THE DYNAMICS OF <u>NOTHOFAGUS CUNNINGHAMII</u> RAINFOREST
ASSOCIATIONS IN TASMANIA - AN ECOPHYSIOLOGICAL APPROACH.
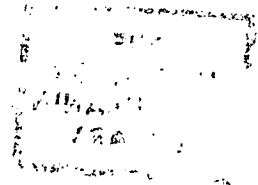

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of Doctor of Philosophy

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DECLARATION

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

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ABSTRACT

Nothofagus cunninghamii is a widespread component of
cool temperate rainforest in Tasmania. It dominates the
canopy on fertile soils, with dominance decreasing with the
soil quality. Elsewhere in the southern hemisphere,
Nothofagus appears either to be restricted to sites away
from the moist, mild, fertile optimum, or to be seral. This
thesis examines regeneration characteristics and comparative
physiology of the major canopy species of Tasmanian cool
temperate rainforest in order to determine the mechanisms
affecting species composition.

Atherosperma moschatum is the most shade-tolerant canopy
species in the Tasmanian rainforest. It regenerates
continuously, primarily by vegetative reproduction (stem
sprouts) and therefore is typically self-replacing. Its
ability to capture the larger gaps created by the death of
old trees of other species is limited by the infrequency of
establishment away from the parent stem. The reproductive
characteristics of A. moschatum where it grows in
rainforest, and the absence of other shade-tolerant canopy
species, explain the dominance of old undisturbed rainforest
by relatively shade-intolerant species in Tasmania.

Nothofagus cunninghamii regenerates continuously on most
sites, primarily by seedling establishment in canopy gaps
created by the death of an old tree. Eucryphia lucida
regenerates continuously by seedling establishment in canopy
gaps, and vegetatively by sprouts from the base of larger
stems. N. cunninghamii and E. lucida have similar light
requirements and are able to regenerate under denser
canopies than Athrotaxis selaginoides and Phyllocladus
aspleniifolius. On the most fertile soils, N. cunninghamii
has the highest growth rate of all the canopy species and
dominates the canopy by establishing in natural canopy gaps
and pre-empting resources (primarily light). The greater
canopy diversity on poor soils appears to be due to the loss
of the competitive advantage in terms of potential size and
growth rate of N. cunninghamii. On the poorest soils, P.

<u>aspleniifolius</u> has the highest growth rate of the co-occurring rainforest canopy species under exposed conditions. However <u>P. aspleniifolius</u> is generally unable to regenerate continuously in closed forest due probably to its shade-intolerance and appears to rely on the higher frequency of fire on poor soils for its regeneration on these sites. <u>A. selaginoides</u> shows more variation in its regeneration patterns. On sites with a relatively closed canopy, regeneration is insufficient to replace the older trees following their death. Where the canopy is more open, regeneration is occurring.

The results of this study indicate that community composition in Tasmanian rainforest is primarily determined by a combination of shade-tolerance, growth rates and reproductive strategies. The growth rates of the species are the sum of responses to environmental features such as light, nutrients, temperature, water availability, and tissue losses due to browsing, frost damage and drought damage. On the more extreme sites (e.g. low temperatures and water shortage), tolerance rather than high growth rates may be of more importance.

The dynamics of the <u>Nothofagus</u>-dominated rainforests in Tasmania are compared with closely related forests in New South Wales and Chile.

TABLE OF CONTENTS

Chapter 1   Introduction

Nothofagus is a characteristic genus of cool temperate
rainforest in southern South America, New Zealand and
Australia with a taxonomically distinct group occurring at
tropical latitudes in New Caledonia and New Guinea (Table
1.1, Fig. 1.1). The fossil record indicates that Nothofagus
was more widespread in these land masses in the Tertiary and
also occurred in Antarctica (Fig. 1.1). The genus is not
confined to rainforest. Some species occur on relatively dry
sites in New Zealand (750-1000 mm rainfall (J. Wardle 1984))
and southern South America (300-400 mm rainfall (McQueen
1976)) and Nothofagus occurs in sub-alpine vegetation in
South America, New Zealand and Australia. Nothofagus is
commonly the dominant canopy species of these varying
vegetation types, often forming almost pure stands (J.
Wardle 1984).

Three species of Nothofagus occur in Australia. N.
gunnii, the only deciduous species of Nothofagus outside
South America (Table 1.1), has a patchy distribution in the
Tasmanian highlands (Fig 1.2). N. moorei is the dominant
tree in cool temperate rainforest in the highlands of
north-eastern New South Wales and south-eastern Queensland
(Fig. 1.2). The closely related N. cunninghamii (Table 1.1;
Hill 1983b) has the most widespread distribution of the
Australian Nothofagus species, occurring in lowland and
montane communities in south-central Victoria and Tasmania
(Figs. 1.2 & 1.3).

The N. cunninghamii associations differ from the
Nothofagus associations of New Zealand and South America in
several respects. Nothofagus species dominate forests at
high altitudes and latitudes in southern South America. They
also dominate some low altitude and mid-elevation sites in
south-central Chile which are exposed to recurrent
catastrophic disturbance. However Nothofagus species are
more light-demanding than many co-occurring species and, in

Table 1.1 List of species in the genus <u>Nothofagus</u>, and their taxonomic position. The letters in brackets following species names refer firstly to the geographic location of the species (A - mainland Australia; NC - New Caledonia; NG - New Guinea; NZ - New Zealand; SA - South America; T - Tasmania), and secondly to the pollen type produced by the species (F - <u>fusca</u>-type; M - <u>menziesii</u>-type; B - <u>brassii</u>-type). The division into Sections is based on the deciduous (Section <u>Nothofagus</u>) and evergreen (Section <u>Calusparassus</u>) habit.   After Hill (1983a).

Nothofagus				
Section *Nothofagus*	Section *Calusparassus*			
	Subsection *quadripartitae*	Subsection *tripartitae*	Subsection *bipartitae*	
N. alessandrii (SA;F)				
N. alpina (SA;M)				
N. antarctica (SA;F)				
N. glauca (SA;M)	*N. betuloides* (SA;F)	*N. solandri* (NZ;F)	*N. aequilateralis*	(NG;B)
N. gunnii (Tas;F)	*N. cunninghamii* (Tas;A;M)		*N. balansae*	(NC;B)
N. obliqua (SA;M)	*N. dombeyi* (SA;F)		*N. baumanniae*	(NC;B)
N. pumilio (SA;F)	*N. fusca* (NZ;F)		*N. brassii*	(NG;B)
	N. menziesii (NZ;M)		*N. carrii*	(NG;B)
	N. moorei (A;M)		*N. codonandra*	(NC;B)
	N. nitida (SA;F)		*N. crenata*	(NG;B)
	N. truncata (NZ;F)		*N. discoidea*	(NC;B)
			N. flaviramea	(NG;B)
			N. grandis	(NG;B)
			N. nuda	(NG;B)
			N. perryi	(NG;B)
			N. pseudoresinosa	(NG;B)
			N. pullei	(NG;B)
			N. resinosa	(NG;B)
			N. rubra	(NG;B)
			N. starkenborghii	(NG;B)
			N. womersleyi	(NG;B)

Fig. 1.1   The distribution of <u>Nothofagus</u>, showing
modern (stippled) and fossil (★) occurrences. After
Humphries (1981).

Fig. 1.2   The present distribution of <u>Nothofagus</u>
in Australia.

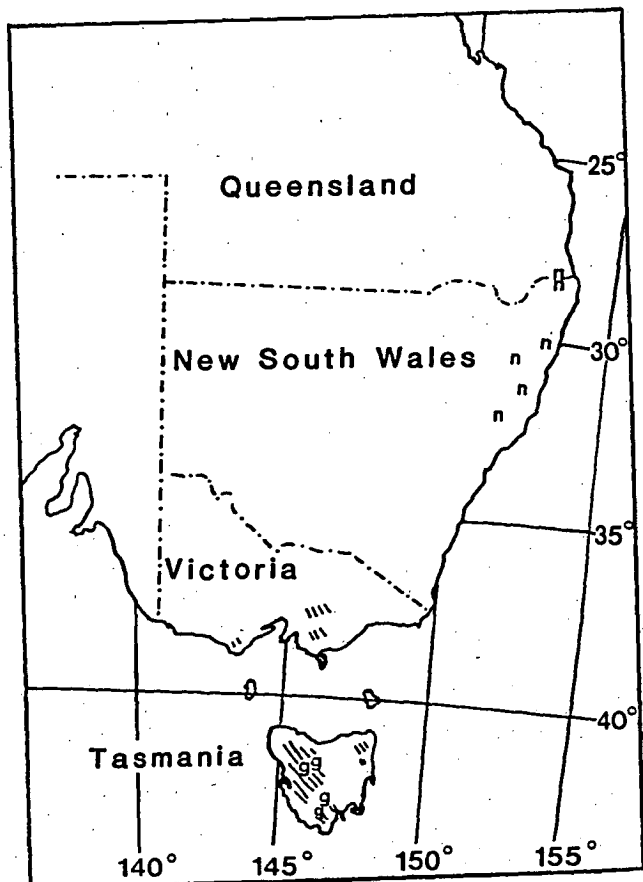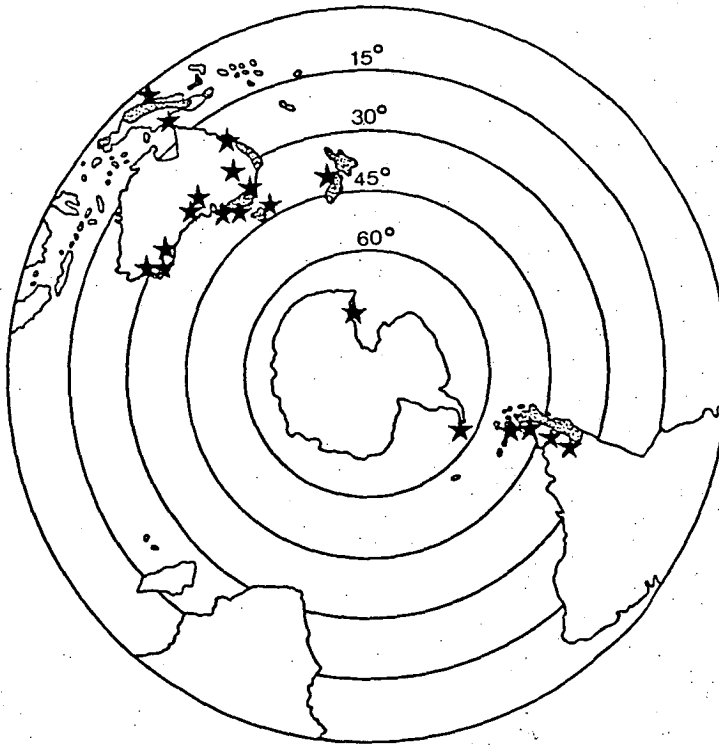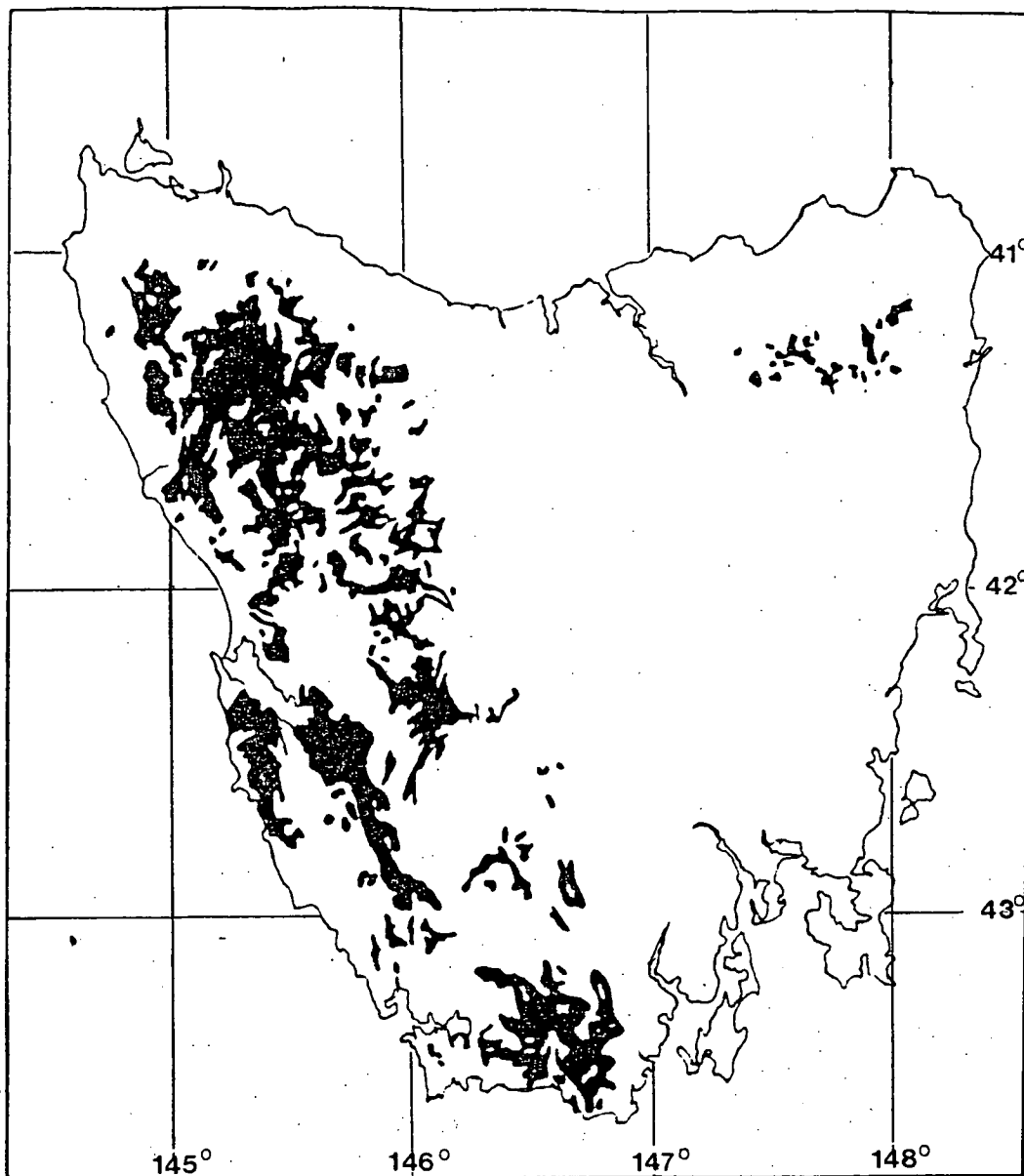<u>N. cunninghamii</u>: ＼＼＼
<u>N. gunnii</u>:   g
<u>N. moorei</u>:   n

Fig. 1.3   The distribution of rainforest in Tasmania.
After Kirkpatrick & Dickinson (1983).

Terminology and definitions

Species nomenclature follows Curtis (1963,1967) and
Curtis & Morris (1975) for the Tasmanian species, Williams
(1982) for the mainland Australia rainforest species, and
Hoffmann J. (1982) for the Chilean species. Terminology
relating to vegetation structure follows Richards (1952) and
Specht (1970).

The difficulties of defining rainforest have often been
noted (Richards 1952; Webb 1959; Jarman & Brown 1983).
Jarman & Brown (1983) define Tasmanian rainforest as "forest
vegetation (trees greater than 8m) dominated by species of
Nothofagus, Atherosperma, Eucryphia, Athrotaxis,
Lagarostrobos, Phyllocladus or Diselma". This definition of
rainforest is followed in this thesis.

Nothofagus cunninghamii associations in
closed forests in Tasmania

Cool temperate rainforest is very localised in Victoria.
A suitable climate (with the associated low fire frequency)
is less widespread in Victoria than in Tasmania and the
rainforest is generally restricted to river gullies and
south-east facing slopes on krasnozem soils and is usually
associated with emergent eucalypts (Howard & Ashton 1973).
The rainforest is most commonly dominated by Nothofagus
cunninghamii, with Atherosperma moschatum sub-dominant up to
1375 m a.s.l. (Howard & Ashton (1973). A. moschatum extends
further east (Errinundra Plateau) and north (Barrington
Tops) than N. cunninghamii, and N. cunninghamii extends west
to the Otway Ranges in the absence of A. moschatum. N.
cunninghamii is also associated with Acacia melanoxylon up
to 650 m a.s.l., and forms low forest with Leptospermum
grandifolium up to 1570 m a.s.l. (Howard & Ashton 1973).

In Tasmania, cool temperate rainforest is more
widespread than on mainland Australia and occurs over a
range of topographies and soils (Jackson 1968), and

consequently has a greater variety of associations (Busby &
Bridgewater 1977; Busby 1984). The floristic associations of
Tasmanian rainforest and their distributions are described
in most detail by Jackson (1958, 1983) and Jarman et al
(1984). The rainforest on fertile, well-drained soils is a
tall closed forest with a canopy of up to 40 m, generally
dominated by N. cunninghamii with A. moschatum sub-dominant.
These forests have a heavily shaded, open understorey,
devoid of shrubs, but sometimes contain a sparse layer of
ground ferns and occasional tree ferns. Epiphytic ferns and
mosses may be abundant on the more humid sites. Lianes and
herbs are rare. Litter on the forest floor can build up
around tree trunks but generally the litter layer is thin.
Species richness of angiosperms is extremely low. This
rainforest is most widespread in the north-west and
north-east of Tasmania, on soils derived from basalts and
granites.

As the site soil quality decreases, the trees of the
lowland rainforest are shorter and the forest structure is
more complex as species of small trees and shrubs become
more common, forming a staggered canopy (Jackson 1965,
1968; Kirkpatrick 1977). N. cunninghamii dominance
decreases and Eucryphia lucida and Phyllocladus
aspleniifolius may be common components of the canopy. On
sites where roots are shallow, windthrow is common, with
some roots retaining contact with the soil and branches
growing vertically to form individual stems. This habit is
characteristic of Anodopetalum biglandulosum, but is also
common in N. cunninghamii, A. moschatum and E. lucida.
Kirkpatrick (1977) describes the rainforest on the poorest
sites on the west coast of Tasmania as a tangled mass of
shrubs and trees, including A. biglandulosum and many
epacrids. On the poorest soils, P. aspleniifolius may assume
almost complete dominance (Jackson 1983). Kirkpatrick (1977)
does not specify the soil characteristics which determine
these changes in lowland rainforest structure and
floristics, but Jackson (1968, 1983) regards the soil

nutrient status as the primary determinant. He further states that climax forests dominated by N. cunninghamii with low diversity can occur on soils of low inherent fertility. He regards the scrub rainforest which occurs on soils derived from infertile substrates as disclimax forest, and suggests that a higher fire frequency on soils derived from low nutrient bedrock commonly depletes the soil nutrients to prevent or slow the development of the climax rainforest. Due to the current lack of data relating forest structure and floristics to soil characteristics, the term "poor soil" will be used in this thesis to denote any soil resulting in relatively slow growth rates and stunted tree form, caused by undetermined soil characteristics.

At higher altitudes on fertile, well-drained soils, N. cunninghamii dominates low closed forests with a decrease in the importance of A. moschatum (Jackson 1983). Athrotaxis selaginoides becomes an important component of rainforest on sites above 610 m in western Tasmania which are topographically protected from fire (Kirkpatrick 1977). It occurs with N. cunninghamii, E. lucida and A. moschatum in tall closed forest, and usually emerges beyond the main canopy. At higher altitudes A. selaginoides occurs in closed forest with N. cunninghamii or N. gunnii (usually above 670 m).

Lagarostrobos franklinii occurs along river banks, on alluvial rainforest flats and on topographically protected sites in south-western Tasmania (Davies 1983). The structure of these communities ranges from closed forest dominated by N. cunninghamii with an open understorey and low species diversity, to poor quality rainforest with a low broken canopy, dense tangled understorey and a relatively high species diversity (Pedley et al. 1980).

The impact of fire in areas of high rainfall

There are two opposing views regarding the successional status of vegetation types occurring in the high rainfall

areas of Tasmania. Jackson (1968) argues that rainforest is
not limited by soil, aspect or topography and that currently
large areas which are climatically suited to rainforest
(1000 mm minimum annual rainfall and 25 mm minimum monthly
summer rainfall) are occupied by vegetation with markedly
xeromorphic characteristics, e.g. sedgeland, heathland and
eucalypt forest. He suggests that interactions between
fire-frequency, vegetation and soil fertility have produced
the anomalous vegetation in high rainfall areas. Due to
these interactions it is likely that fire will occur in
these vegetation types with the appropriate frequency to
maintain the communities, but the vegetation may also drift
towards either rainforest or sedgeland depending on chance
long or short intervals between fires. In contrast, Mount
(1979) argues that the vegetation types are determined by
site characteristics such as geology, drainage, topography
and climate and that vegetation boundaries are stable due to
a characteristic burning cycle determined by the fuel
production of each vegetation type. There is little data
available for testing these hypotheses, but a study by Brown
& Podger (1982) indicates that succession has occurred over
relatively short time spans in a high rainfall area of
south-west Tasmania.

Mixed forests

   Gilbert (1959) introduced the term "mixed forest" to
describe the rainforest-eucalypt associations. These occur
on sites that are burned infrequently, but with a fire-free
interval of less than 350-400 years (the life span of the
eucalypts). Less frequent fire results in pure rainforest,
and a fire frequency of once or twice per century may result
in the loss of the rainforest component (Gilbert 1959).
Acacia species (most commonly A. melanoxylon) also occur
with rainforest species in localised stands. Because of the
disturbance-stimulated germination (fire or flood) the
Acacia species have generally been regarded as seral within

the rainforest (Howard 1981; Jackson 1983; Jarman et al.
1984). In some cases multiple-aged mixed forests occur
through a patchy distribution of fire resulting in a fine
mosaic of survival and regeneration, e.g. fires on thin peat
(Hill 1983; Hill & Read 1984). In north-west Tasmania, N.
cunninghamii, Atherosperma moschatum and Acacia melanoxylon
form mixed stands in lowland swamps where free-standing
water may occur for several weeks annually (Jackson 1983).
A. melanoxylon appears to play a more permanent role in
these forests (Jackson 1983).

