photoassimilate partitioning. *Science*, **225**, 801-808.
- Gilbert, J.M. (1959) Forest succession in the Florentine Valley, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*, **93**, 129-151.
- Gisleröd, H.R., Selmer-Olsen, A.R., & Mortensen, L.M. (1987) The effect of humidity on nutrient uptake of some greenhouse plants. *Plant and Soil*, **102**, 193-196.
- Givnish, T.J. (1979). On the adaptive significance of leaf form. In *Topics in Plant Population Biology* (eds O.T. Solbrig, S. Jain, G.B. Johnson & P.H. Raven), pp. 375-407. Columbia University Press, New York.
- Goldstein, G., Drake, D.R., & Melcher, P. (1996) Photosynthetic gas exchange and temperature-induced damage in seedlings of the tropical alpine species *Argyroxiphium sandwicense*. *Oecologia*, **106**, 298-307.

- Goldstein, G., Meinzer, F.C., & Rača, F. (1994). Environmental biology of a tropical treeline species, *Polylepis sericea*. In *Tropical Alpine Environments. Plant Form and Function* (eds P.W. Rundel, A.P. Smith & F.C. Meinzer), pp. 129-149. Cambridge University Press, Melbourne.
- Good, R.E. & Good, N.F. (1976) Growth analysis of Pitch Pine seedlings under three temperature regimes. *Forest Science*, **22**, 445-448.
- Gowin, T., Lourtoux, A., & Mousseau, M. (1980) Influence of constant growth temperature upon the productivity and gas exchange of seedlings of Scots Pine and European Larch. *Forest Science*, **26**, 301-309.
- Grace, J. (1988). Temperature as a determinant of plant productivity. In *Plants and Temperature* (eds S.P. Long & F.I. Woodward), pp. 91-107. The Company of Biologists Ltd., Cambridge.
- Graham, D. & Patterson, B.D. (1982) Response of plants to low, nonfreezing temperatures: proteins, metabolism and acclimation. *Annual Review Plant Physiology*, **33**, 347-372.
- Grange, R.I. & Hand, D.W. (1987) A review of the effects of atmospheric humidity on the growth of horticultural crops. *Journal of Horticultural Science*, **62**, 125-134.
- Green, J.W. (1969) Temperature responses in altitudinal populations of *Eucalyptus pauciflora* Sieb. ex Spreng. *New Phytologist*, **68**, 399-410.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. Wiley, Chichester, Great Britain.
- Groves, R.H. (1978) Growth of heath vegetation. IV Effects of temperature on growth of *Banksia ornata*, *B. serrata* and *B. serratifolia*. *Australian Journal of Botany*, **26**, 45-51.
- Grubb, P.J. (1977) Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrient. *Annual Review of Ecology and Systematics*, **8**, 83-107.
- Gunderson, C.A., Norby, R.J., & Wullschlegel, S.D. (2000) Acclimation of photosynthesis and respiration to stimulated climatic warming in northern and southern populations of *Acer saccharum*: laboratory and field evidence. *Tree Physiology*, **20**, 87-96.
- Haase, P. (1990) Environmental and floristic gradients in Westland, New Zealand and the discontinuous distribution of *Nothofagus*. *New Zealand Journal of Botany*, **28**, 25-40.
- Hallgren, J.-E., Sundbom, E., & Strand, M. (1982) Photosynthetic responses to low temperature in *Betula pubescens* and *Betula tortuosa*. *Physiologia Plantarum*, **54**, 275-282.
- Han, B., Berjak, P., Pammenter, N., Farrant, J., & Kermode, A. (1997) The recalcitrant plant species, *Castanospermum australe* and *Trichilia dregeana*, differ in their ability to produce dehydrin-related polypeptides during seed maturation and in response to ABA or water-deficit-related stresses. *Journal of Experimental Botany*, **48**, 1717-1726.

- Hand, D.W., Langton, F.A., Hannah, M.A., & Cockshull, K.E. (1996) Effects of humidity on the growth and flowering of cut-flower chrysanthemums (*Dendranthema grandiflora* Tzvelev). *Journal of Horticultural Science*, **71**, 227-234.
- Harden, G.J. (1990) Flora of New South Wales. Volume 1. New South Wales University Press, Sydney.
- Hawkins, B. & Sweet, G.B. (1989) Evolutionary interpretation of a high temperature growth response in five New Zealand forest tree species. *New Zealand Journal of Botany*, **27**, 101-107.
- Haxeltine, A., Prentice, I.C., & Creswell, I.D. (1996) A coupled carbon and water flux model to predict vegetation structure. *Journal of Vegetation Science*, **7**, 651-666.
- Heichel, G.H. & Turner, N.C. (1983) CO₂ assimilation of primary and regrowth foliage of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.): responses to defoliation. *Oecologia*, **57**, 14-19.
- Hellmers, H. (1966) Growth response of Redwood seedlings to thermoperiodism. *Forest Science*, **12**, 276-283.
- Hellmers, H. & Rook, D.A. (1973) Air temperature and growth of Radiata Pine seedlings. *New Zealand Journal of Forestry Science*, **3**, 271-285.
- Henley, W.J. (1993) Measurement and interpretation of photosynthetic light-response curves in algae in the context of photoinhibition and diel changes. *Journal of Phycology*, **29**, 729-739.
- Hermann, R.K. (1977). Growth and production of tree roots. In *The Belowground Ecosystem: a synthesis of plant-associated processes* (ed J.K. Marshall), pp. 7-28. Colorado State University, Fort Collins, Colorado.
- Herwitz, S.R. (1993) Growth rates of selected Australian tropical rainforest tree species under controlled conditions. *Oecologia*, **96**, 232-238.
- Hickey, J.E., Blakesley, A.J., & Turner, B. (1983) Seedfall and germination of *Nothofagus cunninghamii* (Hook.) Oerst., *Eucryphia lucida* (Labill.) Baill. and *Atherosperma moschatum* Labill. Implications for regeneration practice. *Australian Forest Research*, **13**, 21-28.
- Hill, R.S. & Dettmann, M.E. (1996). Origin and diversification of the genus *Nothofagus*. In *The Ecology and Biogeography of Nothofagus Forests* (eds T.T. Veblen, R.S. Hill & J. Read), pp. 11-24. Yale University Press, London.
- Hill, R.S. & Read, J. (1987) Endemism in Tasmanian cool temperate rainforest: alternative hypotheses. *Botanical Journal of the Linnean Society*, **95**, 113-124.
- Hill, R.S., Read, J., & Busby, J.R. (1988) The temperature-dependence of photosynthesis of some Australian temperate rainforest trees and its biogeographical significance. *Journal of Biogeography*, **15**, 431-449.
- Hinckley, T.M., Duhme, F., Hinckley, A.R., & Richter, H. (1983) Drought relations of shrub species: assessment of the mechanisms of drought resistance. *Oecologia*, **59**, 344-350.
- Hodgkinson, K.C. & Quinn, J.A. (1976) Adaptive variability in the growth of *Danthonia caespitosa* Gaud. populations at different temperatures. *Australian Journal of Botany*, **24**, 381-396.