Part A

Studies of forest regeneration

Chapter 2   Population dynamics of the rainforest canopy
             species.

Introduction

    In their successional model based on vital attributes,
Noble & Slatyer (1980) predicted that Tasmanian rainforest
would be dominated by Atherosperma moschatum in the absence
of disturbance by fire, due to its apparent superior
shade-tolerance (inferred from field observations by Gilbert
(1959)) and its subsequent ability to regenerate
continuously within the rainforest. They also noted that
pure rainforest stands are usually a mixture of Nothofagus
cunninghamii and A. moschatum and suggested that some type
of disturbance (other than fire) is responsible for the
persistence of N. cunninghamii (Noble & Slatyer 1978).
Rainforest in Tasmania has also been described as
self-replacing in species composition, with the death of
individuals of a species being compensated by the
establishment of individuals of the same species
(Kirkpatrick 1977) although forests containing Athrotaxis
selaginoides have been observed in which it was not
represented in the small size classes (Ogden 1978;
Kirkpatrick & Harwood 1980).

    In this chapter, patterns of regeneration are examined
in undisturbed rainforest in order to determine the modes of
regeneration of the component species and whether
regeneration is continuous, and subsequently whether these
forests are stable communities in the absence of
disturbance. Rainforest stands were selected over a range of
altitudes and soils to give a range of species associations.
Two aspects of regeneration are examined. Population size
structure of the canopy species was measured on each site in
order to determine whether regeneration was continuous or
sporadic. On some sites the spatial distribution of size
classes of each species was recorded to allow pattern
analysis. Where possible, the methods employed by Veblen et

<u>al</u>. (1981) were used to allow comparison with the Chilean lowland and mid-altitude <u>Nothofagus</u> forests.

<u>Materials and methods</u>

The study sites selected showed no evidence of fire or logging within the lifespan of the living trees. Details of these sites are summarised in Table 2.1, and locations are shown in Figure 2.1.

Spatial patterns of regeneration were examined in 0.39 ha (54 x 72 m) sample plots located in nine forest sites (Table 2.1). The diameter of all trees of 5 cm diameter at breast height (dbh) or greater, and the frequency of all seedlings and saplings (including vegetative shoots from the base of the main stem) less than 5cm dbh and at least 10 cm high were recorded on each study site. This data was collected in contiguous 3 x 3 m quadrats, allowing the formation of nested quadrats and the use of a clumping index at each quadrat size from sides of length one unit (3 x 3 m) to sides of length nine units (27 x 27 m). The index used is Morisita's index (Morisita 1959) which is based on Simpson's diversity index.

$$I_\delta = q \sum_{i=1}^{q} n_i (n_i - 1)/N(N-1)$$

where q is the number of quadrats, n is the number of individuals in the i_{th} quadrat, and N is the total number of individuals in q quadrats. This index has a value of 1 when the distribution is random, is <1 when uniform and is >1 when clumped. It was only applied to a species age class when at least 20 individuals were present. Saplings were recorded as being of seedling or vegetative origin except on the Frodsham's Pass site where it was common to find branches of fallen immature trees growing upright (with adventitious roots), often with their origins obscured by years of litter fall and formation of humus.

The size structure of a population can be used to describe population dynamics by observing the distribution

Fig. 2.1   Map of study sites.

    1. Stephen's Rivulet

    2. Sumac

    3. Dempster

    4. Pipeline

    5. Parrawe

    6. Pieman

    7. Murchison

    8. Howards Road 1&2

    9. Cradle Mt. National Park: Weindorfer 1&2
                                 Ballroom

   10. Diddleum

   11. Mt Michael

   12. Mt Field National Park

   13. Sawback

   14. Frodsham's Pass

   15. Mt Anne

   16. Hastings
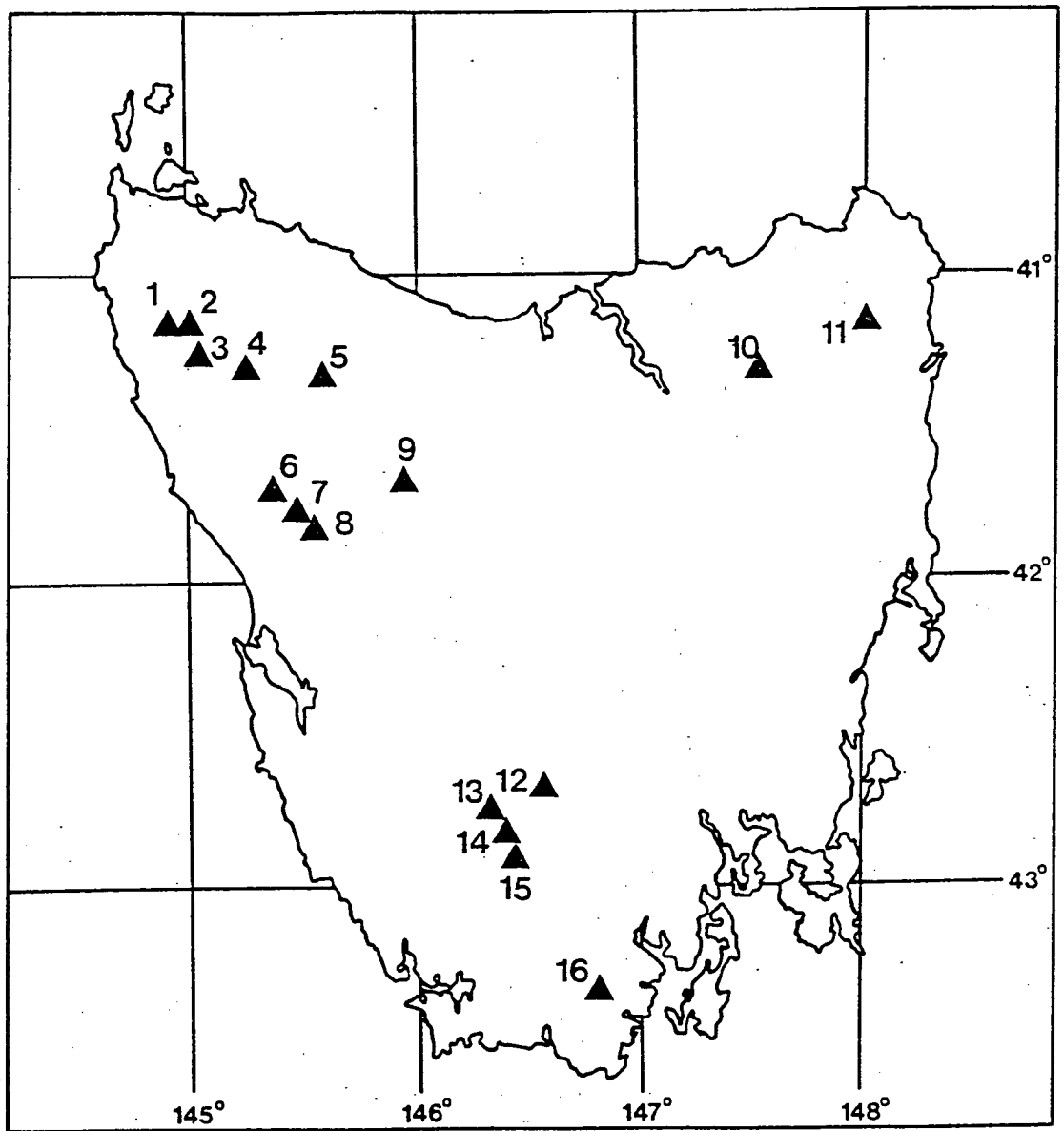
Table 2.1   Summary of study sites. The spatial distribution of stems was analysed on the sites marked with an asterisk. The geology and soil information was taken from Ridgley (1978) and Prikard (1980) with verification by personal observation, unless otherwise stated.

Site location	Soil/Geology	Elevation (m a.s.l.)	Canopy composition	% total basal area
Stephens Rivulet* 41°10'S 144°57'E	Yellowish red gradational soil/ Cambrian volcanic and sedimentary	140	Nothofagus cunninghamii Atherosperma moschatum	86 14
Pipeline Road* 41°19'S 145°16'E	Strong brown gradational soil/ Tertiary basalt	460	N. cunninghamii A. moschatum	85 15
Sumac Road* 41°9'S 145°1'E	Yellowish brown gradational soil/ Cambrian volcanic and sedimentary	180	N. cunninghamii Eucryphia lucida A. moschatum	89 10 1
Parrawe* 41°21'S 145°34'E	Strong brown gradational soil/ Tertiary basalt	580	N. cunninghamii A. moschatum	66 34
Frodsham's Pass* 42°50'S 146°23'E	Yellowish brown duplex soil/ Cambrian mudstone[1]	580	N. cunninghamii A. moschatum E. lucida	53 43 4
Mt Michael* 41°10'S 148°00'E	Brown fibrous peat becoming gravelly with depth/ Quaternary river alluvium & Devonian granite[1]	740	N. cunninghamii A. moschatum	97 3
Diddleum* 41°22'S 147°26'E	Strong brown gradational soil/ Devonian granodiorite	820	N. cunninghamii A. moschatum	95 5
Mt Anne 42°56'S 146°26'E	Soil type was not recorded/ Jurassic dolerite[1]	850	Athrotaxis selaginoides N. cunninghamii A. moschatum	50 39 11
Howard's Road H1 41°51'S 145°33'E	Pale brown gradational soil/ Cambrian volcanics	650	N. cunninghamii A. selaginoides E. lucida A. moschatum	47 43 6 4
H2	Shallow brown fibrous peat over gravelly brownish yellow gradational soil/ Cambrian volcanics	650	Nothofagus gunnii A. selaginoides Phyllocladus aspleniifolius N. cunninghamii E. lucida	41 38 12 5 4
Cradle Mountain N.P. Weindorfer's Forest W1* 41°38'S 145°57'E	Yellowish brown clay soil/ Phyllite & micaceous schists[1]	920	A. selaginoides N. cunninghamii P. aspleniifolius	55 40 5
W2*	''	920	N. cunninghamii A. selaginoides A. moschatum	61 32 7
Ballroom Forest 41°40'S 145°57'E	Deep brown fibrous peat/ Phyllite & micaceous schists[1]	940	N. cunninghamii A. selaginoides A. moschatum	60 24 16
Dempster* 41°12'S 145°03'E	Very dark brown peat, becoming gravelly with depth/ Precambrian dolomite	220	N. cunninghamii P. aspleniifolius E.lucida Anodopetalum biglandulosum	39 28 29 4
Pieman 41°12'S 145°26'E	Greyish brown loam soil/ Lower Devonian-Silurian slate & siltstone	200	P. aspleniifolius N. cunninghamii A. moschatum	56 30 7

cont.			A. biglandulosum	6
			Cenarrhenes nitida	1
Murchison 41°47′S 145°38′E	Greyish brown light clay soil/ Ordovician slate	300	P. aspleniifolius N. cunninghamii E. lucida C. nitida A. biglandulosum Anopterus glandulosus Cyathodes juniperina	42 24 13 11 8 1 1
Sawback 42°49′S 146°21′E	Shallow brown fibrous peat overlying yellowish brown soil/ Ordovician siltstone[1]	480	E. lucida P. aspleniifolius N. cunninghamii A. biglandulosum C. nitida T. gunnii	32 30 19 14 3 2
Hastings 43°24′S 146°51′E	Dark brown fibrous peat over sand/ Silurian sandstone[1]	120	P. aspleniifolius E. lucida N. cunninghamii Agastachys odorata A. biglandulosum C. nitida	40 24 18 9 6 3
Mt Field 42°41′S 146°21′E	Dark grey peat becoming sandy with depth Triassic sandstone	680	P. aspleniifolius A. biglandulosum N. cunninghamii Eucalyptus subcrenulata	82 10 4 4

[1] From 1:250 000 Geological Survey Maps, Dept. of Mines, Hobart.

of frequency of individuals plotted against size classes.
Continuously regenerating populations typically have an
inverse J-shaped distribution (Hett & Loucks 1976). This use
of size structure assumes a significant positive correlation
between tree diameter and age. This was tested by taking
increment cores at breast height from each species at (one core per tree)
several sites and counting the rings to determine tree age.
Diameters of the cored trees ranged from 4-60 cm, though
large trees were often unsuitable because of decayed
centres. The ages of the stems (after reaching 1.3 m in
height) were regressed against size (dbh) for each species.
Correlation analysis indicates a significant positive
relationship between diameter and age for each species at
each site (Table 2.2). Therefore diameter was considered to
be an acceptable approximation of age. The small number of
cores taken at some sites, and the absence of cores from
sites of interest, e.g. H2 and Mt Field, is due to
difficulty of coring some species and consequent breakage of
components of the increment corer.

In addition to these study sites, smaller sample plots
(0.20 and 0.10 ha) were sited in other forests in which
pattern analysis was impractical due to high stem density (H2) or
where seedlings were infrequent (Ballroom, Sawback,
Murchison, Hastings, Pieman and Mt Anne). In these forests a
wide area was searched and the sample plot was placed in a
location considered to be representative of the forest. The
Ballroom Forest graded into closed heath and the interface
was characterised by the establishment of rainforest trees.
In addition to the 0.20 ha study plot, a transect of 20 x 80
metres was laid across the forest edge and the frequency and
height of all stems less than 1 cm dbh, and the dbh and
height of all larger stems was recorded in contiguous 20 x 5
m quadrats.

Percentage cover of the forest floor by ground and tree
ferns was estimated visually on all sites.

Canopy cover was measured by analysis of hemispherical
photographs taken at a height of 1.5 m above the ground in

Table 2.2 Correlation of tree age in years (y) with diameter
at breast height in centimetres (x) from n tree cores of each
species taken at Frodsham's Pass (F), Pipeline Road (P),
Weindorfer's Forest (W), Ballroom Forest (B), Dempster (D)
and Sawback (S). The ages determined from the ring counts
relate to stem age after reaching 1.3 m in height, except
at Dempster where rings were counted on 20 cm high stumps
of felled trees. The time taken to reach the height at which
the trees were aged can be calculated from the data in
Table 9.3, although it relates only to seedlings growing
under full sunlight. All r values are significant at the
99% level.

Species	Site	n	Regression equation	r
N. cunninghami	F	20	$\log_e y = 3.0598 + 0.5078 \log_e x$	0.92
	P	20	$\log_e y = 2.8563 + 0.5380 \log_e x$	0.91
	S	7	$\log_e y = 2.5606 + 0.7161 \log_e x$	0.88
A. moschatum	F	20	$\log_e y = 2.8183 + 0.6208 \log_e x$	0.95
	P	20	$\log_e y = 2.6596 + 0.6692 \log_e x$	0.97
E. lucida	F	20	$\log_e y = 3.1329 + 0.5468 \log_e x$	0.96
	S	8	$\log_e y = 2.7907 + 0.7161 \log_e x$	0.97
A. selaginoides	W	20	$\log_e y = 2.9293 + 0.6930 \log_e x$	0.90
	B	20	$\log_e y = 2.6710 + 0.7358 \log_e x$	0.88
P. aspleniifolius	D	14	$\log_e y = 3.7857 + 0.4957 \log_e x$	0.89
	S	9	$\log_e y = 3.6268 + 0.5037 \log_e x$	0.82

the centre of each of the 48 contiguous 9 x 9 m quadrats in the 0.39 ha sample plots. On the smaller sample plots, photographs were taken at 10 m intervals along transect lines 10 m apart (15 or 25 photographs). The method of analysis used is based on that described by Anderson (1970) for the diffuse site factor and by Veblen et al. (1981) for total potential diffuse and direct light.

Results

Sumac Road

This tall closed forest is dominated by N. cunninghamii trees up to 35 m high and E. lucida up to 30 m high. The understorey is sparse other than ground and tree-ferns covering 11% of the forest floor. The size structure diagrams (Fig. 2.2a) indicates that both canopy species are regenerating continuously. A. moschatum is represented only in the small size classes (Fig. 2.2a) and is poorly dispersed through the forest. It forms clusters of stems with vegetative origins which can be traced back to the original stem. The majority of small stems have originated as sprouts from the base of older stems, and sometimes as branches from fallen stems which have retained root connections with the soil. Adventitious roots have formed from some of these fallen stems.

Pattern analysis indicates clustering of stems <5cm dbh of E. lucida and N. cunninghamii, predominantly at the small quadrat sizes (Fig. 2.3a). Stems 5-14 cm dbh are also predominantly clustered at the small quadrat sizes, and E. lucida stems >15 cm dbh are clustered in the smallest size class although large stems of N. cunninghamii are not clustered (Fig. 2.3a). Since the forest appears to be well into its second generation (where the term "generation" refers to the potential lifespan of a stem) as determined by the presence of well-decayed old logs and stumps of N. cunninghamii, and the young stems are clustered, it is most likely that the absence of clustering in large stems of N.

Fig. 2.2   Population size structures of the major
woody species on each study site. The stem frequency
is calculated per 0.39 ha in a,b,c,d,e,f,g,h,i & n,
per 0.20 ha in j & m and per 0.10 ha on the
remaining sites.

a. Sumac
b. Parrawe
c. Pipeline
d. Stephen's Rivulet
e. Frodsham's Pass
f. Diddleum
g. Mt Michael
h. Weindorfer 1
i. Weindorfer 2
j. Ballroom
k. Howards Road 1
l. Howards Road 2
m. Mt Anne
n. Dempster
o. Murchison
p. Pieman
q. Hastings
r. Sawback
s. Mt Field

d

N. cunninghamii

A. moschatum

e

N. cunninghamii

E. lucida

A. moschatum

f

N. cunninghamii

A. moschatum

g

N. cunninghamii

A. moschatum

P. aspleniifolius

h

N. cunninghamii

A. selaginoides

P. aspleniifolius

i

N. cunninghamii

A. selaginoides

A. moschatum

j

N. cunninghamii

A. selaginoides

A. moschatum

k

N. cunninghamii

A. selaginoides

E. lucida

A. moschatum

No. of stems (log$_e$y+1)

Stem diameter (cm)

l

N. cunninghamii

A. selaginoides

N. gunnii

E. lucida

P. asplenifolius

No. of stems (log$_e$y+1)

Stem diameter (cm)

o

No. of stems $(\log_e y+1)$

N. cunninghamii

E. lucida

P. aspleniifolius

A. biglandulosum

C. nitida

A. glandulosus

Stem diameter (cm)

p

No. of stems $(\log_e y+1)$

N. cunninghamii

P. aspleniifolius

A. moschatum

A. biglandulosum

Stem diameter (cm)

s

P. aspleniifolius   A. biglandulosum

N. cunninghamii

No. of stems (log$_e$y+1)

Stem diameter (cm)

Table 2.3   Percentage of saplings (more than 10 cm high and less than 5 cm dbh) of each species that have regenerated vegetatively from an older stem.

Site		N. cunninghamii	A. moschatum	E. lucida	P. aspleniifolius	A. selaginoides	A. biglandulosum	C. nitida	A. glandulosus	A. odorata
Stephens Rivulet		8	96							
Pipeline Road		43	98							
Sumac Road		19	98	63						
Parrawe		12	82							
Mt Michael		30	99			0				
Diddleum		95	98							
Weindorfer's Forest	W1	38			0	0				
	W2	17	95			18				
Ballroom Forest		89	99			0				
Mt Anne		7	99			0				
Howard's Road	H1	73	99	73		0				
	H2	7		18	2	0				
Dempster		54		75			100	100	100	
Pieman		87	100			0	100		100	
Murchison		45		79		0	100		100	
Sawback		74		100		0	100	100		
Hastings		52	82	93			97	100	100	85

Site   Species

cunninghamii is due to stem thinning rather than to initial random establishment.

Parrawe

This tall closed forest is dominated by N. cunninghamii up to 33 m tall and A. moschatum up to 28 m tall. The understorey is generally open, with occasional Tasmannia lanceolata, Pittosporum bicolor and Coprosma quadrifida and the tree-fern, Dicksonia antarctica, in canopy gaps. Ground and tree-ferns cover 12% of the forest floor, predominantly in canopy gaps.

Size structure diagrams indicate that both A. moschatum and N. cunninghamii are regenerating continuously (Fig. 2.2b), A. moschatum primarily by vegetative reproduction as described for Sumac Road, and N. cunninghamii primarily from seed (Table 2.3).

Pattern analysis indicates clustering of the small stems of both species, particularly N. cunninghamii, at the small quadrat sizes. Some clustering of stems 5-14 cm dbh occurs in the smallest quadrats, but little clustering of larger stems occurs (Fig. 2.3b). As at Sumac Road, the reduced clustering of larger stems is probably due to stem thinning.

Pipeline Road

This tall closed forest is dominated by N. cunninghamii the largest of which reach 38 m in height, with A. moschatum sub-dominant and reaching heights of 32 m. The understorey is devoid of shrubs and tree-ferns are occasional. Total ground cover by ferns is 5%.

Size structure diagrams indicate that both A. moschatum and N. cunninghamii are regenerating continuously (Fig. 2.2c), A. moschatum by vegetative reproduction and N. cunninghamii both vegetatively and from seed (Table 2.3).

Pattern analysis indicates clustering of A. moschatum stems of all sizes at small quadrat sizes (Fig. 2.3c). N. cunninghamii stems <5 cm dbh are highly clustered,

particularly in the small quadrats (Fig. 2.3c). N. cunninghamii stems 5-14 cm dbh are also clustered at small quadrat sizes but the stems >15 cm dbh show little clustering (Fig. 2.3c), as at the previously described sites.

Stephen's Rivulet

This tall closed forest is dominated by N. cunninghamii up to 35 m high with A. moschatum sub-dominant and reaching 30 m in height. The understorey is open and ferns cover 5% of the forest floor.

Size structure diagrams indicate that both A. moschatum and N. cunninghamii are regenerating continuously (Fig. 2.2d), A. moschatum predominantly by vegetative reproduction and N. cunninghamii predominantly from seed (Table 2.3).

Pattern analysis indicates a clustered distribution of stems <5 cm dbh of both species primarily at the small quadrat sizes (Fig. 2.3d). A. moschatum stems are most highly clustered. Stems 5-14 cm are also clustered at the small quadrat sizes (Fig. 2.3d). N. cunninghamii stems >15 cm dbh are randomly distributed, but the large stems of A. moschatum, which are predominantly vegetative in origin, are slightly clustered at quadrat sizes up to 21 x 21 m (Fig. 2.3d).

Frodsham's Pass

This closed forest contains N. cunninghamii trees up to 28 m tall, and A. moschatum and E. lucida up to 26 m tall. The understorey contains occasional Orites diversifolia and Anopterus glandulosus, but is generally open. Fallen stems of A. moschatum, E. lucida and N. cunninghamii which have retained root connections with the soil are common. Branches of these stems grow vertically, often forming a straight line of stems with their origins obscured by years of humus formation. Adventitious roots were observed in A. moschatum, N. cunninghamii and E. lucida. Cover by ferns is less than 5%. The layer of leaf litter is thin and moss is profuse on

the forest floor and the lower stems of trees.

Size structure diagrams indicate that all species are regenerating continuously (Fig. 2.2e). Although the origins of small stems were often difficult to determine without uprooting the plant (and hence data from this site is absent from Table 2.3), small stems of seedling origin are common in both N. cunninghamii and E. lucida, and vegetative stems are common in all species, but particularly in A. moschatum and E.lucida.

Pattern analysis indicates that stems <5 cm dbh of all species are clustered primarily at the smaller quadrat sizes, although E. lucida stems also show some clustering at the larger quadrat sizes (Fig. 2.3e). Large stems of E. lucida are not sufficiently frequent for pattern analysis. Large stems of N. cunninghamii and A. moschatum are clustered at the small quadrat sizes (Fig. 2.3e). This is probably caused by the apparently high frequency of vegetative reproduction on this site.

Diddleum

This tall closed forest has a canopy dominated by N. cunninghamii reaching heights of 35-40 m. A. moschatum is sub-dominant and often forms clusters of stems which can be traced back to an old parent stem (Fig. 2.4). The infrequency of large rotting logs suggests that this may be a relatively young forest (within the first generation of N. cunninghamii). On this site some large N. cunninghamii trees are dead and dying, with tunnels characteristic of Platypus subgranosus abundant on the trunks, in the pattern described by Howard (1973d), creating some large gaps up to ca 20 x 15 m. These gaps are typically occupied by ground ferns and tree ferns which cover 6% of the forest floor. Leaf litter on this site is thin (<2 cm) but a large amount of fine branch litter up to 20 cm deep sits loosely on the forest floor.

The size structure of A. moschatum indicates that it is regenerating continuously (Fig. 2.2f), mainly by vegetative

Fig. 2.3   Values of Morisita's index, I_δ, at quadrat sizes of length 1 unit (3x3 m) to 9 units (27x27 m).

    a. Sumac
    b. Parrawe
    c. Pipeline
    d. Stephen's Rivulet
    e. Frodsham's Pass
    f. Mt Michael
    g. Diddleum
    h. Weindorfer 1
    i. Weindorfer 2.
    j. Dempster
    k.   "

N. cunninghamii total: ● ; of seedling origin only: o
E. lucida total: ■ ; of seedling origin only: □
A. moschatum: ▲
A. selaginoides: ▼
P. aspleniifolius: ◆
A. biglandulosum: △
C. nitida: ◇
A. glandulosus: *

e

≥15 cm dbh

5–14 cm dbh

<5 cm dbh

Quadrat size

f

≥15 cm dbh

5–14 cm dbh

<5 cm dbh

Quadrat size

g

≥15 cm dbh

5–14 cm dbh

<5 cm dbh

Quadrat size
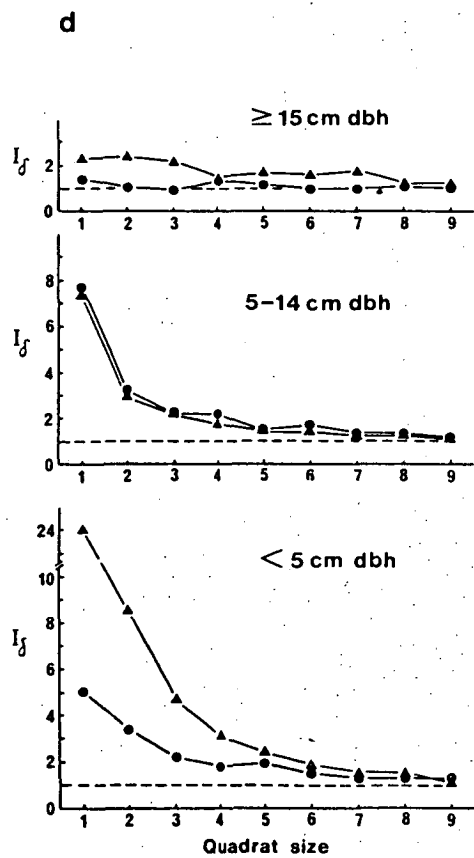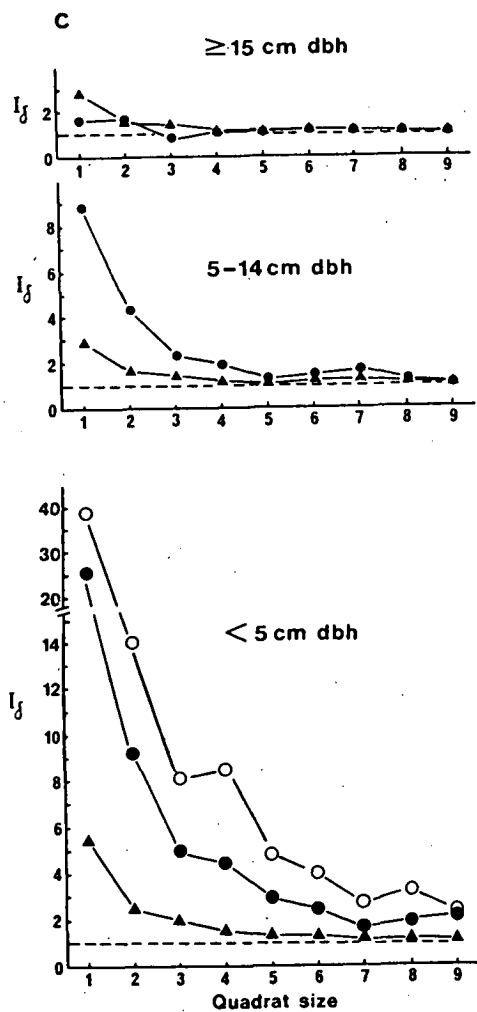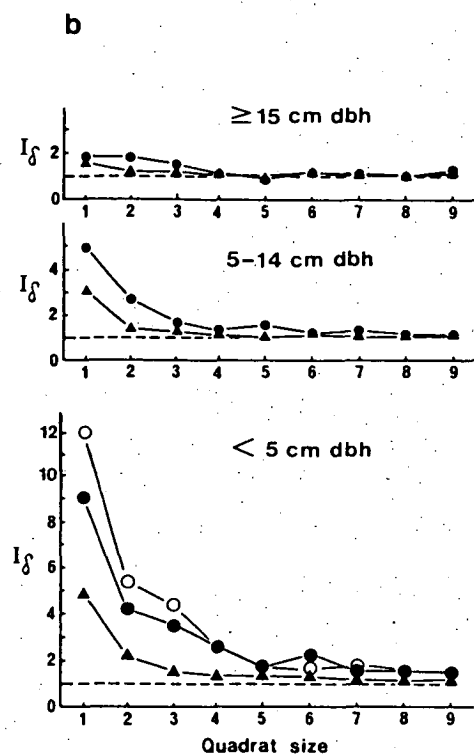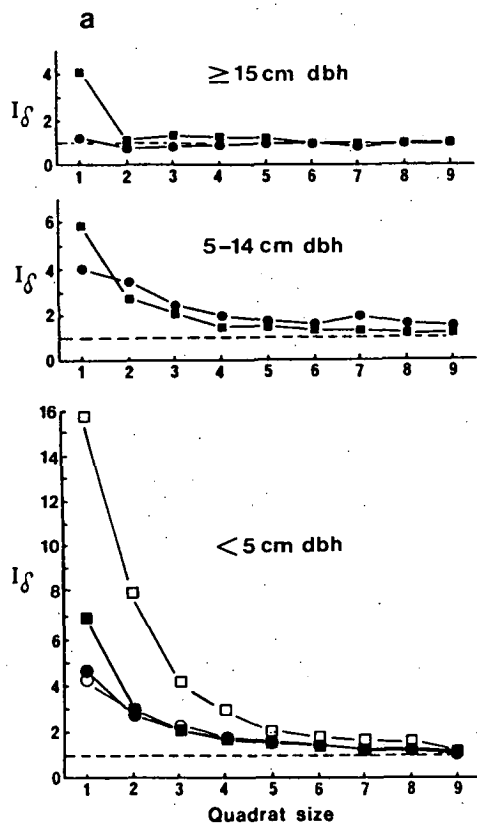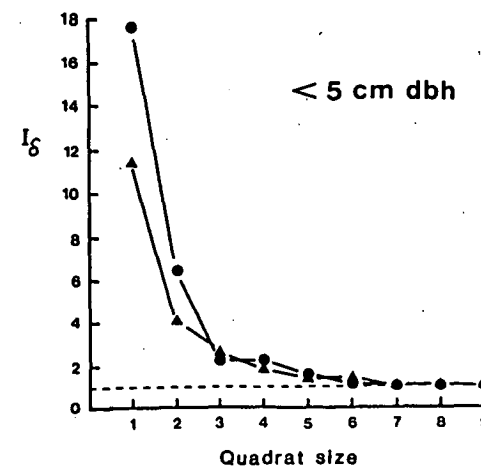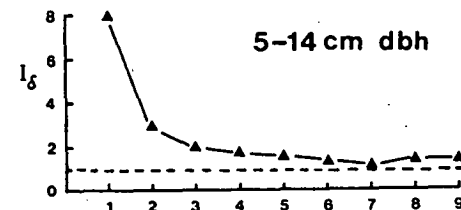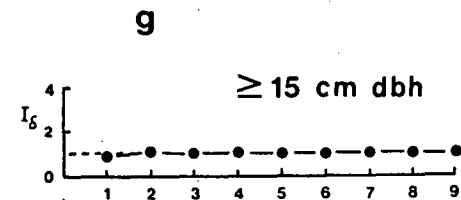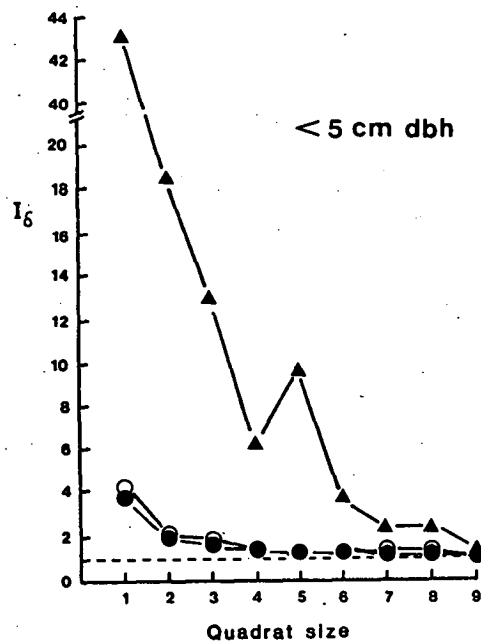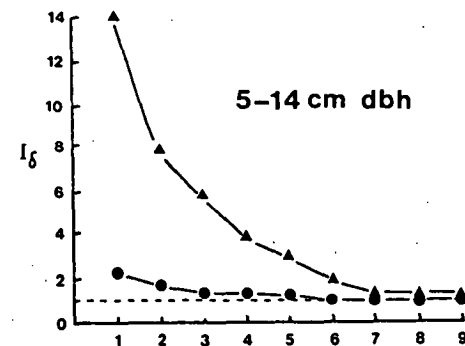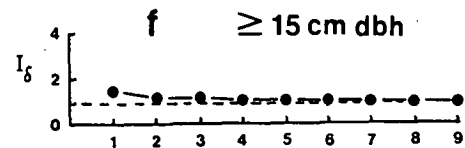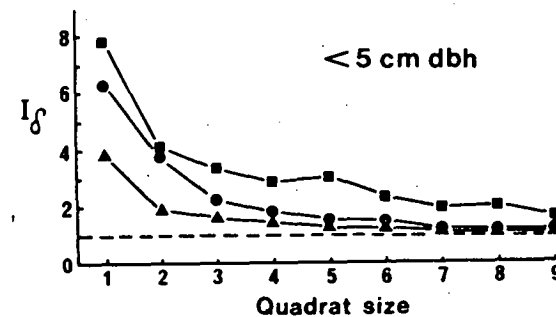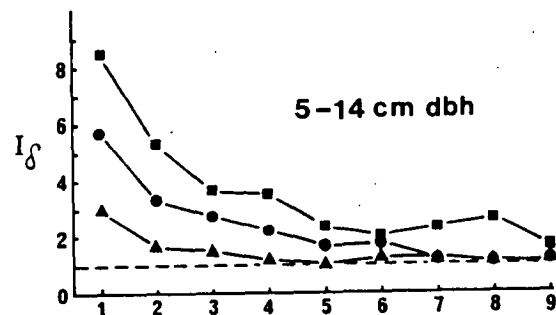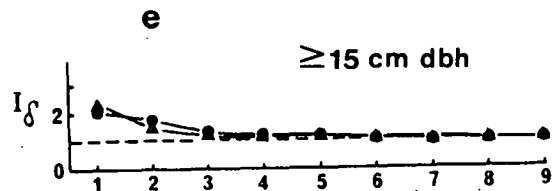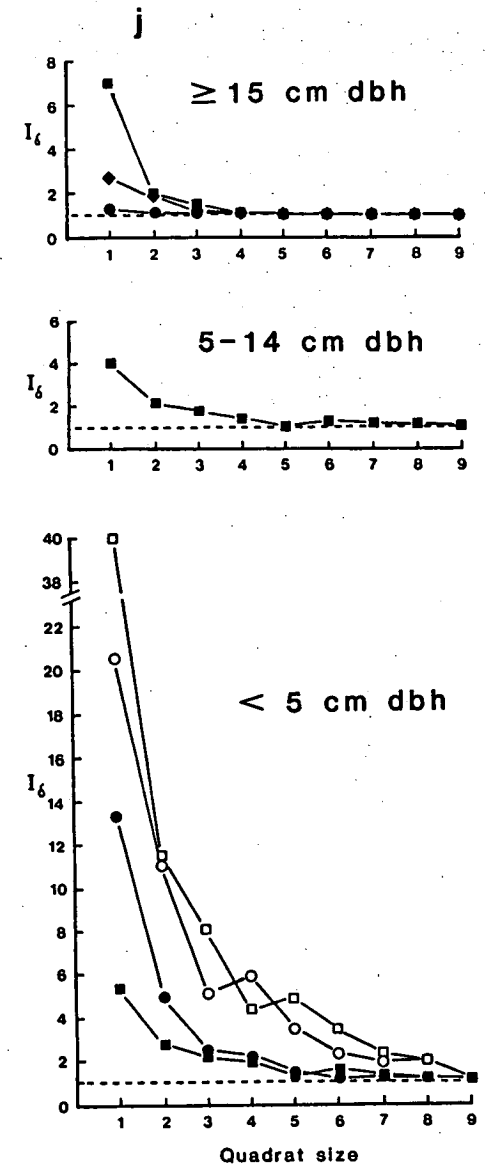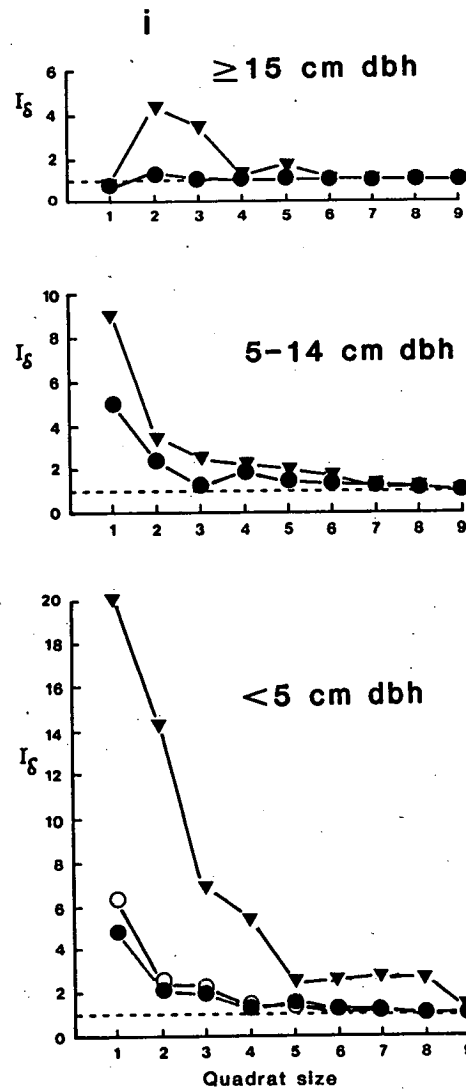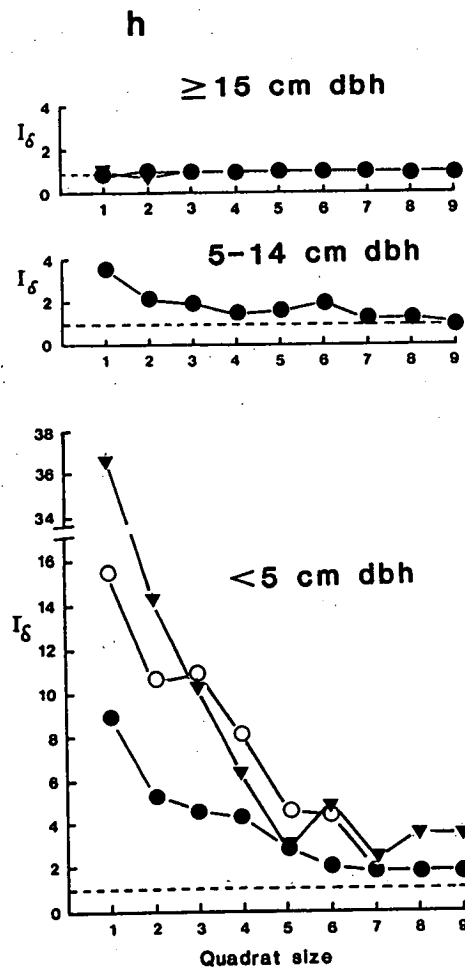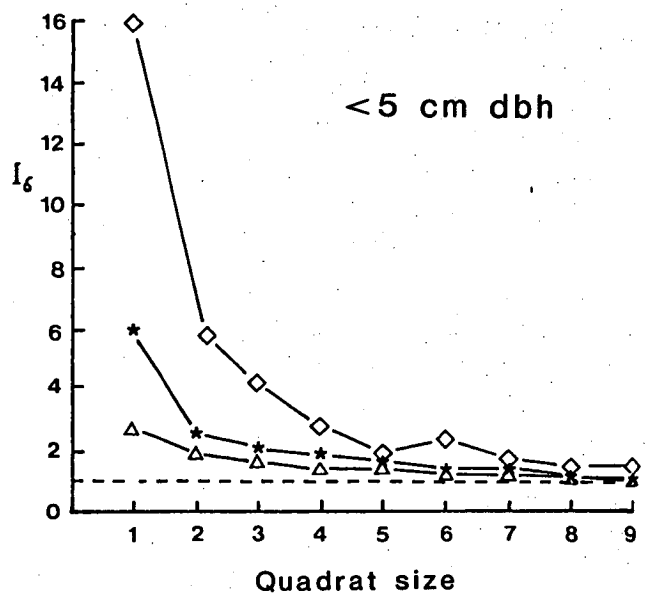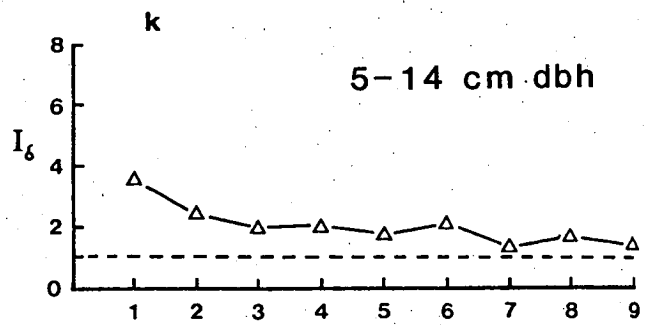
reproduction (Table 2.3). Small stems of N. cunninghamii are also predominantly vegetative in origin (Table 2.3) and there is a peak of larger stems of this species at 35-45 cm dbh (Fig. 2.2f). The clustered dispersion of both A. moschatum and N. cunninghamii stems <5 cm dbh and 5-14 cm dbh, even at the large quadrat sizes (Fig. 2.3g), is caused by the vegetative origin of the stems. There are insufficient large A. moschatum stems and 5-14 cm dbh stems of N. cunninghamii for pattern analysis.

The relatively low number of stems 5-35 cm dbh and the rarity of establishment from seed indicates some instability in the N. cunninghamii population. The stem sprouts which account for 95% of the stems <5 cm dbh are small, and successful replacement by these sprouts is uncertain. _ Vegetative reproduction is rarely as vigorous in N. cunninghamii as it is in A. moschatum. Seedling establishment appears to be retarded first by the deep branch litter, and later by the fern dominance of the canopy gaps.

Mt Michael

This is a closed forest with a canopy dominated by N. cunninghamii up to 20 m tall. A. moschatum is sub-dominant, reaching heights of 17 m and is poorly dispersed through the forest (Fig. 2.4). Litter is generally sparse on the forest floor which is profusely covered by moss. Ground ferns are infrequent. Some large stems of N. cunninghamii are dead and dying from "myrtle dieback" as described at Diddleum.

A. moschatum is regenerating continuously (Fig. 2.2g), mainly by vegetative reproduction (Table 2.3). Stems <5 cm dbh and 5-14 cm dbh are highly clustered even at relatively large quadrat sizes (Fig. 2.3f). This can be related to the vegetative origins of the stems and slow dispersion through the forest.