- Hoffman, G.J. (1979). Humidity. In *Controlled Environment Guidelines for Plant Research* (eds T.W. Tibbitts & T.T. Kozlowski), pp. 141-172. Academic Press, Sydney.
- Hogan, K.P., Smith, A.P., Araus, J.L., & Saavedra, A. (1994) Ecotypic differentiation of gas exchange responses and leaf anatomy in a tropical forest understorey shrub from areas of contrasting rainfall regimes. *Tree Physiology*, **14**, 819-831.
- Holder, R. & Cockshull, K.E. (1990) Effects of humidity on the growth and yield of glasshouse tomatoes. *Journal of Horticultural Science*, **65**, 31-39.
- Holdridge, L.R. (1947) Determination of world plant formations from simple climate data. *Science*, **105**, 367-368.
- Hollinger, D.Y. (1987) Gas exchange and dry matter allocation responses to elevation of atmospheric carbon dioxide concentration in seedlings of three tree species. *Tree Physiology*, **3**, 193-202.
- Hope, G.S. (1994). Quaternary vegetation. In *History of the Australian Vegetation: Cretaceous to Recent* (ed R.S. Hill), pp. 368-389. Cambridge University Press, Cambridge.
- Hopkins, M.S. & Graham, A.W. (1989) Community phenology patterns of lowland tropical rainforest in north-eastern Australia. *Australian Journal of Ecology*, **14**.
- Houlder, D., Hutchinson, M., Nix, H., & McMahon, J. (1999) ANUCLIM user's guide. CRES Publications, Canberra.
- Howard, T.M. (1973) Studies in the ecology of *Nothofagus cunninghamii* Oerst. II. Phenology. *Australian Journal of Botany*, **21**, 79-92.
- Howard, T.M. (1981). Southern closed-forests. In *Australian Vegetation* (ed R.H. Groves), pp. 102-120. Cambridge University Press, Melbourne.
- Howard, T.M. & Ashton, D.H. (1973) The distribution of *Nothofagus cunninghamii* rainforest. *Proceedings of the Royal Society of Victoria*, **85**, 47-75.
- Hunter, J.H., Hsiao, A.I., & McIntyre, G.I. (1985) Some effects of humidity on the growth and development of *Cirsium arvense*. *Botanical Gazette*, **146**, 483-488.
- Huntley, B., Berry, P.M., Cramer, W., & McDonald, A.P. (1995) Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography*, **22**, 967-1001.
- Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbour Symposia on Quantitative Biology*, **22**, 415-427.
- Hyland, B.P.M. (1980) A revision of *Syzygium* in Australia. *Australian Journal of Botany Supplementary Series*, **9** 1-164.
- Jabeen, C. & Abraham, S. (1998) Histological changes in *Lagerstroemia reginae* and *Alstonia scholaris* exposed to air pollutants. *Journal of Environmental Biology*, **19**, 79-82.
- Jackson, R.D., Idso, S.B., Reginato, R.J., & Pinter, P.J. (1981) Canopy temperature as a crop water stress indicator. *Water Resources Research*, **17**, 1133-1138.
- Jackson, W.D. (1968) Fire, air, water and earth - an elemental ecology of Tasmania. *Proceedings of the Ecological Society of Australia*, **3**, 9-16.

- Jacobs, M.R. (1981) Eucalypts for Planting. FAO, Rome.
- Jane, G.T. (1983) Mortality of Native Forest Vegetation in the Kaimai Ranges, University of Waikato.
- Janzen, D.H. (1967) Why mountain passes are higher in the tropics. *The American Naturalist*, **101**, 233-246.
- Jarman, S.J., Kantvilas, G., & Brown, M.J. (1994) Phytosociological studies in Tasmanian cool temperate rainforest. *Phytocoenologia*, **22**, 355-390.
- Jarvis, P.G. (1964) The adaptability to light intensity of seedlings of *Quercus petraea* (Matt.) Liebl. *Journal of Ecology*, **52**, 545-571.
- Jarvis, P.G. & Leverenz, J.W. (1983). Productivity of temperate, deciduous and evergreen forests. In *Physiological Plant Ecology. IV. Ecosystem Processes* (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler), pp. 233-280. Springer, New York.
- Johnson, D.A. & Caldwell, M.M. (1976) Water potential components, stomatal function and liquid phase water transport resistances of four arctic and alpine species in relation to moisture stress. *Physiologia Plantarum*, **36**, 271-278.
- Jones, M.M., Turner, N.C., & Osmond, C.B. (1981). Mechanisms of drought resistance. In *The Physiology and Biochemistry of Drought Resistance in Plants* (eds L.G. Paleg & D. Aspinall), pp. 15-37. Academic Press, Sydney.
- Kam, T.-S., Nyeoh, K.-T., Sim, K.-M., & Yoganathan, K. (1997) Alkaloids from *Alstonia scholaris*. *Phytochemistry*, **45**, 1303-1305.
- Kaspar, T.C. & Bland, W.L. (1992) Soil temperature and root growth. *Soil Science*, **154**, 290-299.
- Kawamitsu, Y., Yoda, S., & Agata, W. (1993) Humidity pretreatment affects the response of stomata and CO₂ assimilation to vapour pressure differences in C₃ and C₄ plants. *Plant and Cell Physiology*, **34**, 113-119.
- Kemp, E.M. (1981). Tertiary palaeogeography and the evolution of Australian climate. In *Ecological Biogeography of Australia* (ed A. Keast), pp. 31-49. Dr. W. Junk bv Publishers, The Hague.
- Kemp, P.R. & Williams, I., G. J. (1980) A physiological basis for niche separation between *Agropyron smithii* (C₃) and *Bouteloua gracilis*. *Ecology*, **61**, 846-858.
- Kemp, P.R., Williams III, G.J., & May, D.S. (1977) Temperature relations of gas exchange in altitudinal populations of *Taraxacum officinale*. *Canadian Journal of Botany*, **55**, 2496-2502.
- Kenkel, N.C. & Orloci, L. (1986) Applying metric and nonmetric multidimensional scaling to some ecological studies: some new results. *Ecology*, **67**, 919-928.
- Kershaw, A.P. (1988). Australiasia. In *Vegetation History* (eds B. Huntley & T.I. Webb), Vol. 7, pp. 237-306. Kluwer Academic Publishers, London.
- Kershaw, P. (1981) Climate and Australian flora. *Australian Natural History*, **20**, 231-234.
- Khairi, M.M.A. & Hall, A.E. (1976) Temperature and humidity effects on net photosynthesis and transpiration of citrus. *Physiologia Plantarum*, **36**, 29-34.

- Khan, A.M., Pandey, V., Yunus, M., & Ahmad, K.J. (1989) Plants as dust scavengers a case study. *Indian Forester*, **115**, 670-672.
- Kirkpatrick, J.B. & Gibson, N. (1999) Towards an explanation of the altitudinal distributions of three species of *Eucalyptus* in central Tasmania. *Australian Journal of Ecology*, **24**, 123-131.
- Kirschbaum, M.U.F. (2000) Forest growth and species distribution in a changing climate. *Tree Physiology*, **20**, 309-322.
- Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, **98**, 419-428.
- Kitajima, K. (1996). Ecophysiology of tropical tree seedlings. In *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 559-596. Chapman & Hill, Melbourne.
- Kleinendorst, A. & Veen, B.W. (1983) Responses of young cucumber plants to root and shoot temperatures. *Netherlands Journal of Agricultural Science*, **31**, 47-61.
- Klepper, B. (1991). Root-shoot relationships. In *Plant Roots. The Hidden Half* (eds Y. Waisel, A. Eshel & U. Kafafi), pp. 265-286. Marcel Dekker, Inc., New York.
- Kohlmann, B., Nix, H., & Shaw, D.D. (1988) Environmental predictions and distributional limits of chromosomal taxa in the Australian grasshopper *Caledia captiva* (F.). *Oecologia*, **75**, 483-493.
- Körner, C. (1991) Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. *Functional Ecology*, **5**, 162-173.
- Körner, C. & Bannister, P. (1985) Stomatal responses to humidity in *Nothofagus menziesii*. *New Zealand Journal of Botany*, **23**, 425-429.
- Körner, C. & Diemer, M. (1987) *In situ* photosynthetic responses to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. *Functional Ecology*, **1**, 179-194.
- Körner, C. & Larcher, W. (1988). Plant life in cold climates. In *Plants and Temperature* (eds S.P. Long & F.I. Woodward), pp. 25-57. The Company of Biologists Ltd., Cambridge.
- Körner, C. & Woodward, F.I. (1987) The dynamics of leaf extension in plants with diverse altitudinal ranges. II. Field studies in *Poa* species between 600 and 3200m altitude. *Oecologia*, **72**, 279-283.
- Kozłowski, T.T. & Pallardy, S.G. (1997a) Growth Control in Woody Plants. Academic Press, San Diego.
- Kozłowski, T.T. & Pallardy, S.G. (1997b) Physiology of Woody Plants. 2nd edn. Academic Press, San Diego.
- Krol, M. & Huner, N.P.A. (1985) Growth and development at cold hardening temperatures. Pigment and benzoquinone accumulation in winter rye. *Canadian Journal of Botany*, **63**, 715-721.
- Kwesiga, F.R., Grace, J., & Sandford, A.P. (1986) Some photosynthetic characteristics of tropical timber trees as affected by the light regime during growth. *Annals of Botany*, **58**, 23-32.