N. cunninghamii is regenerating continuously at Mt Michael (Fig. 2.2g), both vegetatively and from seed (Table 2.3). Small stems are clustered predominantly at the smaller

quadrat sizes, with progressively less clustering of larger
stems (Fig. 2.3f). Seedlings <10 cm high are profuse on the
mossy forest floor (Fig. 2.8b).

Weindorfer's Forest

Both sites (W1 and W2) are closed forests dominated by
A. selaginoides and N. cunninghamii. The two sites are only
50 m apart, both on the same soil and on a level site, but
with varying structures. The trees are largest on W2 where
A. selaginoides reaches heights of up to 30 m and stem
diameters of 200 cm, and N. cunninghamii grows up to 27 m
high with stem diameters of up to 130 cm. A. selaginoides
stems on W1 do not exceed 24 m in height and 90 cm dbh.
Large canopy gaps are less frequent on W1 (Table 2.5) and
the understorey is more dense than W2 (predominantly
Trochocarpa gunnii). Some large logs, 120-150 cm diameter,
lay rotting on the floor of W1. On one of these a 33 cm dbh
tree with an estimated age (from increment cores) of 290
years has established. These observations suggest that W1 is
younger than W2 in terms of tree age, although relatively
large A. selaginoides were present on W1 in a previous
generation. The rate of decay of the fallen logs is
uncertain so the age of the earlier population is unknown
and the time and reason for its demise are unknown. The
forest is close to open plains and therefore may be exposed
to fire. Some A. selaginoides trees close to the forest edge
were fire-scarred.

The size structure diagrams (Figs 2.2h & 2.2i) indicate
that N. cunninghamii is regenerating continuously on both
sites from seed and stem sprouts (Table 2.3). On W1 the
seedlings are most highly clustered in the small quadrat
sizes, but are still clustered in quadrat sizes up to 21 x
21 m (Fig. 2.3h). Stems 5-14 cm dbh are clustered to a
lesser degree and large stems are randomly distributed (Fig.
2.3h). On W2, where the canopy has a higher mean opening
(Table 2.4), N. cunninghamii seedlings show less clustering
(Fig. 2.3i). Stems 5-14 cm dbh are clustered in the smallest

Fig. 2.4   Patterns of establishment of <u>A. moschatum</u> at
Mt Michael and Diddleum.

Individual <u>A. moschatum</u> stems $\geq$15 cm dbh: ▲

Individual <u>A. moschatum</u> stems 5-14 cm dbh: ▲

Presence of <u>A. moschatum</u> stems <5 cm dbh and $\geq$10 cm high
   of vegetative origin in a 3x3 m quadrat: :::

Individual <u>A. moschatum</u> stems <5 cm dbh and $\geq$10 cm high
   of seedling origin: s

Fig. 2.5   The distribution and diameters of
<u>A. selaginoides</u> stems $\geq$15 cm dbh at Weindorfer 2.
The study site is 54x72 m.

Mt Michael
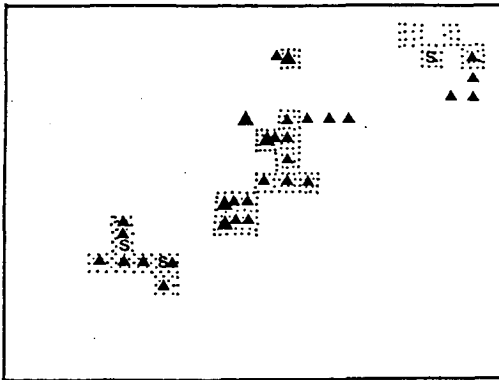
Diddleum
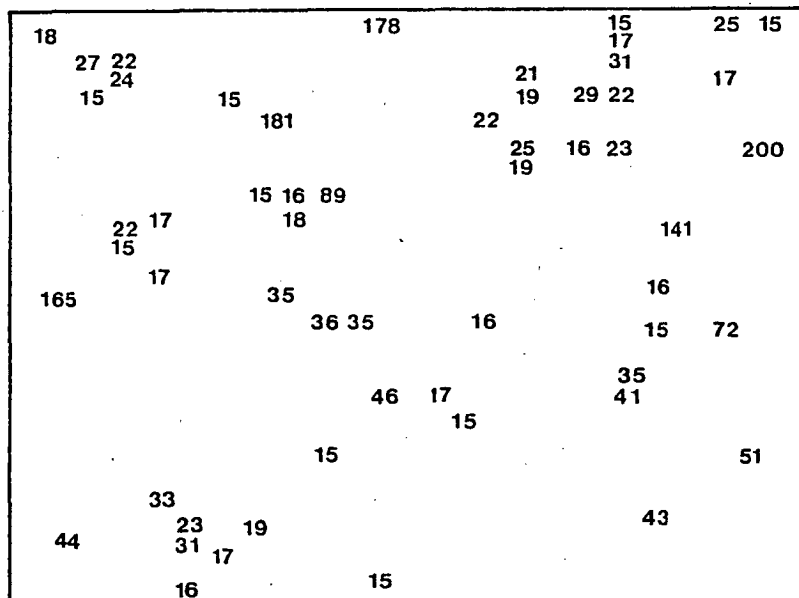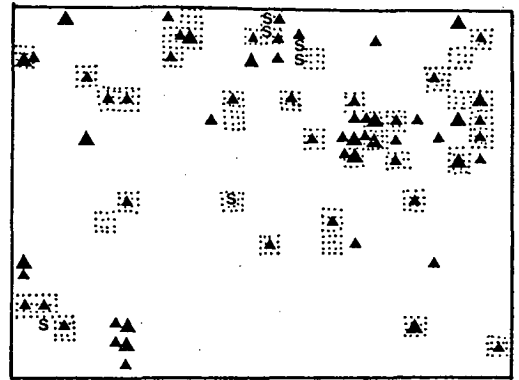
Table 2.4 Mean canopy opening (with standard errors) at each study site, determined from n hemispherical photographs taken 1.5 m from the ground.

Site		n	Canopy opening (%)
Sumac		48	24.8 ± 3.5
Parrawe		48	19.2 ± 4.0
Pipeline Road		48	17.3 ± 4.0
Stephen's Rivulet		48	31.3 ± 3.6
Frodsham's Pass		48	12.8 ± 2.8
Diddleum		48	14.1 ± 2.6
Mt Michael		48	14.0 ± 2.0
Weindorfer's Forest	W1	48	17.0 ± 2.2
	W2	48	30.7 ± 3.4
Ballroom Forest		25	5.0 ± 1.6
Mt Anne		25	22.4 ± 3.6
Howards Road	H1	15	12.3 ± 2.6
	H2	15	35.5 ± 2.0[1]
Dempster		48	15.7 ± 2.7
Pieman		15	7.3 ± 2.6
Murchison		15	10.5 ± 4.2
Sawback		15	6.9 ± 1.1
Hastings		15	9.1 ± 3.7
Mt Field		25	69.6 ± 6.5

[1] Measured while N. gunnii was in full leaf.

Table 2.5 Light conditions on the larger (0.39 ha) study sites: the number of quadrats (9 x 9 m) falling in each of the 10% classes of 0-100% canopy opening, estimated from hemispherical photographs. The total number of quadrats on each site is 48.

Canopy opening (%)	Sumac	Parrawe	Pipeline	Stephens Rivulet	Frodsham's Pass	Diddleum	Mt Michael	W1	W2	Dempster
0-10	17	27	24	13	32	28	27	12	10	27
11-20	9	3	11	8	9	12	11	25	7	9
21-30	7	4	5	6	2	3	5	5	8	7
31-40	4	2	2	6	2	0	2	1	7	0
41-50	5	3	1	4	1	2	1	2	6	2
51-60	2	1	1	4	0	1	1	2	3	0
61-70	2	3	1	2	0	0	1	1	3	1
71-80	1	1	1	3	0	1	0	0	2	2
81-90	0	1	2	2	1	1	0	0	2	0
91-100	1	3	0	0	1	0	0	0	0	0

quadrats, and large stems have a random distribution (Fig. 2.3i). A. moschatum is regenerating continuously (Fig. 2.2i), primarily by vegetative reproduction (Table 2.3). P. aspleniifolius is not sufficiently frequent within the smallest size class to maintain the size distribution on W1 (Fig. 2.2h) and is absent on W2.

The size structure diagrams of A. selaginoides show discontinuous regeneration. On W1, small trees are infrequent (Fig. 2.2h) and 92% of the stems <5 cm dbh occur in two canopy gaps of ca 10 x 15 m, although seedlings <2 cm high are frequent throughout both study sites. The pattern of size structure may either represent episodic regeneration dependent on the infrequent formation of large canopy gaps, or failure of the small saplings to successfully reach the canopy. The pattern analysis (Fig. 2.3h) indicates a high degree of clustering of small A. selaginoides stems at smallest size classes with some clustering occurring throughout the range of quadrat sizes. Stems 5-14 cm dbh are not frequent enough for cluster analysis. Large trees are randomly distributed at all quadrat sizes (Fig. 2.3h), indicating either the effect of stem thinning or original random establishment.

On W2, the size structure of A. selaginoides suggests two temporally distinct populations, the older of five remaining trees with stems 140-200 cm dbh, and the younger population regenerating continuously (Fig. 2.2i). Seedlings of A. selaginoides are most highly clustered at the smallest quadrat sizes but clustering occurs throughout the range of quadrat sizes, and stems 5-14 cm dbh are clustered at the small quadrat sizes (Fig. 2.3i). The large stems are clustered only at 6 x 6 m and 9 x 9 m (Fig 2.3i). Examination of the spatial distributions of stems $\geq$15 cm dbh (Fig. 2.5) shows that stems >50 cm dbh are not clustered but that the smaller stems are often clustered into groups of stems of similar diameter.

Ballroom Forest

This tall closed forest is dominated by N. cunninghamii
and A. selaginoides with A. moschatum sub-dominant. A.
selaginoides reaches heights of 40 m, emerging above the
main canopy of N. cunninghamii (36 m) and A. moschatum (27
m). The canopy is dense (Table 2.4), especially beneath the
canopy of A. moschatum, and the understorey is open.

The size structure diagrams indicate that N.
cunninghamii and A. moschatum are regenerating continuously
in this forest (Fig. 2.2j). The only seedlings of N.
cunninghamii and A. selaginoides occur in a single large
canopy gap (ca 10 x 20 m). However sprouts from the base of
the main stem are common in N. cunninghamii throughout the
forest. A. selaginoides has a discontinuous size structure
with most stems being greater than 65 cm dbh (Fig. 2.2j)
which indicates either a temporal gap in the establishment
of this species or failure of small stems to reach the
canopy.

The transect across the outer edge of the Ballroom
Forest starts in a relatively species-rich closed heath
containing the woody species Bauera rubioides, Baeckia
gunniana, Oxylobium arborescens, Boronia citriodora,
Nothofagus cunninghamii, Nothofagus gunnii, Athrotaxis
selaginoides, Athrotaxis cupressoides, Richea pandanifolia,
Richea sprengelioides, Coprosma quadrifida, Tasmannia
lanceolata, Phyllocladus aspleniifolius and Leptospermum
nitida and terminating in the species-poor tall closed
forest of N. cunninghamii, A. selaginoides and A. moschatum.
(Fig. 2.6d). Stem density of A. selaginoides is highest on
the forest edge (15-40 m along the transect), with very low
density within the forest (Fig. 2.6a). N. cunninghamii also
has high stem densities at the forest edge, decreasing to a
relatively constant density of about 10 stems per 100 m^2
within the forest (Fig. 2.6a). The density of small stems of
A. selaginoides is high only on the forest edge, whereas the
density of small stems of N. cunninghamii remains at a
relatively constant level with a single high peak (at 40 m)

Fig. 2.6   Vegetation changes across the closed heath-
closed forest boundary in the Ballroom Forest, Cradle
Mountain National Park. The transect is 80x20 m, with
data recorded in contiguous 5x20 m quadrats.

a. Frequency of all stems $\geq$10 cm high in each
   quadrat.
b. Mean height of the three tallest stems in each
   quadrat.
c. Frequency of stems 10-100 cm high.
d. Species richness of woody plants in each quadrat.

a,b,c: N. cunninghamii   ●
        A. moschatum   ▲
        A. selaginoides   ■
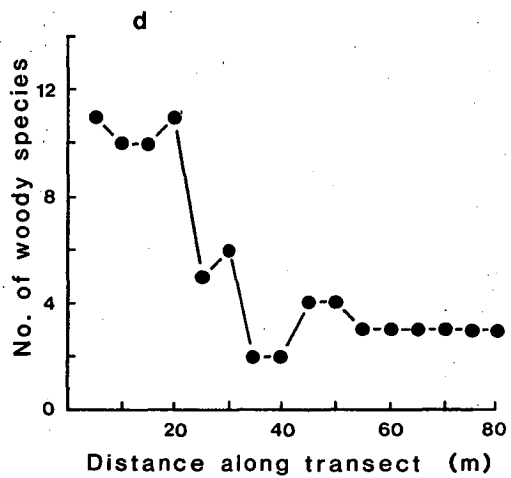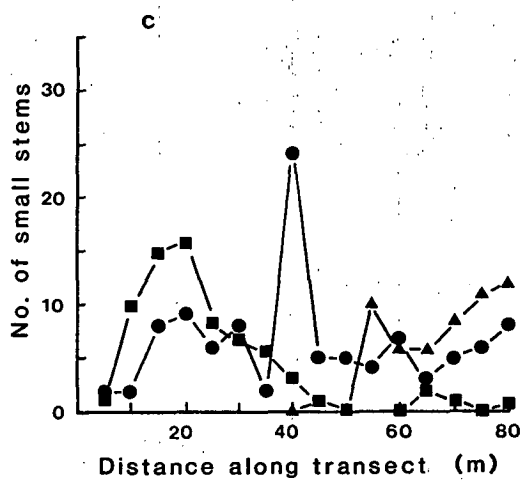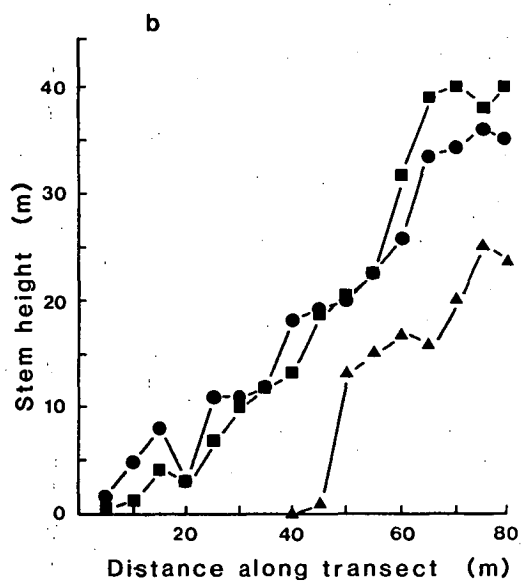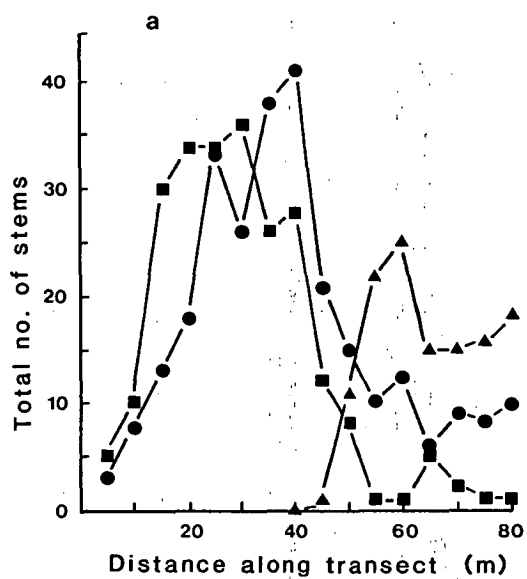
in a canopy gap (Fig. 2.6c). However within the mature forest, small stems of N. cunninghamii are predominantly vegetative in origin, other than in canopy gaps. A. moschatum is not establishing in the heath or at the forest edge (Figs 2.6a&c). A. selaginoides is commonly overtopped by N. cunninghamii except in the mature forest where it emerges above the tallest N. cunninghamii trees, and A. moschatum never reaches the upper canopy (Fig. 2.6b). It is uncertain whether the large A. selaginoides stems established within a rainforest situation, in association with species such as N. cunninghamii, or whether they originated in a heath vegetation similar to that beyond the forest edge. The paucity of regeneration of A. selaginoides in the rainforest suggests that the larger stems originated in a more open vegetation.

Howard´s Road

H1 is a tall closed forest with scattered large A. selaginoides reaching heights of up to 35 m, emerging slightly above a canopy of N. cunninghamii, E. lucida and A. moschatum. The latter three species, together with Anodopetalum biglandulosum, are abundant in the small size classes and are regenerating continuously (Fig. 2.2k). A. selaginoides however is not represented in the small size classes (Fig. 2.2k).

H2 is a low closed forest with a staggered canopy, consisting of a tangled mass of stems of trees and shrubs. N. gunnii occurs in almost krummholz form with prostrate trunks of up to 35 cm diameter within 1 m of the base, eventually forming an erect trunk up to 5 m high. There was no indication of adventitious roots forming from the prostrate trunks and branches. The stem origins were often obscured by years of humus formation and the establishment of other stems, and trunks were prostrate for up to 4 m. The other tree species were growing erect, A. selaginoides reaching heights of 12-15 m and the other tree species forming a staggered canopy of 5-10 m height with the shrub

and small tree species, <u>Agastachys odorata</u>, <u>Anopterus</u>
<u>glandulosus</u>, <u>Tetracarpea tasmanica</u>, <u>Tasmannia lanceolata</u>,
<u>Persoonia gunnii</u>, <u>Trochocarpa gunnii</u>, <u>Cenarrhenes nitida</u>,
<u>Anodopetalum biglandulosum</u> and <u>Richea pandanifolia</u>. The
floor was moss-covered and litter was infrequent. <u>N.</u>
<u>cunninghamii</u>, <u>E. lucida</u> and <u>A. selaginoides</u> are
well-represented in the small size classes, although the
15-24 cm class is under-represented in <u>A. selaginoides</u> (Fig.
2.21). <u>P. aspleniifolius</u> is poorly represented in the
smallest size class and <u>N. gunnii</u> is not represented in the
two smallest size classes (Fig. 2.21). Seedlings and
saplings of all species occur on the bare soil of a nearby
road edge. The <u>N. gunnii</u> trees were estimated to be up to
350 years old (from increment cores). Increment cores of <u>A.</u>
<u>selaginoides</u> from the Cradle Mountain area indicate that
trees on H2 could be of a similar age to the <u>N. gunnii</u>
trees. However the maximum stem size of the other tree
species suggests that they have established more recently.
Age determinations from ring counts of small stems growing
on an adjacent exposed site indicate similarity of height
growth rates of all species except <u>A. selaginoides</u> which has
a considerably lower growth rate (Table 9.3).

Mt Anne

Forests containing <u>A. selaginoides</u> and <u>N. cunninghamii</u>
occur over several hundred metres elevation over the
north-west ridge of Mt Anne. The study site selected was a
closed forest dominated by these two species forming a
canopy up to 30 m high, with <u>A. moschatum</u> sub-dominant and
with a relatively clear understorey. Part of a
recently-formed canopy gap (within the last five years),
approximately 10 x 15 m, occurred within the study site.

The size structures of the <u>N. cunninghamii</u> and <u>A.</u>
<u>moschatum</u> populations indicates that these species are
regenerating continuously (Fig. 2.2m). <u>A. selaginoides</u>
however is not represented in the 5-24 cm classes (Fig.
2.2m). The only stems less than 25 cm dbh are three

seedlings which are 10-30 cm high. This size structure
appears typical of a very large area of forest on Mt Anne.

Dempster

This closed forest has a canopy up to 25 m high formed
by N. cunninghamii, P. aspleniifolius and E. lucida. The
understorey is variable, ranging from clear and open, to
dense thickets of small diameter stems of Anodopetalum
biglandulosum, Anopterus glandulosus and Cenarrhenes nitida.
Ferns form less than 5% cover of the forest floor. Large
fallen and rotting logs occur on the forest floor.

All woody species are well represented in the small size
classes with the exception of P. aspleniifolius which
reaches a peak frequency in the size class 35-44 cm (Fig.
2.2n). Seedlings of P. aspleniifolius <10 cm high occur
within the forest but are most frequent on exposed edges of
the forest, and survival to sapling size is insufficient to
maintain the frequency of P. aspleniifolius within this
forest. Vegetative reproduction is common in all woody
species other than P. aspleniifolius, and forms all of the
reproduction of A. biglandulosum, A. glandulosus and C.
nitida within the forest (Table 2.3), although seedlings of
these species were observed on the forest edge.

Seedlings of N. cunninghamii and E. lucida are most
clustered at the small quadrat sizes, but some clustering is
apparent in all but the largest quadrat size (Fig. 2.3j). N.
cunninghamii stems 5-14 cm dbh are not sufficiently frequent
for pattern analysis. Stems ≥15 cm dbh are randomly
distributed at all quadrat sizes (Fig. 2.3j). E. lucida
stems of the two larger size classes are clustered at the
small quadrat sizes (Fig. 2.3j). This pattern results from
both the clustered dispersion of seedlings and the success
of vegetative reproduction.

P. aspleniifolius stems are frequent enough for analysis
only at stem size ≥15 cm dbh. Pattern analysis indicates
weak clustering at the smallest quadrat sizes (Fig. 2.3j).

C. nitida and A. glandulosus are also clustered at the

small quadrat sizes (Fig. 2.3k) and are poorly dispersed through the forest. A. biglandulosum is widespread through the forest with less clustering of stems than C. nitida and A. glandulosus (Fig.2.3k) although these three species are all reproducing entirely by vegetative means (Table 2.3) – by stem sprouts or by adventitious rooting of fallen stems. Larger stems of A. biglandulosum (5-14 cm) are more highly clustered at the small size quadrat sizes than smaller stems (Fig.2.3k).

Murchison

This closed forest has a staggered canopy formed by P. aspleniifolius, N. cunninghamii and E. lucida of 20-25 m in height,with A. biglandulosum, C. nitida and A. glandulosus up to 15 m high. Understorey species include Trochocarpa gunnii, Richea pandanifolia and occasional Gahnia grandis. Large fallen and rotting logs were absent.