- Lambers, H. (1987) Does variation in photosynthetic rate explain variation in growth rate and yield? *Netherlands Journal of Agricultural Science*, **35**, 505-519.
- Lambers, H. & Dijkstra, P. (1987). A physiological analysis of genotypic variation in relative growth rate: Can growth confer ecological advantage? In *Disturbance in Grasslands* (eds J. van Andel, J.B. Bakker & R.W. Snaydon), pp. 237-252. Dr. W. Junk Publishers, Dordrecht.
- Landsberg, J.J. (1986) *Physiological Ecology of Forest Production*. Academic Press, London.
- Lange, O.L., Schulze, E.-D., Evenari, M., Kappen, L., & Buschbom, U. (1974) The temperature-related photosynthetic capacity of plants under desert conditions I. Seasonal changes of the photosynthetic response to temperature. *Oecologia*, **17**, 97-110.
- Langenheim, J.H., Osmond, C.B., Brooks, A., & Ferrar, P.J. (1984) Photosynthetic responses to light in seedlings of selected Amazonian and Australian rainforest tree species. *Oecologia*, **63**, 215-224.
- Larcher, W. (1969) The effect of environmental and physiological variables on the carbon dioxide gas exchange of trees. *Photosynthetica*, **3**, 167-198.
- Larcher, W. (1980) *Physiological Plant Ecology*. Springer-Verlag, Berlin.
- Larcher, W. & Bauer, H. (1981). Ecological significance of resistance to low temperature. In *Encyclopedia of Plant Physiology. Physiological Plant Ecology. Vol. 12A. Responses to the Physical Environment*. (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler), pp. 403-437. Springer-Verlag, Berlin.
- Leathwick, J.R. (1995) Climatic relationships of some New Zealand forest tree species. *Journal of Vegetation Science*, **6**, 237-248.
- Leathwick, J.R. (1998) Are New Zealand's *Nothofagus* species in equilibrium with their environment? *Journal of Vegetation Science*, **9**, 719-732.
- Leathwick, J.R. & Mitchell, N.D. (1992) Forest pattern, climate and vulcanism in central North Island, New Zealand. *Journal of Vegetation Science*, **3**, 603-616.
- Lechowicz, M.J. (1995) Seasonality of flowering and fruiting in temperate forest trees. *Canadian Journal of Botany*, **73**, 175-182.
- Ledig, F.T. & Korbobo, D.R. (1983) Adaptation of Sugar Maple populations along altitudinal gradients: photosynthesis, respiration, and specific leaf weight. *American Journal of Botany*, **70**, 256-265.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. 2nd edn. Elsevier, New York.
- Leniham, J.M. (1993) Ecological response surfaces for North American boreal tree species and their use in forest classification. *Journal of Vegetation Science*, **4**, 667-680.
- Leverenz, J.W. (1987) Chlorophyll content and the light response curve of shade-adapted conifer needles. *Physiologia Plantarum*, **71**, 20-29.
- Li, W.K.W. (1985) Photosynthetic response to temperature of marine phytoplankton along a latitudinal gradient 16 degrees north to 74 degrees north. *Deep Sea Research Part I Oceanographic Research Papers*, **32**, 1381-1392.

- Lindenmayer, D.B., Mackey, B.G., Cunningham, R.B., Donneily, C.F., Mullen, I.C., McCarthy, M.A., & Gill, A.M. (2000) Factors affecting the presence of the cool temperate rain forest tree myrtle beech (*Nothofagus cunninghamii*) in southern Australia: Integrating climatic, terrain and disturbance predictors of distribution patterns. *Journal of Biogeography*, **27**, 1001-1009.
- Lipton, W.J. (1970) Growth of tomato plants and fruit production in high humidity and high temperature. *Journal of the American Society of Horticultural Science*, **95**, 674-680.
- Lloyd, J. (1991) Modelling stomatal responses to environment in *Macadamia integrifolia*. *Australian Journal of Plant Physiology*, **18**, 649-660.
- Loach, K. (1967) Shade tolerance in tree seedlings. I. Leaf photosynthesis and respiration in plants raised under artificial shade. *New Phytologist*, **66**, 607-621.
- Loehle, C. (1998) Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography*, **25**, 735-742.
- Looman, J. (1983) Distribution of plant species and vegetation types in relation to climate. *Vegetatio*, **54**, 17-25.
- Lösch, R. (1979). Stomatal responses to changes in air humidity. In *Structure Function and Ecology of Stomata* (eds D.N. Sen, D.D. Chawan & R.P. Bansal), pp. 189-216. Bishen Singh Mahendra Pal Singh, Dehra Dun.
- Lowman, M.D. (1992) Leaf growth dynamics and herbivory in five species of Australian rainforest canopy trees. *Journal of Ecology*, **80**, 433-447.
- Ludlow, M.M. (1980). Adaptive significance of stomatal responses to water stress. In *Adaptation of plants to water and high temperature stress* (eds N.C. Turner & P.J. Kramer), pp. 123-138. John Wiley & Sons, Inc., New York.
- Ludlow, M.M. (1989). Strategies of response to water stress. In *Structural and functional responses to environmental stresses* (eds K.H. Kreeb, H. Richter & T.M. Hinckley), pp. 269-281. SPB Academic Publishing bv., The Hague, The Netherlands.
- Lugo, A.E., Gonzales-Liboy, J.A., Cintron, B., & Dugger, K. (1978) Structure, productivity and transpiration of a subtropical dry forest in Puerto Rico. *Biotropica*, **278-291**.
- Luo, Y.-H. & Strain, B.R. (1992) Alteration of components of leaf water potential and water content in Velvetleaf under the effects of long-term humidity difference. *Plant Physiology*, **98**, 966-970.
- MacArthur, R.H. (1972) *Geographical Ecology: Patterns in the Distribution of Species*. Harper & Row, New York.
- Mackey, B.G. (1993a) A spatial analysis of the environmental relations of rainforest structural types. *Journal of Biogeography*, **20**, 303-336.
- Mackey, B.G. (1993b) Predicting the potential distribution of rain-forest structural characteristics. *Journal of Vegetation Science*, **5**, 43-54.
- Macphail, M.K., Alley, N., Truswell, E.M., & Sluiter, I.R.K. (1994). Early Tertiary vegetation: evidence from spores and pollen. In *History of the Australian Vegetation: Cretaceous to Recent* (ed R.S. Hill), pp. 189-262. Cambridge University Press, Cambridge.

- Mahan, J.R., McMichael, B.L., & Wanjura, D.F. (1995) Methods for reducing the adverse effects of temperature stress on plants: A review. *Environmental & Experimental Botany*, **35**, 251-258.
- Mahan, J.R. & Upchurch, D.R. (1988) Maintenance of constant leaf temperature by plants. I. Hypothesis - limited homeothermy. *Environmental and Experimental Botany*, **28**, 351-357.
- Maier, C.A. & Teskey, R.O. (1992) Internal and external control of photosynthesis and stomatal conductance of mature eastern white pine (*Pinus strobus*). *Canadian Journal of Forest Research*, **22**, 1387-1394.
- Mansfield, T.A. & Davies, W.J. (1981). Stomata and stomatal mechanisms. In *The Physiology and Biochemistry of Drought Resistance in Plants* (eds L.G. Paleg & D. Aspinall), pp. 315-346. Academic Press, Sydney.
- Marcelis, L.F.M. (1994) Effect of fruit growth, temperature and irradiance on biomass allocation to the vegetative parts of cucumber. *Netherlands Journal of Agricultural Science*, **42**, 115-123.
- Maroco, J.P., Periera, J.S., & Chaves, M.M. (1997) Stomatal responses to leaf-to-air vapour pressure deficit in Sahelian species. *Australian Journal of Plant Physiology*, **24**, 381-387.
- Marsden, B.J., Lieffers, V.J., & Zwiazek, J.J. (1996) The effect of humidity on photosynthesis and water relations of white spruce seedlings during the early establishment phase. *Canadian Journal of Forest Research*, **26**, 1015-1021.
- Martin, H.A. (1987) Cainozoic history of the vegetation and climate of the Lachlan River region. *Proceedings of the Linnean Society of New South Wales*, **109**, 213-257.
- McCree, K.J. & Anthor, M.E. (1982) Effects of diurnal variation in temperature on the carbon balances of white clover plants. *Crop Science*, **22**, 822-827.
- McNaughton, S.J. (1973) Comparative photosynthesis of Quebec and California ecotypes of *Typha latifolia*. *Ecology*, **54**, 1260-1270.
- McNaughton, S.J., Campbell, R.S., Freyer, R.A., Mylroie, J.E., & Rodland, K.D. (1974) Photosynthetic properties and root chilling responses of altitudinal ecotypes of *Typha latifolia* L. *Ecology*, **55**, 168-172.
- Medina, E. (1983). Adaptations of tropical trees to moisture stress. In *Ecosystems of the World 14A. Tropical Rain Forest Ecosystems. Structure and Function* (ed F.B. Golley). Elsevier Scientific Publishing Company, New York.
- Meena, S., Sirohi, S., & Singh, O.S. (1990) Structure and differentiation of laticifers in the shoot apices of *Alstonia scholaris* (L.) R. Br. *Acta Botanica Indica*, **18**, 64-66.
- Meinzer, C.M. (1982) The effect of vapour pressure on stomatal control of gas exchange in Douglas Fir (*Pseudotsuga menziesii*) saplings. *Oecologia*, **54**, 236-242.
- Meinzer, F., Goldstein, G., & Jaimes, M. (1984) The effect of atmospheric humidity on stomatal control of gas exchange in two tropical coniferous species. *Canadian Journal of Botany*, **62**, 591-595.
- Meinzer, F.C. (1993) Stomatal control of transpiration. *Trends in Ecology & Evolution*, **8**, 289-294.

- Meinzer, F.C., Goldstein, G., Holbrook, N.M., Jackson, P., & Cavelier, J. (1993) Stomatal and environmental control of transpiration in a lowland tropical forest tree. *Plant, Cell and Environment*, **16**, 429-436.
- Melick, D.R. (1990a) Regenerative succession of *Tristaniopsis laurina* and *Acmena smithii* in riparian warm temperate rainforest in Victoria, in relation to light and nutrient regimes. *Australian Journal of Botany*, **38**, 111-120.
- Melick, D.R. (1990b) Relative drought resistance of *Tristaniopsis laurina* and *Acmena smithii* from riparian warm temperate rainforest in Victoria. *Australian Journal of Botany*, **38**, 361-370.
- Melick, D.R. (1990c) Flood resistance of *Tristaniopsis laurina* and *Acmena smithii* from riparian warm temperate rainforest in Victoria. *Australian Journal of Botany*, **38**, 371-81.
- Melick, D.R. & Ashton, D.H. (1991) The effects of natural disturbances on warm temperate rainforests in south-eastern Australia. *Australian Journal of Botany*, **39**, 1-30.
- Milner, H.W. & Hiesey, W.M. (1964) Photosynthesis in climatic races of *Mimulus*. I. Effect of light intensity and temperature on rate. *Plant Physiology*, **39**, 208-213.
- Minchin, P.R. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio*, **69**, 89-107.
- Mitchell, N.D. (1991) The derivation of climate surfaces for New Zealand and their application to the bioclimatic analysis of the distribution of kauri (*Agathis australis*). *Journal of the Royal Society of New Zealand*, **21**, 13-24.
- Monson, R.K. (1984) A field study of photosynthetic temperature acclimation in *Carex eleocharis* Bailey. *Plant, Cell and Environment*, **7**, 301-308.
- Monson, R.K., Littlejohn, R.O., & Williams, G.J. (1983) Photosynthetic adaptation to temperature in four species from Colorado shortgrass steppe: a physiological model for coexistence. *Oecologia*, **58**, 43-51.
- Monson, R.K. & Szarek, S.R. (1979) Ecophysiological studies of Sonoran desert plants. V. Photosynthetic adaptations of *Machaeranthera gracilis*, a winter annual. *Oecologia*, **41**, 317-327.
- Mooney, H.A. (1980) Photosynthetic plasticity of populations of *Heliotropium curassavicum* L. originating from differing thermal regimes. *Oecologia*, **45**, 372-376.
- Mooney, H.A. & Billings, W.D. (1961) Comparative physiological ecology of arctic and alpine populations of *Oxyria digyna*. *Ecological Monographs*, **31**, 1-29.
- Mooney, H.A., Björkman, O., & Collatz, G.J. (1978a) Photosynthetic acclimation to temperature in the desert shrub, *Larrea divaricata*. I. Carbon dioxide exchange characteristics of intact leaves. *Plant Physiology*, **61**, 406-410.
- Mooney, H.A., Björkman, O., Ehleringer, J., & Berry, J. (1976) Photosynthetic capacity of *in situ* Death Valley plants. *Carnegie Institution of Washington Yearbook*, **75**, 410-413.
- Mooney, H.A. & Chiariello, N.R. (1984). The study of plant function - the plant as a balanced system. In *Perspectives on Plant Population Ecology* (eds R. Dirzo & J. Sarukhan), pp. 305-323. Sinauer Associates, Inc., Sunderland, Massachusetts.

- Mooney, H.A. & Chu, C. (1983) Stomatal responses to humidity of coastal and interior populations of a Californian shrub. *Oecologia*, **57**, 148-150.
- Mooney, H.A., Ferrar, P.J., & Slatyer, R.O. (1978b) Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. *Oecologia*, **36**, 103-111.
- Mooney, H.A., Field, C., Gulmon, S.L., Rundel, P., & Kruger, F.J. (1983) Photosynthetic characteristics of South African sclerophylls. *Oecologia*, **58**, 398-401.
- Mooney, H.A. & West, M. (1964) Photosynthetic acclimation of plants of diverse origin. *American Journal of Botany*, **51**, 825-827.
- Mooney, H.A., Wright, R.D., & Strain, B.R. (1964) The gas exchange capacity of plants in relation to vegetation zonation in the White Mountains of California. *American Midland Naturalist*, **72**, 281-297.
- Moore, D.J., Nowak, R.S., & Nowak, C.L. (1998) Photosynthetic acclimation to temperature and drought in the endemic Chelan rockmat, *Petrophytum cinerascens* (Rosaceae). *American Midland Naturalist*, **139**, 374-382.
- Morgan, D.C., Warrington, I.J., & Halligan, E.A. (1985) Effect of temperature and photosynthetic photon flux density on vegetative growth of kiwifruit (*Actinidia chinensis*). *New Zealand Journal of Agricultural Research*, **28**, 109-116.
- Mori, T., Nakashizuka, T., Sumizono, T., & Yap, S.K. (1990) Growth and photosynthetic responses to temperature in several Malaysian tree species. *Journal of Tropical Forest Science*, **3**, 44-57.
- Morris, J.D. (1977) Effects of Temperature on the Growth and Physiology of Eucalypts. Ph.D. Thesis. Department of Forestry, School of General Studies, Australian National University, Canberra.
- Mortensen, L.M. (1986) Effect of relative humidity on growth and flowering of some greenhouse plants. *Scientia Horticulturae*, **29**, 301-308.
- Mortley, D.G., Bonsi, C.K., Loretan, P.A., Hill, W.A., & Morris, C.E. (1994) Relative humidity influences yield, edible biomass, and linear growth rate of sweet potato. *Hortscience*, **29**, 609-610.
- Mueller, R.J. (1985) Determinate branch development in *Alstonia scholaris* (Apocynaceae): the plagiotropic module. *American Journal of Botany*, **72**, 1435-1444.
- Mulkey, S.S., Chazdon, R.L., & Smith, A.P. (1996) Tropical Forest Plant Ecophysiology. Chapman and Hill, London.
- Mulkey, S.S. & Wright, S.J. (1996). Influence of seasonal drought on the carbon balance of tropical forest plants. In *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 187-216. Chapman and Hill, London.
- Murtadha, H.M., Maranville, J.W., Clark, R.B., & Clegg, M.D. (1989) Effects of temperature and relative humidity on growth and calcium uptake, translocation, and accumulation in sorghum. *Journal of Plant Nutrition*, **12**, 535-545.
- Myers, B.J., Robichaux, R.H., Unwin, G.L., & Craig, I.E. (1987) Leaf water relations and anatomy of a tropical rainforest tree species vary with crown position. *Oecologia*, **74**, 81-85.