P. aspleniifolius is absent from the small size classes and has a peak frequency at 25-34 cm dbh (Fig. 2.2o). C. nitida is also absent from the smallest size class (Fig. 2.2o). The other species are regenerating continuously, N. cunninghamii both vegetatively and from seed, and the other species predominantly by vegetative reproduction (Table 2.3). Seedlings of all species are common on bare soil on the forest edge.

Pieman

This tall closed forest is dominated by P. aspleniifolius (up to 32 m high) and N. cunninghamii (up to 29 m high), with A. moschatum and A. biglandulosum subdominant. The interior of the forest is a dense tangle of stems of A. biglandulosum which extend into the few canopy gaps.

P. aspleniifolius is absent from the small size classes (Fig. 2.2p) although seedlings and saplings are frequent at the forest edge. Other tree species are regenerating continuously, primarily by vegetative reproduction (Table

2.3). Only P. aspleniifolius has reached its maximum potential size. It is not clear if this is a reflection of its duration of site occupation relative to the other species, or a differential relationship between site quality and maximum attainable size among the species.

Hastings

This closed forest has a staggered canopy formed by P. asplenifolius and N. cunninghamii trees up to 20 m high, with several small tree species (Table 2.1).The size structure indicates that P. aspleniifolius is absent from the small size classes and has a peak frequency of stems at 35-44 cm dbh (Fig. 2.2q). The other common species of trees are regenerating continuously (Fig. 2.2q). Neither N. cunninghamii, E. lucida or A. moschatum have reached their maximum size potential, although P. aspleniifolius has done so. As on the Pieman site, it is not certain whether this relates to stem age or the effects of site quality on maximum attainable size.

Sawback

This closed forest contains P. aspleniifolius (up to 20 m high), and shorter trees up to 17 m high forming a staggered canopy. The adjacent forest was burnt approximately 15 years ago (determined by sapling ages) along two edges and approximately five years ago along another edge.

P. aspleniifolius is not represented in the smallest size class (Fig. 2.2r). Stems have a peak frequency at 25-34 cm dbh. N. cunninghamii is well represented in the smallest size class but is poorly represented in the 5-14 cm dbh size class (Fig. 2.2r). It is not clear whether this size structure represents a short period of regeneration failure, or the failure of small stems to successfully reach the canopy. The other tree species are regenerating continuously, primarily by vegetative reproduction (Table 2.3). Seedlings of E. lucida, P. aspleniifolius and N.

cunninghamii <5 cm high are common on the forest floor, and
all species currently in the canopy as well as Monotoca
glauca, Cyathodes juniperina and Tasmannia lanceolata are
present as seedlings in the most recently burnt area
adjacent to the forest. Large fallen and rotting logs were
absent from this forest.

Mt Field

This site was selected for study because of the
apparently continuous regeneration of P. aspleniifolius. The
site is on an acid sandy peat with patchy sphagnum moss
distribution in poorly drained hollows. Most establishments
appear to be confined to small mounds, and the few seedlings
which have established in the sphagnum hollows are stunted
and chlorotic. The predominant tree species is P.
aspleniifolius (Table 2.1) reaching heights of up to 6 m,
with A. biglandulosum and occasional N. cunninghamii and
Eucalyptus subcrenulata. The area is a mosaic of low open
forest, with patches of dense low closed forest, and the
whole area of approximately 1 ha is surrounded by eucalypts.
The area used for study is open woodland, selected to show
the size distribution of P. aspleniifolius, indicating
continuous regeneration (Fig. 2.2s) which has not previously
been recorded for this species in this study. The small
clumps of dense forest do not contain seedlings and appear
to have a size structure similar to that recorded on other
study sites in P. aspleniifolius.

Discussion

N. cunninghamii, A. moschatum and E. lucida

The population size structures indicate that these
species are regenerating continuously, with the possible
exceptions of N. cunninghamii at Diddleum and Sawback. This
makes no assumption about the stability of species
proportions since the mortality rates are not known.

At Diddleum and Sawback, where N. cunninghamii is poorly
represented in some small size classes, two alternative
interpretations may be made. Firstly, it may be interpreted
as a temporary deficit, and that the smaller stems are
sufficiently abundant to allow regeneration of the
population. However it may also be interpreted as a failure
of the smaller stems to successfully reach the canopy. At
Sawback, which has a low mean canopy opening, the only
species which are regenerating continuously are doing so
entirely by vegetative reproduction (Table 2.3). Seedling
establishment appears to be less effective in forests with a
dense canopy on poor soils, where death of a tree does not
create an effective gap at ground level due to the high
frequency of small stems of vegetative origin of many
species. For example, a high proportion of vegetative
reproduction in N. cunninghamii and E. lucida is in general
associated with low mean canopy opening (Fig. 2.7). This is
due to the association between seedling frequency and canopy
conditions (Fig. 2.8a&b). This is most noticeable in N.
cunninghamii for which a larger number of sites were
sampled. Seedling establishment patterns with respect to
canopy opening may be complicated by substrate preferences,
with seedlings of all the canopy species most common on bare
mineral soil, moss and rotting logs. Diddleum is the only
odd point on the plot of the percentage of stems of
vegetative origin of N. cunninghamii against mean canopy
opening (Fig. 2.7). The infrequency of establishment from
seed on this site (Fig. 2.8b) is probably related to the
unusually deep layer of fine branch litter on the forest
floor which retards seedling establishment, and to the high
density of ferns in the older canopy gaps. Seedling
establishment is unusually high at Mt Michael (Fig. 2.8b)
which has a very similar canopy cover to Diddleum (Tables
2.4 & 2.5), but has a moss-covered forest floor. Small stems
are infrequent at H2 (Fig. 2.8b) due to the low percentage
of the total basal area formed by N. cunninghamii. There is
no trend in the frequency of stems of vegetative origin with

Fig. 2.7   The proportion of stems $\geq$10 cm high and <5 cm dbh that are of vegetative origin in relation to mean canopy opening of the forest.

N. cunninghamii :   ●

A. moschatum :   ▲

E. lucida :   □

The circled point is from Diddleum.
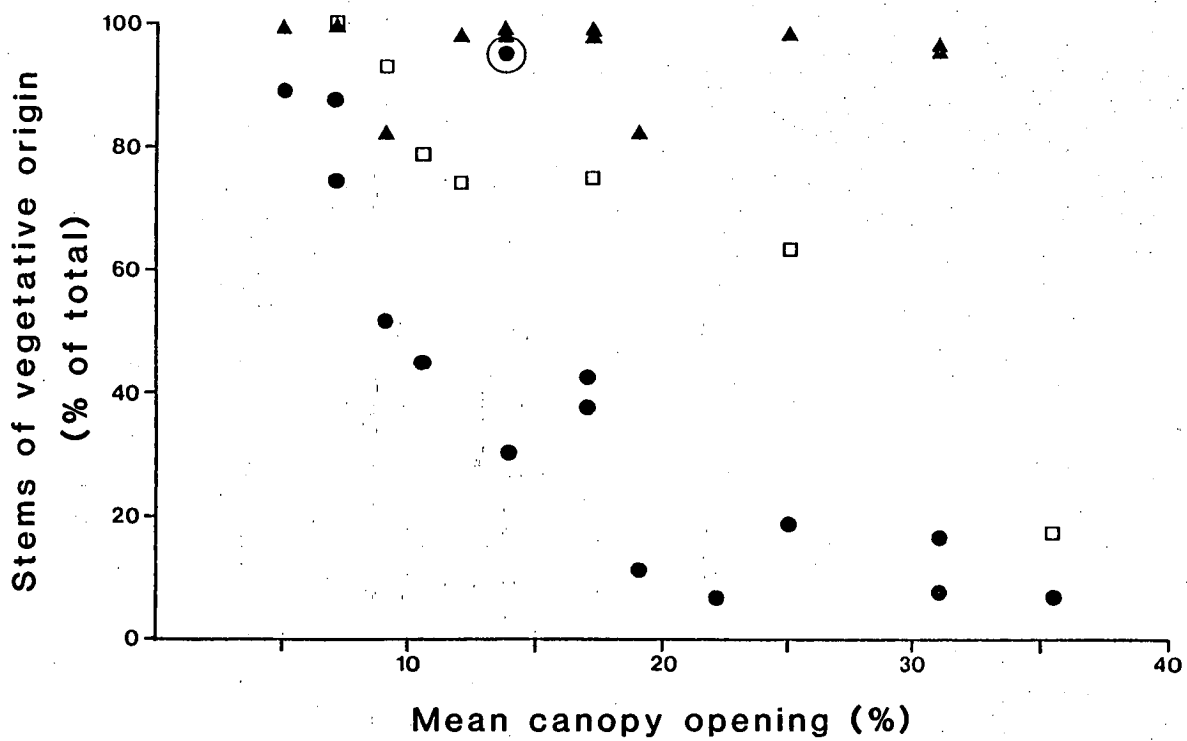
Fig. 2.8   The frequency of stems $\geq$10 cm high and <5 cm dbh (ha^{-1}) in relation to mean canopy opening of the forest. Data points are plotted only for sites where the species forms at least 5% of the total basal area.

a. E. lucida of vegetative origin: □

                  of seedling origin: ■

b. N. cunninghamii of vegetative origin: O

                    of seedling origin: ●

c. P. aspleniifolius (of seedling origin): △

    A. sclaginoides (of seedling origin): ▲

Howard's Road, H2:   h

Mt Michael: m

Diddleum: d

No. of stems (log$_e$)

Mean canopy opening (%)

c
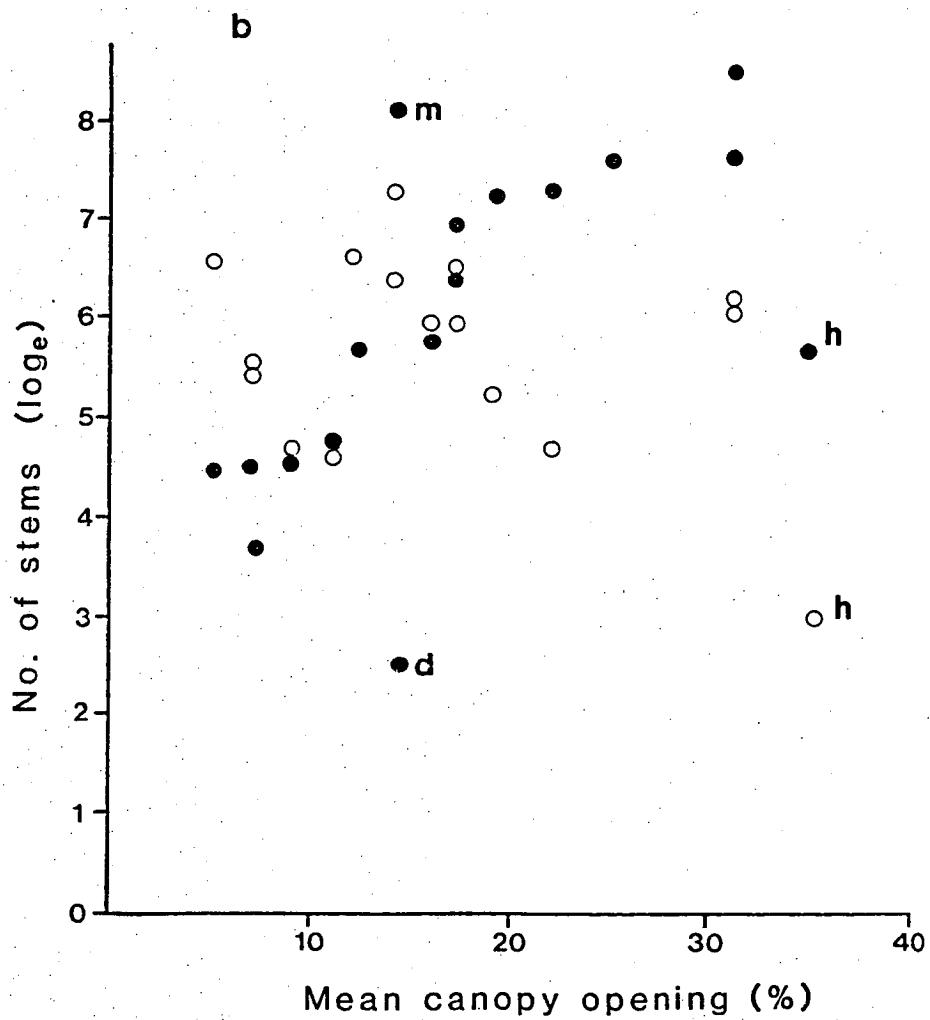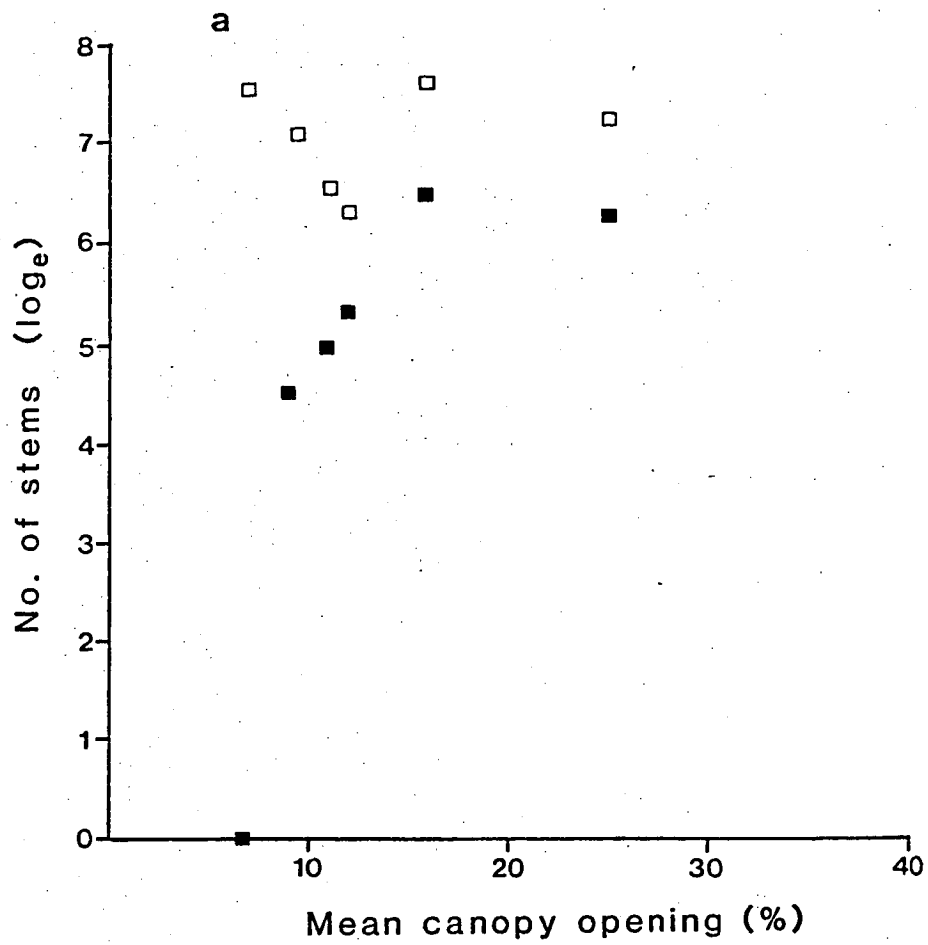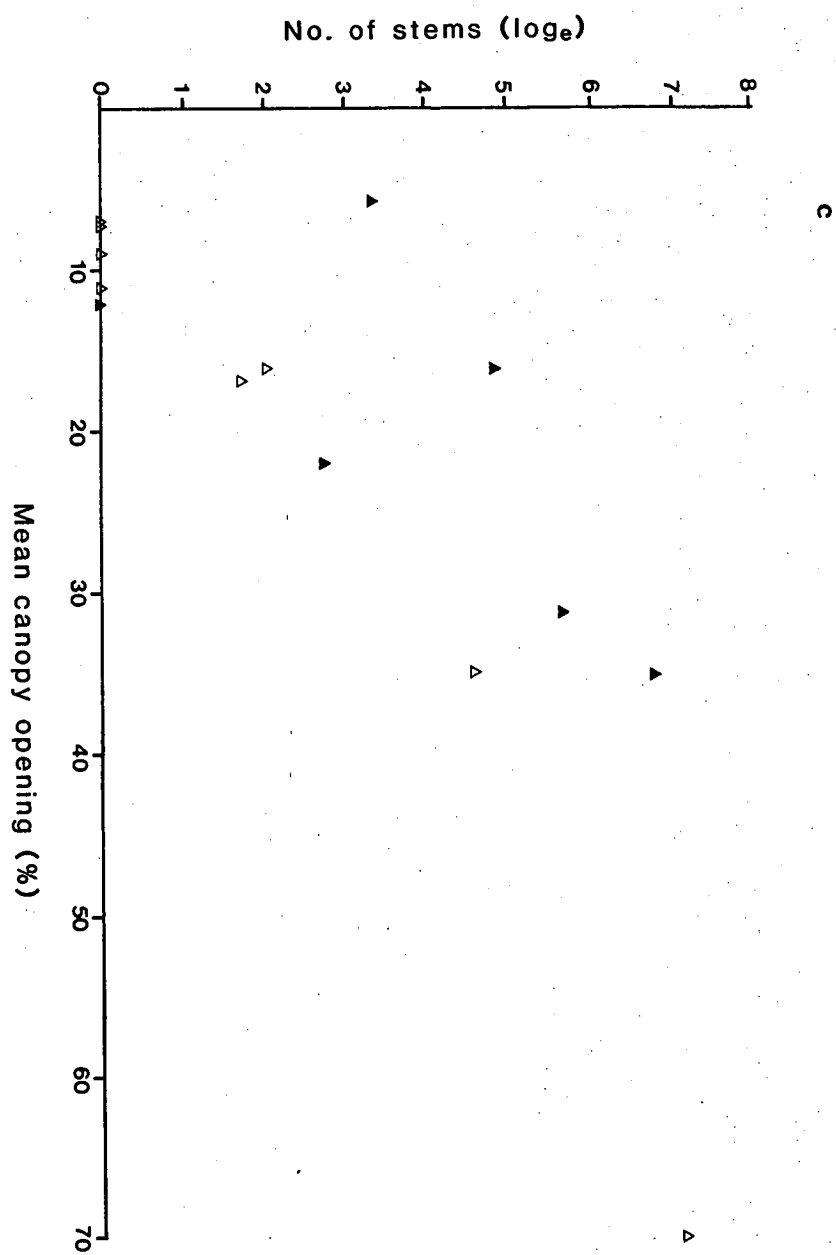
respect to mean canopy opening (Fig. 2.8a&b). Even though
the association between canopy opening and regeneration from
seed is generally clear, the features of the canopy opening
which are determining the success of establishment (e.g.
light and nutrient availability) are not certain.

The clustering patterns of A. moschatum, and to a lesser
extent E. lucida, reflect the vegetative origins of many of
the stems. Clusters of vegetative stems are often large in
size and restricted in frequency which leads to the
clustering apparent at large quadrat sizes in the pattern
analyses. The clustering patterns of smaller stems of
species that reproduce vegetatively is strongly influenced
by the dispersion of the larger parent stems (Fig. 2.5). A.
moschatum is poorly dispersed through many of the sample
plots (Sumac, Diddleum, Mt Michael, Mt Anne, Ballroom
transect and W2) or is absent (W1) although common in
adjacent forest. On these sites there is no evidence of
older parent stems and the largest stems appear to be the
result of random establishment from seed. From these
establishment patterns it appears that these forests will
contain progressively more A. moschatum as it spreads
vegetatively and from rare seedling establishments. For
example A. moschatum is more widely dispersed through
Diddleum than Mt Michael and this is due to the greater
number of stems (sapling and small tree) that have
established from seed on the former site. However, this
dispersal through the forest has occurred very slowly. For
example, the large stems of A. moschatum on the Mt Michael
and Diddleum study sites are up to 40 cm dbh which indicates
a maximum age of approximately 220 years (using the
regression obtained from Pipeline increment cores together
with sapling growth rates (Tables 2.$\overset{2}{1}$ and 9.4)). On sites
where A. moschatum forms a higher percentage of the total
basal area and is well-dispersed through the forest
(Frodsham's Pass, Parrawe and Ballroom Forest) N.
cunninghamii is regenerating successfully in canopy gaps. If
any autogenic replacement of N. cunninghamii by the more

shade-tolerant A. moschatum is occurring, it is over a very
long time scale and as such the frequency and effect of
catastrophic disturbance may make the projected outcome
purely theoretical. Several stands of rainforest dominated
by A. moschatum do occur in Victoria and Tasmania. In
Victoria the absence of N. cunninghamii on the Errinundra
Plateau, which has an apparently suitable climate (Busby
1985), has been attributed to poor seed dispersal and
subsequent inability to cross dry corridors (Howard & Ashton
1973). In Tasmania, A. moschatum sometimes occurs in small
stands, usually in wet gullies, as the dominant rainforest
species, with N. cunninghamii absent. In these stands A.
moschatum is usually growing in association with Eucalyptus
and Acacia species which have fire-stimulated regeneration.
It has been suggested that these outliers of A. moschatum
are due to superior fire and drought resistance (Mount 1964)
and superior dispersal (Gilbert 1959; Jackson 1983) as
compared with N. cunninghamii. The only report of A.
moschatum autogenically replacing N. cunninghamii was made
by Gilbert (1959) in the Florentine Valley. He reported poor
regeneration of N. cunninghamii in pure rainforest and mixed
forest and suggested that A. moschatum, which was well
represented in the small size classes, would progressively
replace N. cunninghamii. Unfortunately that site was cleared
many years ago. The factors controlling the success of A.
moschatum establishment from seed are not certain. There is
no relationship between the proportion of vegetative
reproduction and the mean canopy opening (Fig. 2.7).

On a shorter time-scale, however, these three species
tend to be self-replacing in old, undisturbed forests. This
is probably influenced by the following features:
1. Reproduction characteristics: Vegetative reproduction
(basal sprouts from the stem base) predominates in A.
moschatum, and is common in E. lucida, thereby allowing
indefinite replacement. These stems are often already part
of the canopy at the time of death of the main stem.
Sprouting of shoots from a basal burl is common in N.

cunninghamii in Victoria and parts of north-west Tasmania (Howard 1973) but is generally less frequent elsewhere in Tasmania. Viable seed of N. cunninghamii and E. lucida is poorly dispersed (Hickey et al. 1983), especially within the rainforest where air movement is reduced by the density of the canopy. The seed pool is therefore concentrated around trees of the same species.

2. Establishment preferences with respect to gap size: A. moschatum trees have a deep, conical crown with a diameter at the widest point of 5-12 metres. The effective canopy gap created by the death of an old A. moschatum stem is relatively small, especially when the tree is multi-stemmed. Successful regeneration of N. cunninghamii or E. lucida in such gaps is relatively infrequent. Seedling frequency of N. cunninghamii and E. lucida is associated with the forest light climate (Figs 2.7, 2.8 & 2.9). The results of pattern analysis indicate that N. cunninghamii and E. lucida seedlings are most highly clustered at small quadrat sizes. Cluster size depends on the availability of a suitable substrate as well as the size of the gap, and therefore may be lower than the actual size of the gap. N. cunninghamii trees have a larger crown with a diameter of 8-18 metres, which casts heavy shade. Death of an old stem results in a relatively large gap, and other trees may be knocked over by its fall. Gaps created by the initial fall of an old N. cunninghamii of up to 550 m^2 were recorded on the study sites. Establishment by A. moschatum is less likely in these gaps largely due to the generally infrequent establishment from seed. Lateral outgrowth of branches or coppice of existing stems of A. moschatum may utilise some of the canopy gap. Seedlings of N. cunninghamii and E. lucida readily establish in such gaps. Where seedlings of both these species establish (or with other gap-regenerating species), the replacement species is the result of competition processes which are considered in Chapters 9 and 10.

In dis-climax rainforests, such as the late stage mixed

forests, the composition of this rainforest component may not be so stable. For example, Ogden & Powell (1979) suggest that N. cunninghamii increases its basal area as the eucalypts die out, but that the basal area of A. moschatum remains unchanged. Lowland rainforest can regenerate after fire so long as the fire-free interval is long (Gilbert 1959) and there is an available seed source. However little is known about the early stages of post-fire regeneration and the stability of species composition. The probabalistic model of species replacement described above suggests the importance of the initial floristic composition (Egler 1954), i.e. if N. cunninghamii, E. lucida and A. moschatum establish early on a widely disturbed site, through chance dispersal or differential survival of fire, they will tend to persist.

Myrtle dieback as described by Howard (1973d, 1981) was observed only on the Mt Michael and Diddleum study sites, although it was observed on road edges near some other study sites. The effect on differential establishment of the three species described in this paper in terms of gap formation is uncertain although Howard (1981) noted that seedling, sapling and pole trees of N. cunninghamii were present in these gaps. Although the large amount of leaf and branch litter from the dying trees at Diddleum appeared to retard seedling establishment, at Mt Michael seedlings were common, and therefore the effect of the dieback on regeneration is probably determined by site characteristics such as those which determine the rate of litter decomposition.

The persistence of N. cunninghamii in lowland cool temperate rainforest in Tasmania is due to its ability to regenerate in canopy gaps created by the fall of old trees. A similar pattern of regeneration of N. cunninghamii was noted by Howard (1973a) in Victoria. Although this gap replacement is a feature of high altitude forests in New Zealand (June & Ogden 1978) and Chile, and at high latitudes in Chile, it is less frequent in forests occurring on optimal sites (Veblen et al. 1981; Wardle 1983). In the

mixed rainforests in south-central Chile <u>N. dombeyi</u> occurs
in large even-aged patches with no clustering within the
patch and is generally unable to regenerate in canopy gaps
created by the death of old trees (Veblen <u>et al</u>. 1981). The
difference between this situation and that observed in
Tasmania may be caused by differences in physiology (such as
light requirements) between the <u>Nothofagus</u> species, or in
characteristics of the co-occurring species. These
hypotheses are examined in Chapter 12.

A. selaginoides

A. selaginoides is regenerating continuously only on the
edge of the Ballroom Forest, and at H2. In the closed
forests, <u>A. selaginoides</u> either has temporally distinct
populations (W2) or is failing to regenerate sufficiently to
maintain its abundance in the canopy (W1, H2, Mt Anne and
possibly Ballroom)., Kirkpatrick & Harwood (1980) observed
the absence of seedlings and saplings of <u>A. selaginoides</u> at
Mt Bobs (southern Tasmania) with no evidence of recruitment
over the last 300 years. Ogden (1978) found a similar
population size structure on his study site at Mt Anne with
infrequent recent establishments and infrequent recruitment
of established stems less than 50 cm dbh to the canopy.
Ogden's Swift Creek study site has a similar population size
structure to W2, with two temporally distinct populations,
the younger of which is regenerating continuously. He also
records the age of establishment of these trees from
increment cores which verifies the temporal distinction. The
group of larger trees on W2 could not be aged because of
their large size (relative to the increment corer). The
population size structures on W2 and on Ogden's Swift Creek
site suggest that regeneration is failing in closed forests
with unbroken canopies, but that where the canopy is opening
due to the death of large old trees, the gaps are of
sufficient size to permit successful regeneration of <u>A.</u>
<u>selaginoides</u>. It is possible, therefore, that the small

stems observed in W1 and Mt Anne may represent the start of a regeneration phase with opening of the canopy. Similarly, the Ballroom Forest site indicates infrequent regeneration of A. selaginoides, with seedlings occurring only in the large canopy gaps created by the death of large old trees and on the edge of the forest. N. cunninghamii has higher seedling numbers in smaller canopy gaps than A. selaginoides (Fig. 2.9), and may also regenerate from basal sprouts (Table 2.3). Consequently it is less affected than A. selaginoides by the density of the canopy and regenerates continuously on sites where A. selaginoides has a discontinuous size distribution. Therefore it is also possible to interpret the low numbers of small trees on sites such as H1, W1 and Mt Anne as failure of recruitment to the canopy due to vigorous growth of co-occurring species in the canopy gaps, especially on sites with higher species richness forming a closed canopy, such as H1. Further study sites with an emphasis on historical vegetation reconstruction are necessary to clarify the regeneration status of A. selaginoides on sites such as these. Even on sites where regeneration is occurring in A. selaginoides (W2 and H2) there is no indication of the stability of the proportion of A. selaginoides in the canopy.

Kirkpatrick & Harwood (1980) reject low light intensity as the reason for regeneration failure of A. selaginoides, due to the frequency of seedlings of N. cunninghamii, A. moschatum and P. aspleniifolius in the study area, and because regeneration of A. selaginoides was observed in forest in the Cradle Mountain area of similar canopy cover (no confirming data was presented). However the first reason is not a meaningful explanation since it does not allow for differences among species in their light requirements. In this study, regeneration of A. selaginoides is clearly greater on sites with greater opening of the canopy (W2, H2 and the edge of the Ballroom forest), although it is not a simple relationship at the lower levels of canopy opening (Fig. 2.8c). Seedlings of both A. selaginoides and N.

Fig. 2.9   The mean frequency of seedlings in relation
to canopy conditions (in 10% class intervals) of the
9x9m quadrats within study sites.
a. Weindorfer 2
b. Weindorfer 1
c. Sumac

N. cunninghamii: white
A. selaginoides: black

* indicates a canopy opening class for which only one
value was recorded.
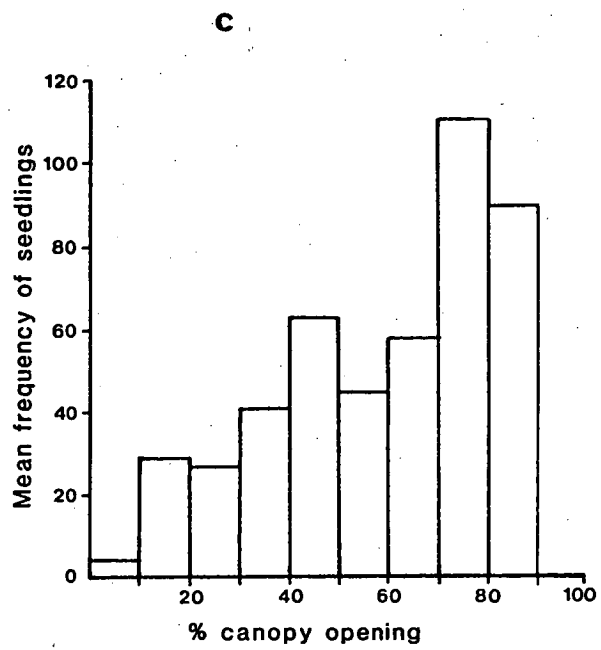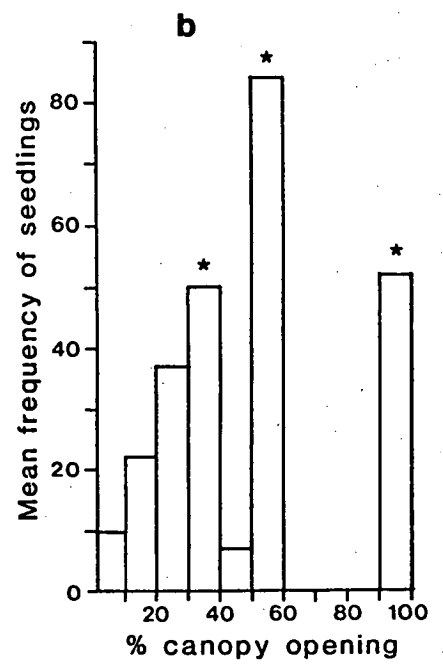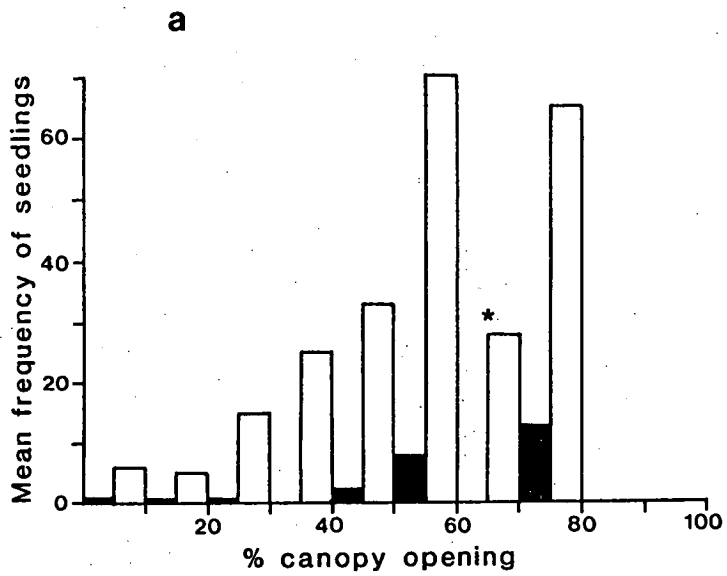
cunninghamii have a more clustered distribution on W1 which
has a higher overall canopy cover than W2 (Table 2.4) and a
low frequency of large canopy gaps (Table 2.5). In addition,
seedlings of A. selaginoides are more highly clustered than
those of N. cunninghamii which suggests a tighter
association with the canopy gaps. Even though the
association of A. selaginoides seedling establishment with
canopy opening is clear, the features of the canopy opening
(e.g. light and nutrients) which are determining the success
of establishment is not certain.

Seedlings of A. selaginoides less than 2 cm high occur
within the forests, even where regeneration is failing, and
it is unlikely that germination and early establishment are
the primary factors limiting regeneration of this species on
most of the sites studied here. However little is known of
the seeding behaviour of A. selaginoides or the relationship
between tree age and the amount of viable seed produced and
these factors may be important on other sites where the
forest is relatively old before canopy gaps are formed and
if seed production is not coincident with the formation of
canopy gaps or with climate suited to establishment.

Non-regenerating size structures have also been observed
in Athrotaxis cupressoides in Tasmania (Ogden 1978) and are
common in some of the New Zealand gymnosperms. Cockayne
(1958) suggested that the mixed conifer-broadleaved forests
of New Zealand are a seral stage from the pioneering
conifer-dominated forests to the climax broadleaved forests
and several authors have attributed a regeneration gap in
New Zealand gymnosperms to climatic changes which favoured
broadleaved tree species (Robbins 1962; Holloway 1964).
Several studies indicate that the absence of small stems on
some sites can be attributed to regeneration of the
gymnosperms following catastrophic disturbance and
subsequent failure to regenerate in the more mature closed
forests (Clayton-Greene 1977; P. Wardle 1978; Veblen &
Stewart 1982), although some gap regeneration may occur with
thinning of the old forest on sites where the vigour of the

broadleaved species is relatively low (Veblen & Stewart 1982). On many sites, catastrophic disturbance occurs within the lifetime of the gymnosperms, thereby maintaining their importance in the forests. Veblen & Stewart (1982) suggest that these size structures can be attributed to the regeneration ecology of these species without invoking climatic change as a causal factor. These observations are not totally incompatible with earlier theories in that any changes in climate may differentially affect growth rates and consequently the outcome of competition in canopy gaps or on widely disturbed sites. The limited evidence from regeneration patterns suggests that A. selaginoides regenerates poorly in many closed forests, at levels insufficient to maintain its importance in the canopy. The conditions under which it became a canopy dominant of these forests, and the importance of catastrophic disturbance and gradual climatic change in creating these patterns of regeneration is uncertain.

P. aspleniifolius

P. aspleniifolius is regenerating continuously only at the Mt Michael and Mt Field study sites, and at the former site is represented only by relatively small stems. On the other sites the number of small stems is insufficient to allow stability of the P. aspleniifolius population. All other species on the study sites on which P. aspleniifolius is common in the canopy (Dempster, Pieman, Murchison, Sawback, Mt Field and Hastings), are regenerating continuously, with the exception of Cenarrhenes nitida at Murchison and possibly N. cunninghamii at Sawback. All these species, other than P. asplenifolius, have the capacity to regenerate vegetatively. N. cunninghamii and E. lucida are regenerating from seed on some of these sites. The other species (A. glandulosus, C. nitida, A. biglandulosum and A. odorata) rarely establish from seed inside these rainforests (Table 2.3), although seedlings occur on open sites such as

road edges. These forests have a high degree of canopy cover in comparison with many of the other closed forests (Table 2.4) and the proportion of vegetative stems in small size classes is higher in the forests with more closed canopies. The ability of these forests to regenerate is therefore dependent largely on the vegetative capacity of the component species and the failure of P. aspleniifolius to regenerate must be related in part to the inability to reproduce vegetatively. Similarly, the relatively poor regeneration of N. cunninghamii at Sawback may be related to its less vigorous vegetative reproduction.

Trees were aged at Dempster and Sawback. The results indicate that the oldest P. aspleniifolius trees at Dempster are approximately 500 years old. Large canopy gaps have been created by the death of large trees, but other species have quickly established in these gaps. The oldest trees at Sawback (P. aspleniifolius and N. cunninghamii) are approximately 300 years old. This is considerably less than the maximum ages recorded for P. aspleniifolius of 750 years (Dunwiddie & LaMarche 1980) and N. cunninghamii of 450 years (Gilbert 1959) and this, together with the absence of recent large tree falls and large rotting logs, indicates that the Sawback forest has not completed a full generation. The absence of large rotting logs at Pieman and Murchison indicates that these sites may also not have completed a full generation (i.e. a full lifespan). This suggests that the closed forests containing large proportions of P. aspleniifolius have originated after large scale disturbance, with recruitments to the canopy showing a general decrease with time. These forests have a very closed canopy and P. aspleniifolius fails to regenerate even though seedlings less than 5 cm high are common in the forest. At Dempster where large trees are falling and the canopy has a greater mean canopy opening, due to more frequent canopy gaps, P. asplenifolius is also failing to regenerate. This site has similar canopy conditions to Mt Michael where P. aspleniifolius is establishing, while forming a very small

proportion of the canopy (<1%). This appears due in part to the presence of the small tree species at Dempster which coppice vigorously or produce vertical branches from prostrate stems, thereby reducing the light reaching the forest floor in the canopy gaps. These species, including A. biglandulosum, A. glandulosus, C. nitida and Trochocarpa gunnii, are common components of all the closed forests where P. aspleniifolius is a major component of the canopy. Therefore, death of old trees on other sites is unlikely to result in a regeneration phase of P. aspleniifolius. The future of such sites is uncertain with respect to the effect of the small tree species on the continued regeneration of other canopy species. Little is known of the ecology and dynamics of the small tree species. While they rarely establish under a closed canopy, they may vigorously occupy small canopy gaps by vegetative reproduction, and may prevent establishment of the taller canopy species.

The Mt Field site represents the extreme in poor soil quality (indicated by the very low growth rates, Table 9.4) with the resultant low frequency of the faster-growing canopy species which are common on higher quality soils. P. aspleniifolius is regenerating continuously under the open canopy, with competing species limited predominantly to the low shrubs and Gahnia grandis. Pattern analysis was not performed on this site, but some clustering due to soil patterning amongst the mounds and hollows of sphagnum moss due to low pH and poor drainage might be expected. The age of this site (with respect to past disturbance) is unknown. Although the P. aspleniifolius stems are small relative to their potential size, the site quality is limiting the growth rate of seedlings (Table 9.4) and therefore may be limiting the size potential of this species.

Jackson (1968, 1983) has suggested that tall closed forest dominated by N. cunninghamii can develop on any soil or bedrock within the climatically suitable area and that the species composition of forests on low nutrient soils changes gradually due to a necessary improvement in the soil

nutrient status before a climax forest dominated by N. cunninghamii is achieved. He noted that this is rarely achieved on poor soils because of the long fire-free interval required and that scrub rainforest may therefore be persistant on these sites. The results of the present study indicate that there is a more rapid change in canopy composition caused by short-term autogenic processes and suggest that infrequent disturbances, such as fire, may be necessary for the regeneration of P. aspleniifolius on these sites.

This pattern of stand establishment followed by regeneration failure has some similarity with regeneration patterns of A. selaginoides, although in the higher altitude habitats of A. selaginoides fire may be devastatingly destructive rather than regenerative (Kirkpatrick 1977). In addition, there is also some evidence of renewed regeneration of A. selaginoides in forests where the canopy is opening up due to death of large old trees, but this pattern has not been observed in P. aspleniifolius, due apparently to the vigour of co-occurring species in the closed forests. The regeneration pattern of P. aspleniifolius also has similarity with the native conifers of New Zealand and Chile in which regeneration appears to be disturbance-initiated (Wardle 1978; Veblen & Stewart 1982), except on sites where the vigour of co-occurring species is low enough to allow competitive regeneration in gaps (Veblen & Stewart 1982).

Part B

Studies of comparative physiology

Chapter 3   Introduction to studies of comparative
              physiology.

        Community dynamics are determined by propagule
availability and the responses of component species to the
total environment, both physico-chemical and biotic. The sum
of these responses for an individual species is termed its
"niche" and can be divided into four components (Grubb
1977):
1. The habitat niche, i.e. the physical and chemical limits
tolerated by the mature plant in nature.
2. The life-form niche.
3. The phenological niche.
4. The regeneration niche
For each of these components there is a "potential niche"
(in the absence of competitors and predators) and a
"realised niche" (in the presence of competitors and
predators), although these concepts particularly apply to
the habitat niche (Grubb 1977).
        Some aspects of the niche of individual species in a
community can be determined from the spatial and temporal
patterns of regeneration observed in field studies, as in
Chapter 2. However many of the details of a species´ niche
are most easily determined by experimental studies of plant
responses to specific environmental factors. This approach
also recognises the importance of studying comparative
species responses rather than the responses of individual
species in order to understand species niches and community
dynamics. The difficulties of establishing causal mechanisms
of plant density and vigour from field correlations in space
and time include difficulties in measuring environmental
variables, eliciting which variable is determining the
response, the time lag between event and response, and the
importance of rare events in determining species
distributions (Grime 1965; McCune & Allen 1985). The value

of comparative experiments lies in the ability to measure plant responses to controlled variables. Differential species responses may be observed in experiments in which the environment is simplified, with no attempt to reconstruct the field environment (Grime 1965). However there is still the problem that a response may be peculiar to the experimental conditions, or may not play any part in determining field distributions (Grime 1965). At best one can correlate the results of comparative experiments with field data to suggest the probable importance of the cause-effect relationship. The greater the suite of plant-environment responses studied, the greater is the understanding possible of a particular cause-effect relationship. Grime suggests that susceptibilities (plant characteristics which lead to reduced survival, yield or reproduction in the experimental conditions) often recorded in comparative experiments are incidental effects of adaptation to a particular environment and may give some clue to the nature and role of the adaptations.

The previous chapters have recorded spatial and temporal patterns of regeneration in Nothofagus cunninghamii, Atherosperma moschatum, Eucryphia lucida, Phyllocladus aspleniifolius and Athrotaxis selaginoides. Although there has been extensive ecophysiological study of N. cunninghamii, primarily in Victoria (Howard 1970, 1973), nothing has been reported of the comparative physiology of the other rainforest canopy species. The following chapters further examine the niches of the rainforest canopy species by 1) field observations and 2) comparative physiological responses of the rainforest canopy species to experimental environments. The results are discussed in terms of the niches of the individual species and their determination of community dynamics, and consequently the mechanisms determining community composition.

The physiological experiments are predominantly conducted on seedlings for two reasons. Firstly, in a practical sense they are suitable for comparative

experiments due to their small size which allows growth in controlled conditions. Secondly, seedling responses are very relevant to the dynamics of the forest since they represent the early establishment phase. The early seedling leaves of all species except <u>P. aspleniifolius</u> are similar in gross morphology to the foliage of mature plants except in size and the degree of mesomorphy. <u>P. aspleniifolius</u> produces true leaves while the seedlings are relatively small (up to 4-8 cm high). The mature foliage consists of phylloclades. The age of the seedlings used varies among experiments (but is consistant among species within an experiment) and is stated in each case.