- Neilson, R.E., Ludlow, M.M., & Jarvis, P.G. (1972) Photosynthesis in Sitka Spruce (*Picea sitchensis* (Bong.) Carr.). II Response to temperature. *Journal of Applied Ecology*, 9, 721-745.
- Neilson, R.P. (1995) A model for predicting continental-scale vegetation distribution and water balance. *Ecological Applications*, 5, 362-385.
- Newell, E.A., McDonald, E.P., Strain, B.R., & Denslow, J.S. (1993) Photosynthetic responses of *Miconia* species to canopy openings in a lowland tropical rainforest. *Oecologia*, 94, 49-56.
- Ni, B.R. & Pallardy, S.G. (1991) Response of gas exchange to water stress in seedlings of woody angiosperms. *Tree Physiology*, 8, 1-10.
- Nix, H.A. (1982). Environmental determinants of biogeography and evolution in Terra Australis. In *Evolution of the Flora and Fauna of Arid Australia* (eds W.R. Barker & P.J.M. Greensdale), pp. 47-66. Peacock Publications, Frewville, SA.
- Nix, H.A. (1991). An environmental analysis of Australian rainforests. In *The Rainforest Legacy. Australian National Rainforests Study Vol. 2 Flora and Fauna of the Rainforests* (eds G. Werren & P. Kershaw), pp. 1-26. Australian Government Publishing Service, Canberra.
- Oberbauer, S.F. & Strain, B.R. (1984) Photosynthesis and successional status of Costa Rican rain forest trees. *Photosynthesis Research*, 5, 227-232.
- Oberbauer, S.F. & Strain, B.R. (1985) Effects of light regime on the growth and physiology of *Pentaclethra macroloba* (Mimosaceae). *Journal of Tropical Ecology*, 1, 303-320.
- Odening, W.R., Strain, B.R., & Oechel, W.C. (1974) The effect of decreasing water potential on net CO₂ exchange of intact desert shrubs. *Ecology*, 55, 1086-1095.
- Odum, H.T., Lugo, A., Cintron, G., & Jordan, C.F. (1970). Metabolism and evapotranspiration in some rain forest plants and soils. In *A Tropical Rainforest* (eds H.T. Odum & F. Pigeon), pp. H3-H52. U. S. Atomic Energy Commission, Oak Ridge.
- Oechel, W.C., Lawrence, W., Mustafa, J., & Martinez, J. (1981). Energy and carbon acquisition. In *Resource Use by Chaparral and Matorral. A comparison of vegetation function in two Mediterranean type ecosystems* (ed P.C. Miller), pp. 151-183. Springer-Verlag, New York.
- Opeke, L.K. (1982) Tropical Tree Crops. Wiley, New York.
- Öquist, G. (1983) Effects of low temperature on photosynthesis. *Plant Cell and Environment*, 6, 281-300.
- Osmond, C.B. (1987) Photosynthetic and carbon economy of plants. *New Phytologist*, 106, 161-175.
- Osonubi, O. & Davies, W.J. (1980) The influence of plant water stress on stomatal control of gas exchange at different levels of atmospheric humidity. *Oecologia*, 46, 1-6.
- Osunkoya, O.O., Ash, J.E., Hopkins, M.S., & Graham, A.W. (1992) Factors affecting survival of tree seedlings in North Queensland rainforests. *Oecologia*, 91, 569-578.

- Park, S.-Y. & Furukawa, A. (1999) Photosynthetic and stomatal responses of two tropical and two temperate trees to atmospheric humidity. *Photosynthetica*, **36**, 181-186.
- Parker, A.J. (1994) Latitudinal gradients of coniferous tree species, vegetation, and climate in the Sierran-Casade axis of Northern California. *Vegetatio*, **115**, 145-155.
- Parkhurst, D.F., Duncan, P.R., Gates, D.M., & Kreith, F. (1968) Wind-tunnel modelling of convection of heat between air and broad leaves of plants. *Agricultural Meteorology*, **3**, 241-246.
- Parkhurst, D.F. & Loucks, O.L. (1972) Optimal leaf size in relation to environment. *Journal of Ecology*, **60**, 505-537.
- Paton, D.M. (1980) *Eucalyptus* physiology. II. Temperature responses. *Australian Journal of Botany*, **28**, 555-566.
- Patterson, D.T. (1980). Light and temperature adaptation. In *Predicting Photosynthesis for Ecosystem Models* (eds J.D. Hesketh & J.W. Jones), Vol. 1, pp. 205-235. CRC Press, Boca Raton, FL.
- Patterson, D.T. & Mortensen, D.A. (1985) Effects of temperature and photoperiod on Common Crupina (*Crupina vulgaris*). *Weed Science*, **33**, 333-339.
- Paul, M.J., Lawlor, D.W., & Driscoll, S.P. (1990) The effect of temperature on photosynthesis and carbon fluxes in sunflower and rape. *Journal of Experimental Botany*, **41**, 547-555.
- Pearcy, R.W. (1976) Temperature responses of growth and photosynthetic CO₂ exchange rates in coastal and desert races of *Atriplex lentiformis*. *Oecologia*, **26**, 245-255.
- Pearcy, R.W. (1977) Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex lentiformis* (Torr.) Wats. *Plant Physiology*, **59**, 795-799.
- Pearcy, R.W. (1986). Photosynthetic responses of tropical forest trees. In *Proceedings, International Conference on Tropical Plant Ecophysiology* (eds D. Doley, C.B. Osmond & W. Wongkaew). Biotrop Special Publication No. 31, Bogor.
- Pearcy, R.W. (1987) Photosynthetic gas exchange responses of Australian tropical rainforest trees in canopy, gap and understorey micro-environments. *Functional Ecology*, **1**, 169-178.
- Pearcy, R.W. & Harrison, A.T. (1974) Comparative photosynthetic and respiratory gas exchange characteristics of *Atriplex lentiformis* (Torr.) Wats. in coastal and desert habitats. *Ecology*, **55**, 1104-1111.
- Pearcy, R.W. & Sims, D.A. (1994). Photosynthetic acclimation to changing light environment: scaling from the leaf to the whole plant. In *Exploitation of Environmental Heterogeneity by Plants* (eds M.M. Caldwell & R.W. Pearcy), pp. 145-174. Academic Press, Sydney.
- Penfold, G.C. & Lamb, D. (1999) Species co-existence in an Australian subtropical rain forest: evidence for compensatory mortality. *Journal of Ecology*, **87**, 316-329.
- Penman, H.L. (1948) Natural evaporation from open water, bare soil and grass. *Proceedings of the Royal Society of America*, **193**, 120-145.

- Pereira, J.S. (1994). Gas exchange and growth. In *Ecophysiology of Photosynthesis* (eds E.-D. Schulze & M.M. Caldwell), pp. 147-181. Springer-Verlag, London.
- Pereira, J.S., Tenhunen, J.D., Lange, O.L., Beyschlag, W., Meyer, A., & David, M.M. (1986) Seasonal and diurnal patterns in leaf gas exchange of *Eucalyptus globulus* trees growing in Portugal. *Canadian Journal of Forest Research*, 16, 177-184.
- Pigott, C.D. & Huntley, J.P. (1981) Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. III. Nature and causes of seed sterility. *New Phytologist*, 87, 817-839.
- Pinkard, E.A. & Beadle, C.L. (1998) Regulation of photosynthesis in *Eucalyptus nitens* (Deane and Maiden) Maiden following green pruning. *Trees: Structure and Function*, 12, 366-376.
- Poole, A.L. (1987) Southern Beeches. Science Information Publishing Centre, Wellington.
- Poorter, H. (1990). Interspecific variation in relative growth rate: on ecological causes and physiological consequences. In *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants* (ed H. Lambers). SPB Publishing bv., The Hague, The Netherlands.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A., & Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, 19, 117-134.
- Prentice, I.C., Sykes, M.T., & Cramer, W. (1993) A simulation model for the transient effects of climate change on forest landscapes. *Ecological Modelling*, 65, 51-70.
- Prioul, J.L. & Chartier, P. (1977) Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO₂ fixation: a critical analysis of the methods used. *Annals of Botany*, 41, 789-800.
- Ramos, J. & Grace, J. (1990) The effects of shading on gas exchange of seedlings of four neotropical trees from Mexico. *Functional Ecology*, 4, 667-677.
- Ratkowsky, D.A., Lowry, R.K., McMeekin, T.A., Stokes, A.N., & Chandler, R.E. (1983) Model for bacterial culture growth rate throughout the entire biokinetic temperature range. *Journal of Bacteriology*, 154, 1222-1226.
- Rawson, H.M., Begg, J.E., & Woodward, R.G. (1977) The effect of atmospheric humidity on photosynthesis, transpiration and water use efficiency of leaves of several plant species. *Planta*, 134, 5-10.
- Read, J. (1985) Photosynthetic and growth responses to different light regimes of the major canopy species of Tasmanian cool temperate rainforest. *Australian Journal of Ecology*, 10, 327-334.
- Read, J. (1990) Some effects of acclimation temperature on net photosynthesis in some tropical and extra-tropical Australasian *Nothofagus* species. *Journal of Ecology*, 78, 100-112.
- Read, J. (1991). The dynamics of cool temperate rainforest in Tasmania. In *The Rainforest Legacy. Australian National Rainforest Study*, pp. 147-151. Australian Government Publishing Service, Canberra.