The terminology relating to stress and strain used in the subsequent chapters is derived from Levitt (1980).

Chapter 4   Phenology

Introduction

Temperate trees have a limited growing season in natural
conditions and there is considerable variation among species
in the timing and patterns of foliage expansion, and the
timing of flowering and seed release. Variation may also
occur within a single species at different sites. These
features are examined in N. cunninghamii, E. lucida, A.
moschatum, P. aspleniifolius and A. selaginoides at Mt Field
National Park (42°41´S 146°40´E) in order to determine
whether differences among species in these features may
contribute to the observed patterns of species regeneration
and distribution.

Methods

Four sites were selected over an altitudinal range of
820 m from 180 m to 1000m a.s.l.. The species observed at
each site and the features recorded are listed in Table 4.1.
At each site, five lateral branches were tagged on three
trees of each species on exposed forest edges. Saplings (of
seedling origin) of N. cunninghamii, E. lucida and P.
aspleniifolius were also tagged at Site 2 (no saplings of
seedling origin were found in A. moschatum). The following
features were recorded:
1. The timing of bud-break.
2. Leaf production and abscission.
3. The time of flowering, seeding and germination (where
possible). Germination is often difficult to record directly
in the field and is here recorded indirectly as the first
appearance of seedlings (with only cotyledonary leaves).
    Growth patterns were also observed from 1982 to 1985 in
seedlings raised in Hobart from seed or cotyledonary
seedings collected from Mt Field in June 1982. One group of
five seedlings was grown outside under natural daylengths,

Table 4.1   Species, study sites and features recorded in phenological studies
             at Mt Field.

Altitude (m a.s.l.)	Species	Observations
180	N. cunninghamii A. moschatum	Leaf expansion, 1982-83 observations fortnightly.
720	N. cunninghamii A. moschatum E. lucida P. aspleniifolius	Leaf expansion, 1982-83 observations fortnightly. Flowering, seeding and seedling appearance, 1982, 1984 and 1985, observations monthly, but with some gaps in the observation period.
920	N. cunninghamii A. moschatum P. aspleniifolius A. selaginoides	Leaf expansion, 1982-83 observations fortnightly. Flowering, seeding and seedling appearance, 1982, 1984 and 1985, observations monthly, but with some gaps in the observation period.
1000	N. cunninghamii A. selaginoides	Leaf expansion, 1982-83 observations fortnightly.

and another group of seedlings was grown in a glasshouse
under natural daylengths.

Results

Bud-break and shoot expansion

Only <u>N. cunninghamii</u> and <u>E. lucida</u> have specific
adaptations for the protection of dormant buds, the former
with the axillary buds sheathed by bracts, and in <u>E. lucida</u>
the apical buds are enclosed in a yellow wax.

Bud-break occurred later with increasing altitude for
each species, except in <u>N. cunninghamii</u> at 920 m and 1000 m
(Fig. 4.1). There was no distinct pattern in the timing of
bud-break among species, other than the later bud-break of
<u>P. aspleniifolius</u> compared with the other species (Fig.
4.1). At 180 m, <u>N. cunninghamii</u> buds broke earlier than
those of <u>A. moschatum</u>, but there was no difference between
these species at 700 m and 920 m. Similarly, <u>A. selaginoides</u>
buds opened earlier than those of <u>N. cunninghamii</u> at 920 m
but there was no difference among these species at 1000 m.
Bud-break was up to 2-4 weeks earlier in saplings of <u>P.
aspleniifolius</u> and <u>N. cunninghamii</u> at 700 m than in adults.
In 1985, leaf production was delayed in <u>A. moschatum</u> and <u>P.
aspleniifolius</u>, so that at the 920 m study site, leaves of
these species were not fully mature by June. In contrast,
leaves of the other species had matured by late summer-early
autumn.

<u>N. cunninghamii</u> shoots from saplings and mature plants
showed predominantly determinate growth, with a single flush
of growth from axillary buds during the spring, usually
bearing 5-16 leaves. Many axillary buds remained dormant
during the three years of observations. Axillary buds formed
during the growth flush occasionally break in saplings in
the late summer to form a second flush of growth (this was
not observed at 920 or 1000 m), and some continuous
production of leaves after the initial determinate growth

Fig. 4.1 Timing of leaf production at Mt Field at each
altitude, examined at two-week intervals in 1982-1983.

●—● The period during which bud-break occurred in
       mature plants.
○—○ The period during which bud-break occurred in
       saplings (of seedling origin) 1.0-1.5 m high.
The dots preceding the marked period indicate the time of
the previous observation.

    Most N. cunninghamii leaves were produced during the
spring growth flush, but some expanded shoots of saplings
continued to produce new leaves at the apices.
    e   The date at which N. cunninghamii leaves were
           fully expanded.
    *   The date at which N. cunninghamii leaves produced
           in the spring growth flush were fully expanded,
           with further leaf production occurring at the
           shoot apices or in a later growth flush.

    ▲   The date by which leaf production had ceased.

Fig. 4.2   Timing of flowering at Mt Field at each
altitude, examined at monthly intervals in 1983-84 (■)
and 1984-85 (▲). Flowering was not observed in
A. selaginoides and N. cunninghamii during this period.
The dots preceding the marked period indicate the date of
the preceding observation.
    The date shown for P. aspleniifolius indicates
only the first appearance of the cones. The dates shown
for both P. aspleniifolius and A. moschatum refer only
to the appearance of female cones/flowers.

A. selaginoides 1000

920

P. aspleniifolius 920

700

E. lucida 700

N. cunninghamii 1000

920

700

180

A. moschatum 920

700

180

A S O N D J F M

Month

E. lucida 700

P. aspleniifolius 920

700

A. moschatum 920

700

A S O N D J F M A M J J

Month
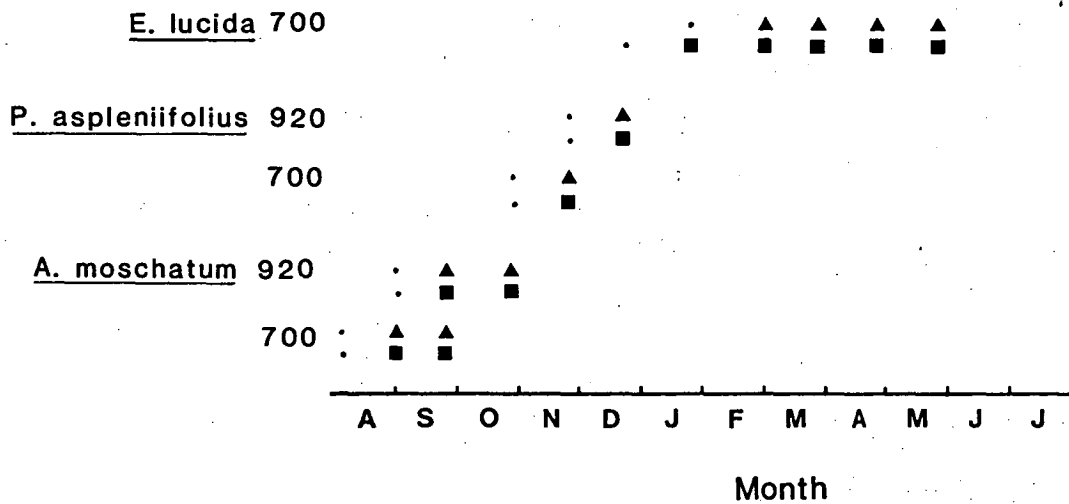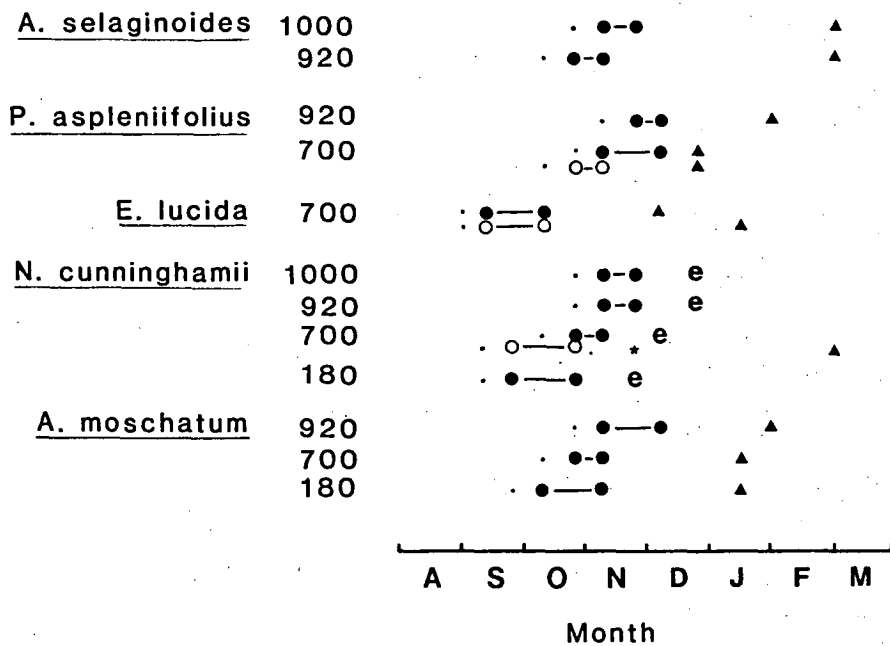
was occasionally observed in saplings. Shoots were fully
extended within 4-6 weeks at all sites and leaves were fully
expanded within 6-8 weeks at all sites (Fig. 4.1). N.
cunninghamii seedlings which had germinated in Hobart in
June 1982 showed continuous apical growth in the glasshouse

through the winter and axillary buds broke in August.
Seedlings growing outside in Hobart showed some apical
growth through winter until October, when axillary buds
broke. Subsequent growth in seedlings both inside and
outside the glasshouse was a combination of growth flushes
from axillary buds with continuous growth at the shoot
apices until early autumn, when growth ceased outside the
glasshouse, but continued inside the glasshouse primarily as
continuous apical growth. This pattern of growth, with
slight variations in timing of events, was observed in the
same seedlings until observations ceased in October 1985.

All other species produced foliage indeterminately. A.
moschatum and E. lucida usually produced 2-4 leaves on each
shoot during the growing season. P. aspleniifolius usually
produced a single whorl of 5-7 phylloclades, although in
shaded branches of some trees, growth was limited to a
single phylloclade arising from an older phylloclade. The A.
selaginoides shoots produced 11-23 leaves. Leaf production
in mature plants of A. selaginoides, A. moschatum, E. lucida
and P. aspleniifolius ceased during summer and did not
resume until the following spring (Fig. 4.1). Leaf
production ceased later at the higher altitudes (Fig. 4.1).
In seedlings raised in Hobart, leaf production was
continuous in the glasshouse, and continued very slowly
outside the glasshouse, during the first winter after
germination. Growth continued until in May in seedlings
growing outside and did not resume until October. Seedlings
inside the glasshouse showed continuous growth throughout
the year. These growth patterns remained constant until
observations ceased in October 1985, with slight variations
in the the timing of events.

The foliage of P. aspleniifolius seedlings at Mt Field

consisted entirely of leaves for the first three years of growth, but grown outside in Hobart produced phylloclades within the first six months of growth.

No leaf loss was recorded in any of these species other than due to browsing. Therefore the leaf life span was greater than 41 months.

Flowering, seeding and germination

In 1984-85, flowering and seed maturation of E. lucida were delayed apparently by the cool temperatures during the growing season (Figs 4.2 & 4.3). Seed maturation and germination were also delayed in A. moschatum in 1984-85, and flowering in this species was delayed in 1985 (Figs 4.2 & 4.3). These events may all have been caused by the cool 1984-85 growing season. The timing of cone development was not affected in P. aspleniifolius but seed maturation was delayed in 1985 at 920 m (Fig. 4.3). There was no difference observed in the time of seedling appearance of P. aspleniifolius (Fig. 4.3). Seeding of N. cunninghamii and A. selaginoides at Mt Field occurred only in 1982, a year of extremely heavy seeding. Flowering of A. selaginoides and N. cunninghamii was not observed at Mt Field in subsequent years, either in the tagged trees or in nearby trees, although occasional empty husks of N. cunninghamii seed were observed which indicated that flowering was occurring in this species at very low frequency. No viable seeds were found. No quantitative records of seed production in A. moschatum, E. lucida and P. aspleniifolius were made. A. moschatum and E. lucida flowered prolifically each year, and P. aspleniifolius produced cones each year but was most prolific in 1981-82.

Germination of N. cunninghamii normally occurs during autumn at low altitudes and may occur later at high altitudes, with seedlings not appearing until spring (Fig. 4.3). Howard (1973b) recorded the same feature in N. cunninghamii in Victoria. E. lucida was only studied at 700

Fig. 4.3   Timing of the period of seed maturation and release (1982: ● ; 1984: ■ ; 1985: ▲), and the first appearance of seedlings (s) at Mt Field at each study site, examined at two- or four-week intervals.

The dots indicate the dates of observations prior to seed maturation and following the majority of seed release.

A. selaginoides 920 • •-•——• . s

E. lucida 700 : ▲——▲——▲ . s
: ■-■ . s
: •-•——•s .

N. cunninghamii 920 . . •-•——•——• . s

700 . •-•-• —$\substack{\text{s} \\ \text{o}}$.

P. aspleniifolius 920 : ▲——▲ .
: ■——■ . ▲ .
: •——•——• .

700 : ▲——▲ .
: ■——■ .
: •-•——• .
s
s

A. moschatum 920 . ■-■ . ▲——▲——▲——▲ .

700 . s
■-■-■s ▲——▲——▲
. .

	J	F	M	A	M	J	J	A	S

Month
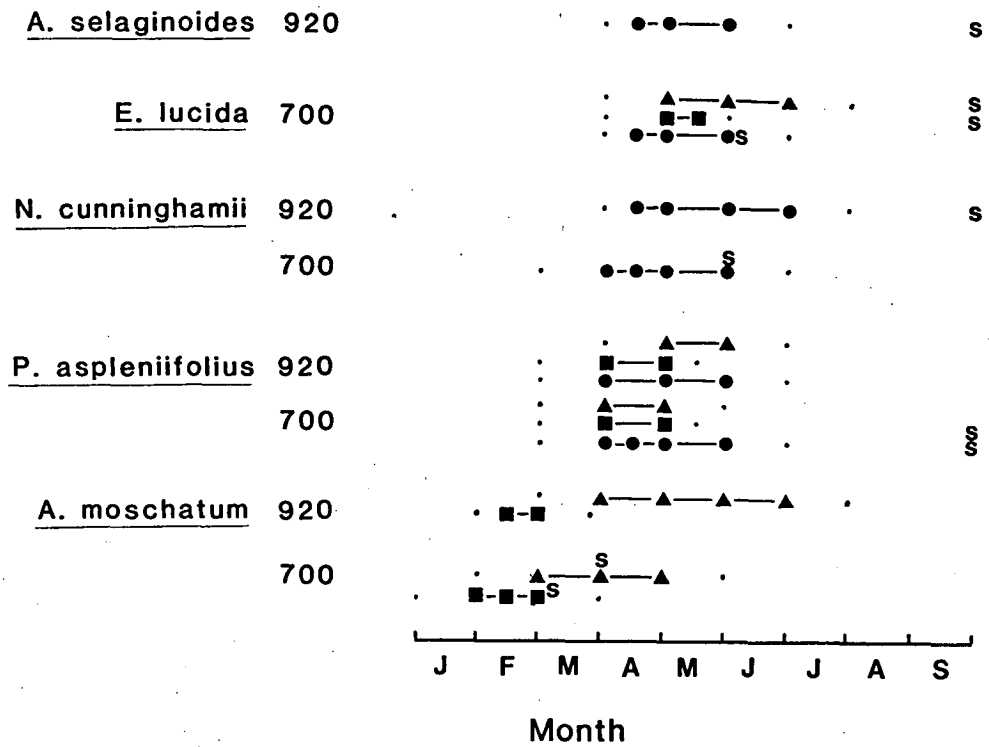
m elevation at Mt Field. Autumn germination was recorded there in 1982 and spring germination was recorded in other years. E. lucida seed does not mature until the autumn following the year of flowering. A. selaginoides seedlings first appeared in spring at 920 m. A. moschatum seedlings appeared in autumn at low altitudes (700 m). At 920 m seeding was profuse and seed collected and germinated in the laboratory showed 92% viability of selected apparently sound seed, which was equivalent to 36% of the total seed collected. However successful germination of A. moschatum was very rare at this altitude in 1985. Many hundreds of seeds were present around the base of the parent trees, but only two cotyledonary seedlings were observed, and these were not apparent until September. The seed crop of P. aspleniifolius at 920 m was small, with the exception of 1982, and no seedlings were observed in the vicinity of the trees.

Discussion

The patterns of shoot growth in N. cunninghamii are identical to those recorded in Victoria by Howard (1973b), although the appearance of a second growth flush in N. cunninghamii appears to be more frequent in Victoria than at Mt Field. Howard noted that the incidence of a second flush decreased with increasing altitude at Mt Donna Buang, and therefore the low incidence of second growth flushes at the lower altitude at Mt Field and the absence of second growth flushes at high altitudes probably reflects the cooler climate. No data is available from other sites in Tasmania. The only feature of the timing of bud-break that appears to be significant to patterns of regeneration and species distribution, is the delaying effect of a cool growing season on the shoot expansion of A. moschatum and P. aspleniifolius so that these leaves may be vulnerable to frost damage.

Seedfall was recorded in N. cunninghamii and A.

selaginoides in this study only in 1982, but occurred
annually in the other three species. Hickey et al. (1982)
recorded seedfall of N. cunninghamii, E. lucida and A.
moschatum at two sites in north-west Tasmania from 1975 to
1981 and summarised N. cunninghamii seedfalls back to 1963.
This data indicates sporadic production of seed in N.
cunninghamii, with heavy falls in 1967, 1969, 1971, 1975,
1977 and 1980, interspersed with years of low or moderate
seedfall. They did not find any clear relationship between
seed production and the temperatures of the previous growing
season, but noted that the pattern of seed production was
consistent at several sites around Tasmania. The times of
flowering and seed release reported by Hickey et al. (1982)
are in general earlier than those reported at Mt Field and
is likely to be related to the cooler climate at Mt Field.
The sporadic nature of the seed production of N.
cunninghamii and A. selaginoides, and the association of low
seed viability with the years of low seed production (Howard
1973b; Hickey et al. 1982; Chapter 5) must have a
detrimental effect on the colonisation by these species of
sites which are disturbed during periods of low seed
production. The greater consistency of seedfall in A.
moschatum and E. lucida has been shown quantitatively by
Hickey et al. (1982). There is no long-term data available
on seed production in A. selaginoides and P.
aspleniifolius.

The time of onset of germination within a species with
respect to altitude is probably related both to differences
in the time of seed release and the time taken for
germination to occur, both factors being affected by
climate. This appears to be particularly critical in A.
moschatum, since observations indicate that the late seed
release at 920 m in 1985 led to very low rates of
germination, although this seed was germinated successfully
in the laboratory soon after its release. This is further
discussed in Chapter 5. Since observations were made only at
monthly intervals, fine-scale differences in the onset of

germination among species were not detected.

Chapter 5   Germination

Introduction

     The importance of the relationships between the physical
environment and seed germination on the distribution of a
species in space and time, and the variability of these
relationships has been noted by many authors (e.g. Grubb
1977; Bazzaz 1979). In this chapter, the gross environmental
requirements for germination are studied in seeds of N.
cunninghamii, A. moschatum, E. lucida, A. selaginoides and
P. aspleniifolius collected from Mt Field National Park
(42°41´S 146°40´E), in order to determine the impact of
germination characteristics on species´ patterns of
distribution and regeneration.

Materials and methods

     Seed was collected in 1982, a year of exceptionally high
seed production for all of these species, from three trees
of N. cunninghamii (Nc700), E. lucida, P. aspleniifolius and
A. moschatum at 700 m a.s.l. and from N. cunninghamii
(Nc980)and A. selaginoides at 980 m a.s.l. All seeds were
collected on 1.5.82 and sown on 25.5.82 following dry
storage at room temperature.
     The seed treatments for each species were as follows:
1. Incubated moist in light at 4, 12, 17, 25 and 32°C.
2. Incubated moist in dark conditions at 25°C.
3. Incubated moist in light at 4°C for four weeks, followed
by 25°C.
     The failure of P. aspleniifolius to germinate in any of
the above treatments led to the following treatments for
this species only:
4. Seed soaked for 24 hours in HCl (pH 2) followed by
incubation moist in light at 20°C.
5. Seed scarified and incubated moist in light at 20°C.
6. Seed coat removed and seed incubated moist in light at

$20^{o}C$.

7. Seed boiled for 5 minutes then incubated moist in light at $20^{o}C$

8. Seed sown in pots of sandy loam and placed outside in full sunlight, with daily watering.

In treatments 1 to 7, 30-40 seeds of each tree were placed in a petri dish on a pad of Whatman's Seed Test Thick filter paper (three dishes per species for each treatment, one for each parent tree). "Thiram" fungicide was dusted onto the seed pad prior to the addition of distilled water. The petri dishes were incubated in controlled environment growth cabinets under incandescent and fluorescent lights (150 μmol quanta $m^{-2}s^{-1}$). The "dark" treatment was provided by cardboard boxes lined with black cartridge paper and seeds placed in this treatment were sown and observed under green light.

Seeds were observed every 1-2 days for the first 50 days, then every 3-5 days until Day 100, followed by irregular observations. Observations of Treatments 1-3 were continued for 25 days after the last seed germinated. Observations of the $12^{o}C$ treatment ceased after 125 days due to fungal infection of the remaining seeds. Observations of treatments 4-7 were discontinued after 90 days. Treatment 8 was observed for 30 months.

Results

A. selaginoides, N. cunninghamii, A. moschatum and E. lucida neither required light for germination, nor were inhibited by light (Table 5.1). The onset of germination and the time taken to reach 50% of the final germination was most rapid at $25^{o}C$ for all species, although with little difference at $17^{o}C$ (Tables 5.2 & 5.3). Incubation temperature did not affect the final germination percentage, other than at $32^{o}C$, where no germination occurred and seed had deteriorated after 28 days, and at 4° in A. moschatum (Table 5.1). At $12^{o}C$ a substantial proportion of seeds of N.