- Read, J. (1992). The long-term survivability of *Nothofagus cunninghamii*-dominated forest. In *Victoria's Rainforests: Perspectives on definition, classification and management* (eds P. Gell & D. Mercer), pp. 133-140. Department of Geography and Environmental Science, Monash University, Melbourne.
- Read, J. (1995) The importance of comparative growth rates in determining the canopy composition of Tasmanian rainforest. *Australian Journal of Botany*, 43, 243-271.
- Read, J. (1998). Pattern and process in rainforest. In *Vegetation of Tasmania* (eds J.B. Reid, R.S. Hill & M.J. Brown). Government Printer, Hobart.
- Read, J. & Brown, M.J. (1996). Ecology of Australian *Nothofagus* forests. In *The Ecology and Biogeography of Nothofagus Forests* (eds T.T. Veblen, R.S. Hill & J. Read), pp. 131-181. Yale University Press, London.
- Read, J. & Busby, J.R. (1990) Comparative responses to temperature of the major canopy species of Tasmanian cool temperate rainforest and their ecological significance. II. Net photosynthesis and climate analysis. *Australian Journal of Botany*, 38, 185-205.
- Read, J. & Farquhar, G. (1991) Comparative studies in *Nothofagus* (Fagaceae). I. Leaf carbon isotope discrimination. *Functional Ecology*, 5, 684-695.
- Read, J. & Hill, R.S. (1985) Photosynthetic responses to light of Australian and Chilean species of *Nothofagus* and their relevance to the rainforest dynamics. *New Phytologist*, 101, 731-742.
- Read, J. & Hill, R.S. (1988a) Comparative responses to temperature of the major canopy species of Tasmanian cool temperate rainforest and their ecological significance. I. Foliar frost resistance. *Australian Journal of Botany*, 36, 131-143.
- Read, J. & Hill, R.S. (1988b) The dynamics of some rainforest associations in Tasmania. *Journal of Ecology*, 76, 558-584.
- Read, J. & Hill, R.S. (1989) The response of some Australian temperate rainforest tree species to freezing temperatures and its biogeographical significance. *Journal of Biogeography*, 16, 21-27.
- Read, J. & Hope, G.S. (1989) Foliar frost resistance of some evergreen tropical and extratropical Australasian *Nothofagus* species. *Australian Journal of Botany*, 37, 361-373.
- Read, J., Hope, G.S., & Hill, R.S. (1990). Integrating historical and ecophysiological studies in *Nothofagus* to examine the factors shaping the development of cool rainforest in southeastern Australia. In *Proceedings of the 13th International Organisation of Palaeobotany* (eds J.G. Douglas & D.C. Christophel), pp. 97-106.
- Regehr, D.L. & Bazzaz, F.A. (1976) Low temperature in successional winter annuals. *Ecology*, 57, 1297-1303.
- Reich, P.B. (1995) Phenology of tropical forests - patterns, causes and consequences. *Canadian Journal of Botany*, 73, 164-174.
- Reich, P.B., Walters, M.B., Krause, S.C., Vanderklein, D.W., Raffa, K.F., & Tabone, T. (1993) Growth, nutrition and gas exchange of *Pinus resinosa* following artificial defoliation. *Trees*, 7, 67-77.

- Reich, P.B., Walters, M.B., Tjoelker, M.G., Vanderklein, D., & Buschena, C. (1998) Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Functional Ecology*, 12, 395-405.
- Richter, H. & Wagner, S.B. (1983). Water stress resistance of photosynthesis: some aspects of osmotic relations. In *Effects of Stress on Photosynthesis* (eds R. Marcelle, H. Clijsters & M. van Poucke), pp. 45-53. Martinus Nijhoff/Dr. W. Junk Publishers, The Hague.
- Ridloch, I., Lehto, T., & Grace, J. (1991) Photosynthesis of tropical tree seedlings in relation to light and nutrient supply. *New Phytologist*, 119, 137-147.
- Roberds, J.H., Hyun, J.O., Namkoong, G., & Rink, G. (1990) Height response functions for white ash provenances grown at different latitudes. *Silvae Genetica*, 39, 121-129.
- Robichaux, R.H., Rundel, P.W., Stemmermann, L., Canfield, J.E., Morse, S.R., & Friedman, W.E. (1984). Tissue water deficits and plant growth in wet tropical environments. In *Physiological ecology of plants of the wet tropics* (eds E. Medina, H.A. Mooney & C. Vasquez-Yanez), pp. 99-112. Dr. W. Junk Publishers, The Hague.
- Roden, J.S., Wiggins, D.J., & Ball, M.C. (1997) Photosynthesis and growth of two rain forest species in simulated gaps under elevated CO₂. *Ecology*, 78, 385-393.
- Rook, D.A. (1969) The influence of growing temperature on photosynthesis and respiration of *Pinus radiata* seedlings. *New Zealand Journal of Botany*, 43-55.
- Roy, J. & Mooney, H.A. (1982) Physiological adaptation and plasticity to water stress of coastal and desert populations of *Heliotropium curassavicum* L. *Oecologia*, 52, 370-375.
- Russel-Smith, J. (1991) Classification, species richness and environmental relations of monsoon rain forest in northern Australia. *Journal of Vegetation Science*, 2, 259-278.
- Rütten, D. & Santarius, K.A. (1992) Age-related differences in frost sensitivity of the photosynthetic apparatus of two *Plagiomnium* species. *Planta*, 187, 224-229.
- Sa-ardavut, P., Shepard, K.R., & Awe, J.O. (1984) Effects of air and soil temperatures on growth of provenances of *Eucalyptus camaldulensis* Dehnh. seedlings. *Australian Forest Research*, 14, 57-66.
- Sakai, A. & Larcher, W. (1987) Frost Survival of Plants. Responses and Adaptation to Freezing Stress. Springer-Verlag, Berlin.
- Sale, P.J.M. (1970) Growth and flowering of cacao under controlled atmospheric relative humidities. *Journal of Horticultural Science*, 45, 119-132.
- Salim, M. (1989) Effects of salinity and relative humidity on growth and ionic relations of plants. *New Phytologist*, 113, 13-20.
- Sall, T. & Pettersson, P. (1994) A model of photosynthetic acclimation as a special case of reaction norms. *Journal of Theoretical Biology*, 166, 1-8.
- Sandford, A.P. & Jarvis, P.G. (1986) Stomatal responses to humidity in selected conifers. *Tree Physiology*, 2, 89-103.

- Santhakumaran, L.N. (1992) Natural resistance of twenty species of Indian timbers to marine borer attack in Goa waters. *Proceedings of the National Academy of Sciences India Section B*, **62**, 23-30.
- Sarmiento, G., Goldstein, G., & Meinzer, F. (1985) Adaptive strategies of woody species in neotropical savannas. *Biological Review*, **60**, 315-355.
- Schaffer, B. & Andersen, P.C. (1994a) Handbook of environmental physiology of fruit crops. I. Temperate crops. CRC Press, Boca Raton, Florida.
- Schaffer, B. & Andersen, P.C. (1994b) Handbook of environmental physiology of fruit crops. II. Tropical crops. CRC Press, Boca Raton, Florida.
- Schenk, H.J. (1996) Modelling the effects of temperature on growth and persistence of tree species: a critical review of tree population models. *Ecological Modelling*, **92**, 1-32.
- Schreiber, L. & Riederer, M. (1996) Ecophysiology of cuticular transpiration: Comparative investigation of cuticular water permeability of plant species from different habitats. *Oecologia*, **107**, 426-432.
- Schulze, E.-D. (1986) Carbon dioxide and water vapour exchange in response to drought in the atmosphere and in the soil. *Annual Review of Plant Physiology*, **37**, 247-274.
- Schulze, E.-D. & Hall, A.E. (1982). Stomatal responses, water loss and CO₂ assimilation rates of plants in contrasting environments. In *Encyclopedia of Plant Physiology. Vol. 12B. Physiological Plant Ecology. II. Water Relations and Carbon Assimilation* (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler), pp. 181-230. Springer-Verlag, Berlin.
- Scott, D. (1970) CO₂ exchange of plants. 3. Temperature acclimatisation of three species. *New Zealand journal of Botany*, **8**, 369-379.
- Scurfield, G. (1961) The effects of temperature and day length on species of *Eucalyptus*. *Australian Journal of Botany*, **9**, 37-56.
- Shackel, K.A., Matthews, M.A., & Morrison, J.C. (1987) Dynamic relation between expansion and cellular turgor in growing grape (*Vitis vinifera* L.) leaves. *Plant Physiology*, **84**, 1166-1171.
- Shao, G. & Halpin, P.N. (1995) Climatic controls of eastern North American coastal tree and shrub distributions. *Journal of Biogeography*, **22**, 1083-1089.
- Sharkey, T.D. (1984) Transpiration-induced changes in the photosynthetic capacity of leaves. *Planta*, **160**, 143-150.
- Shepherd, K.R., Banks, J.C.G., & Atyeo, W.J. (1976) Variation in *Eucalyptus nitens* Maiden in response to temperature and seed source. *Australian Journal of Botany*, **24**, 167-176.
- Shugart, H.H. (1984) A Theory of Forest Dynamics. The ecological implications of forest succession models. Springer-Verlag, New York.
- Singh, A.P., Nilsson, T., & Daniel, G.F. (1993) *Alstonia scholaris* vestures are resistant to degradation by tunnelling bacteria. *IAWA Journal*, **14**, 119-126.

- Slatyer, R.O. (1977a) Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. III Temperature response of material grown in contrasting thermal environments. *Australian Journal of Plant Physiology*, 4, 301-312.
- Slatyer, R.O. (1977b) Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. IV Temperature response of four populations grown at different temperatures. *Australian Journal of Plant Physiology*, 4, 583-594.
- Slatyer, R.O. & Ferrar, P.J. (1977) Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. II Effects of growth temperature under controlled conditions. *Australian Journal of Plant Physiology*, 4, 289-299.
- Slatyer, R.O. & Morrow, P.A. (1977) Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. I Seasonal changes under field conditions in the Snowy mountains area of South-eastern Australia. *Australian Journal of Botany*, 25, 1-20.
- Slavik, B. (1973). Transpiration resistance in leaves of maize grown in humid and dry air. In *Plant Response to Climatic Factors. Proceedings of the Uppsala Symposium* (ed R.O. Slatyer), pp. 267-269. United Nations Educational, Scientific and Cultural Organization, Paris.
- Smith, B.G. (1989) The effects of soil water and atmospheric vapour pressure deficit on stomatal behaviour and photosynthesis in the Oil Palm. *Journal of Experimental Botany*, 40, 647-651.
- Smith, E.M. & Hadley, E.B. (1974) Photosynthetic and respiratory acclimation to temperature in *Ledum groenlandicum* populations. *Arctic and Alpine Research*, 6, 13-27.
- Sobrado, M.A. (1986) Aspects of tissue water relations and seasonal changes of leaf water potential components of evergreen and deciduous species coexisting in tropical dry forests. *Oecologia*, 68, 413-416.
- Sowell, J.B. (1985) A predictive model relating North American plant formations and climate. *Vegetatio*, 60, 103-111.
- Specht, A. (1985) Temperature Effects on Eucalypt Shoot Growth in the Brisbane Region. Hons. Thesis. Botany Department, University of Queensland, Brisbane.
- Specht, R.L. (1981) Growth indices, - Their role in understanding the growth, structure and distribution of Australian vegetation. *Oecologia*, 50, 347-356.
- Specht, R.L. (1986). Phenology. In *Tropical Plant Communities. Their resilience, functioning and management in northern Australia* (eds H.T. Clifford & R.L. Specht), pp. 78-90. Department of Botany, University of Queensland, Brisbane.
- Specht, R.L. & Brouwer, Y.M. (1975) Seasonal shoot growth of *Eucalyptus* species in the Brisbane area of Queensland (with notes on shoot growth and litter fall in other areas of Australia). *Australian Journal of Botany*, 23, 459-474.
- Specht, R.L. & Specht, A. (1999) *Australian Plant Communities. Dynamics of structure, growth and biodiversity*. Oxford University Press, Oxford.

- Sperry, J.S. & Sullivan, J.E.M. (1992) Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous and conifer species. *Plant Physiology*, **100**, 603-613.
- Sperry, J.S. & Tyree, M.T. (1990) Water stress-induced xylem embolism in three species of conifers. *Plant Cell and Environment*, **13**, 427-436.
- Stephenson, N.L. (1990) Climatic control of vegetation distribution the role of the water balance. *American Naturalist*, **135**, 649-670.
- Stephenson, N.L. (1998) Actual evapotranspiration and deficit: Biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography*, **25**, 855-870.
- Stirzaker, R.J., Hayman, P.T., & Sutton, B.G. (1997) Misting of tomato plants improves leaf water status but not leaf growth. *Australian Journal of Plant Physiology*, **24**, 9-16.
- Stoneman, G.L. & Dell, B. (1993) Growth of *Eucalyptus marginata* (Jarrah) seedlings in a greenhouse in response to shade and soil temperature. *Tree Physiology*, **13**, 239-252.
- Strain, B.R., Higginbotham, K.O., & Mulroy, J.C. (1976) Temperature preconditioning and photosynthetic capacity of *Pinus taeda* L. *Photosynthetica*, **10**, 47-53.
- Strauss-Debenedetti, S. & Bazzaz, F.A. (1996). Photosynthetic characteristics of tropical trees along successional gradients. In *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 162-186. Chapman and Hill. London.
- Strauss-Debenedetti, S. & Bazzaz, F.A. (1991) Plasticity and acclimation to light in tropical Moraceae of different successional positions. *Oecologia*, **87**, 377-387.
- Sun, G.C. & Ehleringer, J.R. (1986) Gas exchange in *Schima superba*, a subtropical monsoonal forest tree. *Photosynthetica*, **20**, 158-163.
- Swaine, M.D. & Hall, J.B. (1983) Early succession on cleared forest land in Ghana. *Journal of Ecology*, **71**, 601-627.
- Swanborough, P.W., Doley, D., Keenan, R.J., & Yates, D.J. (1998) Photosynthetic characteristics of *Flindersia brayleyana* and *Castanospermum australe* from tropical lowland and upland sites. *Tree Physiology*, **18**, 341-347.
- Sykes, M.T., Prentice, I.C., & Cramer, W. (1996) A bioclimatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography*, **23**, 203-233.
- Taylor, S.E. (1975). Optimal leaf form. In *Perspectives in Biophysical Ecology* (eds D.M. Gates & R.B. Schmerl), pp. 73-86. Springer-Verlag, Berlin.
- Tenhunen, J.D., Pearcy, R.W., & Lange, O.L. (1987). Diurnal variations in leaf conductance and gas exchange in natural environments. In *Stomatal Function* (eds E. Zeiger, G.D. Farquhar & I.R. Cowan), pp. 323-351. Stanford University Press, Stanford, California.
- Teskey, R.O., Fites, J.A., Samuelson, L.J., & Bongarten, B.C. (1986) Stomatal and nonstomatal limitations to net photosynthesis in *Pinus taeda* L. under different environmental conditions. *Tree Physiology*, **2**, 131-142.

- Teskey, R.O., Whitehead, D., & Linder, S. (1994) Photosynthesis and carbon gain by pines. *Ecological Bulletins*, **43**, 35-49.
- Teskey, R.O. & Will, R.E. (1999) Acclimation of loblolly pine (*Pinus taeda*) seedlings to high temperatures. *Tree Physiology*, **19**, 519-525.
- Tewolde, H., Dobrenz, A.K., & Voigt, R.L. (1993) Seasonal trends in leaf photosynthesis and stomatal conductance of drought stressed and nonstressed pearl millet as associated to vapor pressure deficit. *Photosynthesis Research*, **38**, 41-49.
- Thompson, W.A., Huang, L.-K., & Kriedemann, P.E. (1992a) Photosynthetic response to light and nutrients in sun-tolerant and shade-tolerant rainforest trees II. Leaf gas exchange and component processes of photosynthesis. *Australian Journal of Plant Physiology*, **19**, 1-18.
- Thompson, W.A., Kriedemann, P.E., & Craig, I.E. (1992b) Photosynthetic response to light and nutrients in sun-tolerant and shade-tolerant rainforest trees. I. Growth, leaf anatomy and nutrient content. *Australian Journal of Plant Physiology*, **19**, 1-18.
- Thompson, W.A., Stocker, G.C., & Kriedemann, P.E. (1988) Growth and photosynthetic response to light and nutrients of *Flindersia brayleyana* F. Muell., a rainforest tree with broad tolerance to sun and shade. *Australian Journal of Plant Physiology*, **15**, 299-315.
- Toft, N.L. & Pearcy, R.W. (1982) Gas exchange characteristics and temperature relations of two desert annuals: a comparison of a winter-active and a summer-active species. *Oecologia*, **55**, 170-177.
- Tranquillini, W., Havranek, W.M., & Ecker, P. (1986) Effects of atmospheric humidity and acclimation temperature on the temperature response of photosynthesis in young *Larix decidua* Mill. *Tree Physiology*, **1**, 37-45.
- Treharne, K.J. & Eagles, C.F. (1970) Effect of temperature on photosynthetic activity of climatic races of *Dactylis glomerata* L. *Photosynthetica*, **4**, 107-117.
- Treharne, K.J. & Nelson, C.J. (1975). Effect of growth temperature on photosynthetic and photo-respiratory activity in Tall Fescue. In *Environmental and Biological Control of Photosynthesis* (ed R. Marchelle), pp. 61-69. Dr. W. Junk b.v. Publishers, The Hague.
- Truswell, E.M. (1990). Australian rainforests: the 100 million year record. In *Australian Tropical Rainforests. Science - Values - Meaning* (eds L.J. Webb & J. Kikkawa), pp. 7-22. CSIRO Publications, Melbourne.
- Truswell, E.M. (1993) Vegetation changes in the Australian Tertiary in response to climatic and phytogeographic forcing factors. *Australian Systematic Botany*, **6**, 533-557.
- Turnbull, M.H. (1991) The effect of light quantity and quality during development on the photosynthetic characteristics of six Australian rainforest tree species. *Oecologia*, **87**, 110-117.
- Turner, N.C., Schulze, E.-D., & Gollan, T. (1984) The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. I. Species comparisons at high soil water contents. *Oecologia*, **63**, 338-342.

- Turner, N.C., Schulze, E.-D., & Gollan, T. (1985) The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. II. In the mesophytic herbaceous species *Helianthus annuus*. *Oecologia*, **65**, 348-355.
- Tyree, M.T., Davis, S.D., & Cochard, H. (1994) Biophysical perspectives of xylem evolution: Is there a trade-off of hydraulic efficiency for vulnerability to dysfunction? *IAWA Journal*, **15**, 335-360.
- Tyree, M.T. & Ewers, F.W. (1991) the hydraulic architecture of trees and other woody plants. *New Phytologist*, **119**, 345-360.
- Tyree, M.T. & Ewers, F.W. (1996). Hydraulic architecture of woody tropical plants. In *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 217-243. Chapman and Hill, London.
- Unwin, G.L. & Kriedemann, P.E. (1990) Drought tolerance and rainforest tree growth on a north Queensland rainfall gradient. *Forest Ecology and Management*, **30**, 113-123.
- Vallejos, C.E. & Percy, R.W. (1987) Differential acclimation potential to low temperatures in two species of *Lycopersicon*: photosynthesis and growth. *Canadian Journal of Botany*, **65**, 1303-1307.
- van de Sanden, P.A.C.M. & Veen, B.W. (1992) Effects of Air Humidity and Nutrient Solution Concentration On Growth Water Potential and Stomatal Conductance of Cucumber Seedlings. *Scientia Horticulturae*, **50**, 173-186.
- van der Heyden, F. & Lewis, O.A.M. (1990) Environmental control of photosynthetic gas exchange characteristics of fynbos species representing three growth forms. *South African Journal of Botany*, **56**, 654-658.
- Vázquez-Yanes, C. (1974) Studies on the germination of seeds of *Ochroma lagopus* Swartz. *Turrialba*, **24**, 176-179.
- Walter, H. (1971) Ecology of tropical and subtropical vegetation. Van Nostrand Reinhold, New York.
- Wardle, P. (1964) Facets of the distribution of forest vegetation in New Zealand. *New Zealand Journal of Botany*, **2**, 352-366.
- Warren-Wilson, J. (1966) Effect of temperature on net assimilation rate. *Annals of Botany*, **30**, 753-761.
- Warren-Wilson, J. (1967) Effects of seasonal variation in radiation and temperature on net assimilation and growth rates in an arid climate. *Annals of Botany*, **31**, 41-57.
- Webb, L.J. (1959) A physiognomic classification of Australian rain forests. *Journal of Ecology*, **47**, 551-570.
- Webb, L.J. (1968) Environmental relationships of the structural types of Australian rain forest vegetation. *Ecology*, **49**, 296-311.
- Webb, L.J. & Tracey, J.G. (1981a). Australian rainforests: patterns and change. In *Ecological Biogeography of Australia* (ed A. Keast), Vol. 1, pp. 607-694. Dr. W. Junk Publishers, The Hague.
- Webb, L.J. & Tracey, J.G. (1981b). The rainforests of northern Australia. In *Australian Vegetation* (ed R.H. Groves), pp. 67-101. Cambridge University Press, Melbourne.

- Webb, L.J. & Tracey, J.G. (1994). The rainforests of northern Australia. In *Australian Vegetation* (ed R.H. Groves), pp. 87-129. Cambridge University Press, Melbourne.
- Webb, L.J., Tracey, J.G., & Williams, W.T. (1984) A floristic framework of Australian rainforests. *Australian Journal of Ecology*, **9**, 169-198.
- Went, F.W. (1953) The effect of temperature on plant growth. *Annual Review of Plant Physiology*, **4**, 347-362.
- Wheeler, R.M., Tibbitts, T.W., & Fitzpatrick, A.H. (1989) Potato growth in response to relative humidity. *Hortscience*, **24**, 482-484.
- Whitehead, D., Okali, D.U.U., & Fasehun, F.E. (1981) Stomatal response to environmental variables in two tropical forest species during the dry season in Nigeria. *Journal of Applied Ecology*, **18**, 571-587.
- Whittaker, R.H. (1975) *Communities and Ecosystems*. MacMillan Publishing Company Inc., New York.
- Williams, D.G. & Black, R.A. (1993) Phenotypic variation in contrasting temperature environments: growth and photosynthesis in *Pennisetum setaceum* from different altitudes on Hawaii. *Functional Ecology*, **7**, 623-633.
- Williams, G.J. (1974) Photosynthetic adaptations to temperature in C₃ and C₄ grasses. *Plant Physiology*, **54**, 709-711.
- Williams, J.B., Harden, G.J., & McDonald, W.J.F. (1984) *Trees and Shrubs in Rainforests of New South Wales and Southern Queensland*. Botany Department, University of New England, Armidale.
- Wilson, P.G. & Waterhouse, J.T. (1982) A review of the genus *Tristania*. *Australian Journal of Botany*, **30**, 435.
- Woledge, J. & Jewiss, O.R. (1969) The effect of temperature during growth on the subsequent rate of photosynthesis in leaves of Tall Fescue (*Festuca arundinacea* Schreb.). *Annals of Botany*, **33**, 897-913.
- Woodward, F.I. (1975) The climatic control of the altitudinal distribution of *Sedum rosea* (L.) Scop. and *S. telephium* L. II. The analysis of plant growth in controlled environments. *New Phytologist*, **74**, 335-348.
- Woodward, F.I. (1979) The differential temperature responses of the growth of certain plant species from different altitudes. I. Growth analysis of *Phleum alpinum* L., *P. bertolonii* D. C., *Sesleria albicans* Kit. and *Dactylis glomerata* L. *New Phytologist*, **82**, 385-395.
- Woodward, F.I. (1987) *Climate and Plant Distribution*. Cambridge University Press, Cambridge.
- Woodward, F.I., Körner, C., & Crabtree, R.C. (1986) The dynamics of leaf extension in plants with diverse altitudinal ranges. I. Field observations on temperature responses at one altitude. *Oecologia*, **70**, 222-226.
- Woodward, F.I. & Pigott, C.D. (1975) The climatic control of the altitudinal distribution of *Sedum rosea* (L.) Scop. and *S. telephium* L. I. Field observations. *New Phytologist*, **74**, 323-334.
- Woodward, R.G. & Begg, J.E. (1976) The effect of atmospheric humidity on the yield and quality of soya bean. *Australian Journal of Agricultural Research*, **27**, 501-508.

- Xiong, F.S., Mueller, E.C., & Day, T.A. (2000) Photosynthetic and respiratory acclimation and growth response of Antarctic vascular plants to contrasting temperature regimes. *American Journal of Botany*, **87**, 700-710.
- Yates, D.J. & Hutley, L.B. (1995) Foliar uptake of water by wet leaves of *Sloanea woollsii*, an Australian subtropical rainforest tree. *Australian Journal of Botany*, **43**, 157-167.
- Yates, D.J., Unwin, G.L., & Doley, D. (1988). Rainforest environment and physiology. In *The Ecology of Australia's Wet Tropics* (ed R.L. Kitching). Surry Beatty & Sons Pty. Ltd., Chipping Norton, NSW.
- Zotz, G. & Winter, K. (1996). Diel patterns of CO₂ exchange in rainforest canopy plants. In *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 89-113. Chapman and Hall, London.