Table 5.1 Final germination percentages of each species. Each value is the mean of results of seed from three trees at the same site.

Species	Site	Incubation temperature (°C)						
		32	25 light	25 dark	17	12	4	4-25[1]
N. cunninghamii	700 m	0	21	20	22	12[2]	24	25
	980 m	0	48	50	48	26[2]	51	46
E. lucida	700 m	0	93	91	93	60[2]	95	93
A. moschatum[3]	700 m	0	92	97	93	49[2]	0	99
A. selaginoides	980 m	0	61	59	63	60	67	63

[1] 4°C for 4 weeks, then incubated at 25°C.
[2] The final count was at 125 days, with remaining seeds infected by fungus.
[3] Poorly formed seeds (small, shrivelled or discoloured) were not included.

Table 5.2 The number of days to the onset of germination and to reach 50% of the final germination percentage, expressed as a range.

Species	Site	Incubation temperature (°C)			
		25	17	12	4-25[1]
N. cunninghamii	700	7-9	9-11	23-125[2]	7-10
	980	5-6	7-8	14-115[2]	4-7
E. lucida	700	7-15	12-25	23-115[2]	1-1
A. moschatum	700	7-10	11-13	26-	9-11
A. selaginoides	980	8-15	13-23	20-80	1-8

[1] 4°C for 4 weeks, then incubated at 25°C.
[2] Final germination percentage is assumed to be the same as at 25°C.

Table 5.3 Cumulative percentages of germination at 4°C.

Species	Site	Days from sowing				
		129	136	140	151	223
N. cunninghamii	700	0	0	0	1	24
	980	0	0	0	19	51
E. lucida	700	0	0	0	0	95
A. moschatum	700	0	0	0	0	0
A. selaginoides	980	0	9	17	67	

cunninghamii, A. moschatum and E. lucida were infected by fungus after 125 days (Tables 5.1 & 5.2) and observations ceased. The final germination percentage is assumed to be the same as at 25, 17 and 4°C for N. cunninghamii and E. lucida. However, since A. moschatum fails to germinate at 4°C, the reduced germination percentage of A. moschatum at 12°C may not be due only to fungal infection.

The 4°C pre-treatment increased the rate of germination for E. lucida and A. selaginoides (Table 5.2) but had no effect on the final germination percentage (Table 5.1). A. selaginoides germinated earlier at 4°C than the other species (Table 5.3), including Nc980, and germination of A. selaginoides at 12°C was complete within 125 days (Tables 5.1 & 5.2). All species, except A. moschatum germinated at 4°C within 224 days. A. moschatum had not germinated within 323 days and seeds taken from this treatment and transferred to 20°C failed to germinate within 60 days under a 24 hour photoperiod but 98% germination occurred within 9 days in seeds transferred from 4°C to darkness at 20°C.

P. aspleniifolius failed to germinate in Treatments 1-7, although seeds had fully imbibed water within 24 hours. Observations on Treatment 3 ceased on Day 151 due to fungal attack, and on Day 125 for the other treatments. However, seeds germinated in soil left outside (Treatment 8), in the spring of 1983 i.e. after two winters. Seedlings appeared in September and there were no later germinations, with a final germination percentage of 62%.

Seed of N. cunninghamii, E. lucida and A. selaginoides stored dry at room temperature germinated with 50-80% of their original viability after 32 months. Seed of A. moschatum could not be germinated at 20°C under a 24 hour photoperiod after 2 months dry storage at room temperature. Seed of A. moschatum stored dry at 4°C was successfully germinated at its original level of viability after 4 months, but with only 3% germination after 5 months. However, A. moschatum seed stored in these conditions germinated (96%) after incubation in darkness at 20°C.

Discussion

The early germination of A. selaginoides at low
temperatures is also a feature of Athrotaxis cupressoides
and Nothofagus gunnii (Read unpublished data), all of which
are primarily restricted to high altitudes. The ecological
importance of this feature is uncertain. Cotyledonary
seedlings of A. selaginoides, A. cupressoides, N. gunnii and
N. cunninghamii were observed in September 1982 at 980 m
a.s.l., Mt Field (4-5 months after seed release, see Chapter
4), but the actual time of germination is unknown. Many
seedlings of all species died during summer, apparently due
to desiccation. Early germination may therefore be important
in allowing early growth and establishment during periods of
low evaporative loss. The data obtained in the present study
indicate that the timing of germination in the field is due
to the slow germination at low temperatures rather than any
pre-chilling requirement. This has been previously reported
in N. cunninghamii (Howard 1970b). The lack of any
requirement for pre-chilling treatment in high altitude
species has also been recorded in N. gunnii and A.
cupressoides (Read unpublished data), and in a study of
alpine plants of the U.S.A. where only 3 out of 60 species
had a chilling requirement (Amen 1966). Sayers & Ward (1966)
observed that temperatures resulting in the best germination
of alpine species in the U.S.A. (20-30°C) were similar to
species native to lowlands. Similarly, in the present study,
germination was most rapid at 25°C for all species, with
seed of all species killed by incubation at 32°C. However,
ecologically significant differences may occur at a finer
scale of temperatures than those tested here. There was no
evidence of reduced viability of N. cunninghamii seed with
increasing altitude, as suggested by Howard (1973b) and
Hickey et al. (1982).

Germination failure at 30-35°C has been reported
previously in A. moschatum by Read (1981) and in N.

cunninghamii by Howard (1973b). Seed of A. moschatum, E.
lucida and N. cunninghamii was successfully germinated in a
$20^\circ/30^\circ$C regime by Hickey et al. (1982). The importance of
high temperatures in seed deterioration is uncertain.
Prolonged high temperatures in the range 30-35° are unusual
in the current distribution of forests containing these
species, both in Victoria and Tasmania, but this feature may
be relevant to the absence of these species from warmer
climates.

A suitable combination of moisture and temperature is
probably the most important factor determining seed
germination under natural conditions (Mayer &
Poljakoff-Mayber 1982). Howard (1973b) noted that N.
cunninghamii would rarely germinate after one year in the
field since suitable conditions for germination occur within
8-9 months of seed-fall. The same is true for E. lucida, A.
moschatum and A. selaginoides. At low altitudes N.
cunninghamii, A. moschatum and E. lucida usually germinate
in autumn, within 1-2 months of seed release (Chapter 4) and
it is unlikely that the apparent secondary dormancy recorded
in stored A. moschatum seed (also noted by Hickey et al.
(1982)), would be a significant occurrence in the natural
lowland environment. The environmental feature which is
initiating this dormancy is uncertain since it is induced
experimentally at both low temperatures and at room
temperature, and in both dry and moist conditions. It may
therefore be a general response to delayed germination. At
high altitudes, particularly in seasons when seed release is
late, the delay of temperature conditions suitable for
germination appears to cause a greatly reduced germination
percentage in apparently sound seed of A. moschatum (Chapter
4). This is consistent with the secondary dormancy induced
experimentally by cold moist and dry storage. However, in
the field the dormancy does not appear to be broken to any
significant degree. This must depend on the light
environment of the site of seed deposition, if light is the
only factor which leads to release from dormancy. Any delays

in germination will also result in greater mortality due to fungal and insect attack.

Only P. aspleniifolius with its hard testa, together with seed dormancy, may be soil-stored. However there is no data to indicate storage times of this species. P. aspleniifolius seedlings commonly appear on rainforest sites after fire (Kirkpatrick 1977; Hill & Read 1984). This may be the result of either soil storage and release from dormancy by the disturbance, or efficient dispersal. Kirkpatrick (1977) has suggested that the early appearance of P. aspleniifolius on disturbed sites is due to bird dispersal. However, there is no evidence to my knowledge of P. aspleniifolius being found in pellets deposited by birds or mammals, so the frequency of animal dispersal and its effect on seed germination is uncertain for this species. The seed dormancy of P. aspleniifolius appears to be similar to that of Tasmannia lanceolata, a species that commonly invades forest disturbances and which has seeds that are bird-dispersed (Read & Hill 1982). Howard (1974) noted that most T. lanceolata seedlings appeared 12 months after soil containing the seeds was collected from the field (18 months after the latest seedfall). She suggested that this was due to leaching of a germination inhibitor from the seed.

With the exception of the poorly understood germination requirements of P. aspleniifolius there are no gross differences in germination requirements of the rainforest species which can be related to their regeneration niche or habitat niche. However the faster rate of germination of A. selaginoides than other species at low incubation temperatures, and the observed failure of A. moschatum seed to germinate at low incubation temperatures, are fine scale differences which are consistent with the general pattern of distribution of these species with respect to altitude.

Chapter 6   Photosynthetic and growth responses to
            different light regimes.

Introduction

A. moschatum has been described as more shade-tolerant
than N. cunninghamii on the basis of its ability to
regenerate under the forest canopy (Gilbert 1959). The
dominance of climax forest on equable sites by the
supposedly less shade-tolerant N. cunninghamii represents an
anomaly in terms of forest dynamics, both with respect to
successional theory which predicts dominance by the most
shade-tolerant species on equable sites (Connell & Slatyer
1977; Noble & Slatyer 1978), and to the trends observed in
mesic forests of the northern hemisphere (Jones 1945) and in
the cool temperate rainforests of Chile and New Zealand
(Veblen et al. 1981; Wardle 1984). This chapter examines the
comparative light requirements of the rainforest canopy
species and discusses these in relation to the patterns of
regeneration described in Chapter 2.

Materials and methods.

Instantaneous photosynthetic
responses to light

Seedlings of each species were grown from seed (N.
cunninghamii, A. moschatum, E. lucida and A. selaginoides)
or cotyledonary seedlings (P. aspleniifolius) collected from
Mt Field (42°41′S 146°40′E). A. selaginoides seed was
collected from 980 m a.s.l., and the other species were
collected from 700 m a.s.l. All plants were grown outdoors
in a shade-house in sandy loam with slow release fertiliser,
and were watered daily. After 24 months the seedlings were
transferred to contrasting light regimes in a glasshouse
from August to December, 1984. Eight plants of each species
were grown unshaded in the glasshouse (approximately 80% of

the photosynthetically active radiation of natural sunlight, reaching a maximum value of 1600 µmol quanta m^{-2}s^{-1}) and the same number were shaded from direct sunlight so that the maximum photon flux density (PFD) of the unfiltered diffuse light was 30-80 µmol quanta m^{-2} s^{-1}. The daily maximum temperatures in the glasshouse for the seven weeks prior to and during measurement ranged from 23-31°C with a mean maximum daily temperature of 26°C. Leaf temperature varied by less than 1°C between the treatments.

Another group of plants was grown for 12 months outdooors in a shadehouse under a eucalypt woodland canopy of approximately 60% canopy cover (measured by hemispherical photograph). The daily maximum temperature for the seven weeks prior to and during measurement ranged from 11-24°C with a mean maximum daily temperature of 16°C.

An open gas exchange system incorporating a Series 225 infra-red gas analyser (Analytical Development Co. Ltd.) was used to measure the net rate of CO_2 assimilation at different PFDs. The light source was a Sylvania 400W metalarc lamp. Photosynthetically active radiation was measured with a LiCor LI-185 meter with quantum sensor. Light intensity reaching the leaf was varied using a combination of distance from the light source and shade cloth screens. Humidified air (317-340 ppm CO_2) was passed through a leaf chamber of cross-sectional area 10 cm^2 at a flow rate of 0.4 l min^{-1}. Moisture was condensed from the gas lines prior to analysis. CO_2 differentials were recorded on chart.

Responses were first measured at 750 µmol quanta m^{-2} s^{-1} and subsequently at decreasing light intensities. Responses at PFD greater than 750 µmol quanta m^{-2} s^{-1} were measured last because of potential photoinhibition at high PFD. Leaf temperature was monitored and maintained at 21$\pm$1°C. Temperatures of 18-23°C were optimal for all species. Leaf photosynthesis was measured only on young fully expanded leaves of N. cunninghamii, A. moschatum, E. lucida and P. aspleniifolius (phylloclades). A. selaginoides

has small leaves appressed to the stem. Photosynthesis was measured in shoot sections rather than individual leaves of this species. Total replicates were 5-8, one leaf (or phylloclade or shoot) per plant. Foliage area was measured photometrically and varied in the range 3-10 cm^2 and leaf (or phylloclade) dry weight was measured. The leaf area value of <u>A. selaginoides</u> used in the calculation of photosynthetic rate was taken from the projected area of the whole shoot in the leaf chamber. This was considered to be more accurate than total leaf area due to self-shading and leaf curvature. Leaves from the undersurface were trimmed from the stem two weeks prior to measurement, so that during measurement only the upper surface of the stem was bearing leaves. The leaf area and dry weight values used in the calculation of the specific leaf area for <u>A. selaginoides</u> involved measurement of the total area and dry weight of individual leaves. Leaf chlorophylls of <u>N. cunninghamii</u>, <u>A. moschatum</u>, <u>E. lucida</u> and <u>P. aspleniifolius</u> were extracted in 80% (v/v) acetone and were estimated spectrophotometrically.

Growth responses to light

Total plant response to light was examined by growing seedlings of the same species in four light intensities in a controlled environment growth cabinet. The light source consisted of a 400W metalarc lamp, eight 40W fluorescent lamps and four 60W incandescent lamps for a 12 hour photoperiod. Day temperature was 23°C and night temperature was 20°C. PFD was measured at the highest leaf of each seedling. The mean PFDs of the treatments were 6 ,48, 102 and 180 µmol quanta m^{-2} s^{-1} giving daily photon fluxes of 0.26, 2.07, 4.40 and 7.78 mol quanta m^{-2} day^{-1} respectively with no significant difference between species within treatments. Leaf temperature between treatments varied by less than 1°C. Ten seedlings of each species were transferred from the glasshouse to each treatment and

harvested after 35 days. Some deaths occurred and final
replicates were 5-10 seedlings. Ten seedlings were harvested
at the beginning of the experiment. Dry weight of each
seedling was measured at each harvest. Mean relative growth
rate was calculated as

$$\frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where W_1 and W_2 are initial and final dry weights
respectively, and $t_2 - t_1$ is the period of growth.

Results

Some details of the light-dependence curves (Figs. 6.1 &
6.2) and leaf characteristics are summarised in Table 6.1.
All species acclimated to shade conditions during growth by
decreasing the dark respiration rate (DRR), instantaneous
light compensation point (LCP) (except P. aspleniifolius)
and light saturation point and increasing the specific leaf
area (SLA). Apparent quantum yield does not differ
significantly between light regimes or species (with a mean
value of 0.066 ± 0.001 mol CO_2.mol quanta^{-1}). There were no
indications of photoinhibition at incident PFD of up to 2500
µmol quanta m^{-2} s^{-1}.

The maximum rate of photosynthesis (P_{max}) of A.
moschatum is unchanged by the growth light conditions,
whereas N. cunninghamii, E. lucida and P. aspleniifolius
have lower P_{max} values in shade-raised seedlings ($p < 0.05$).
A. moschatum has a low LCP and DRR in shade-grown plants and
a low P_{max} in sun-raised plants compared with other species.
Sun-raised plants are bleached, and have low chlorophyll
values (Table 6.1). The SLA increases in shade conditions,
with shade-raised A. moschatum having the highest SLA, and
subsequently the highest chlorophyll/leaf dry weight and
P_{max} on a leaf dry weight basis (Table 6.1).
Shadehouse-raised A. moschatum show less acclimation. These

plants have a lower SLA, chlorophyll content and P_{max} ($p<0.05$) than shade-raised plants (Table 6.1).

N. cunninghamii, E. lucida and P. aspleniifolius have a lower P_{max} in shade-raised plants than sun-raised plants (Fig. 6.1)(N. cunninghamii 57%, E. lucida 43% and P. aspleniifolius 69%). Shade-raised N. cunninghamii and E. lucida plants have a lower LCP and DRR than sun-raised plants (Table 6.1)($p<0.05$). In P. aspleniifolius these values are not significantly different ($p<0.05$) for sun- and shade-raised plants (Table 6.1). The LCP and DRR of shade-raised N. cunninghamii, E. lucida and P. aspleniifolius are not as low as those of shade-raised A. moschatum and A. selaginoides and they show relatively less change in chlorophyll per unit leaf area in the different light regimes than A. moschatum (Table 6.1) (leaf tissue of A. selaginoides that was being used for chlorophyll determinations was lost in an accident). N. cunninghamii and E. lucida have their highest P_{max} on a dry weight basis in sun-raised plants (Table 6.1).

P. aspleniifolius has a higher P_{max} on a leaf area basis in sun-raised plants (Fig. 6.1d), though a low SLA in these plants reduces the P_{max} on a leaf dry weight basis (Table 6.1). Seedlings of P. aspleniifolius and A. selaginoides grown in full light in the glasshouse showed evidence of stress, possibly due to high light-high temperature interactions. One of the A. selaginoides seedlings died and three seedlings failed to produce sufficient growth for use in this experiment and therefore only one sun-raised plant of A. selaginoides was suitable for use. Growth of A. selaginoides seedlings at the lower temperatures characteristic of its natural habitat (predominantly above 600 m elevation) would require a very long period in a controlled environment growth cabinet (approximately twelve months) in order to produce sufficient fully expanded leaves for measurement of photosynthesis. This was not practicable. Several P. aspleniifolius seedlings also failed to produce new growth and the phylloclades produced on the remaining

Fig. 6.1   Light-dependence curves of photosynthesis of
seedlings grown in full sunlight (-▲-) and shade (-△-) in a
glasshouse. Each point is the mean of 5-8 replicates. The
largest standard error is shown on each curve, where it is
greater than 0.25.
a) <u>N. cunninghamii</u>
b) <u>E. lucida</u>
c) <u>A. moschatum</u>
d) <u>P. aspleniifolius</u>
e) <u>A. selaginoides</u>

a

b

c
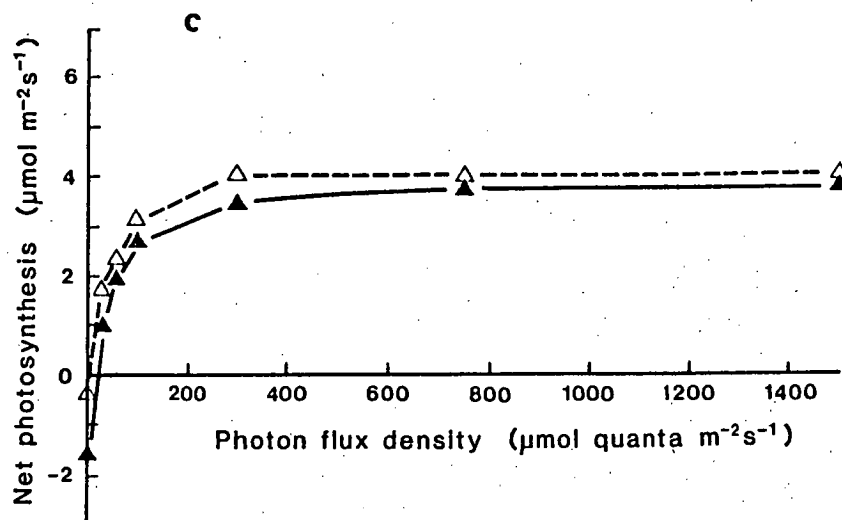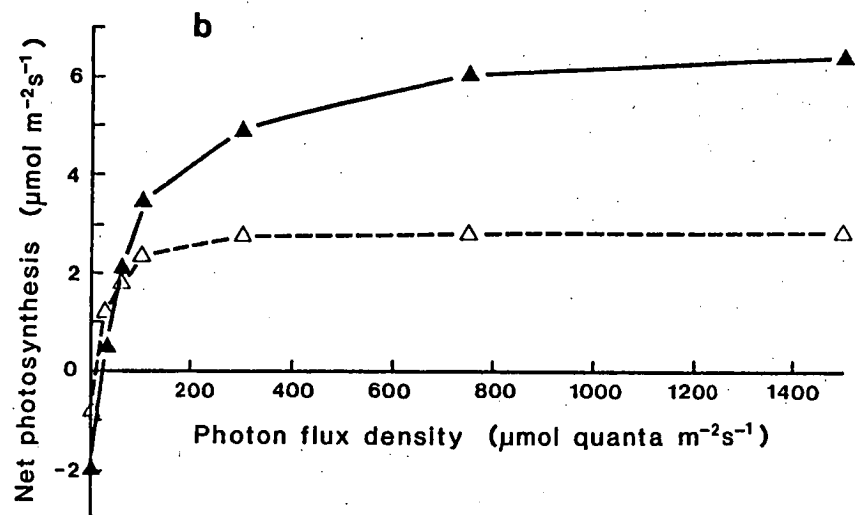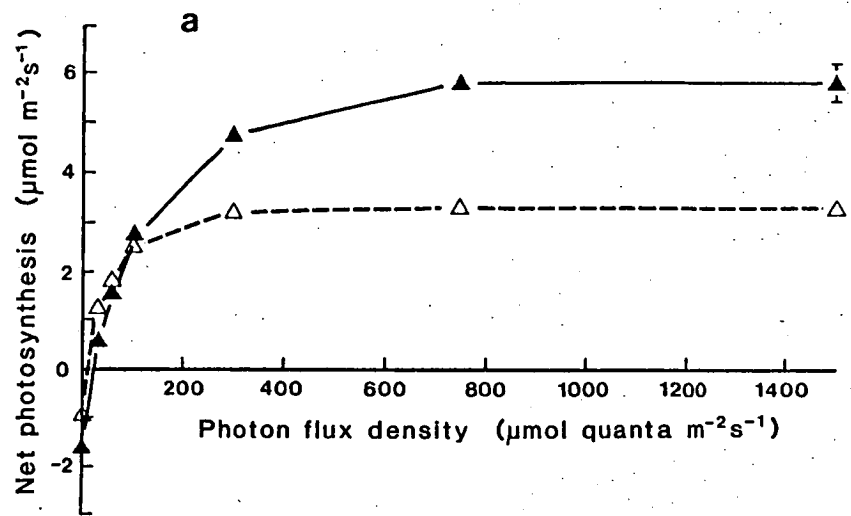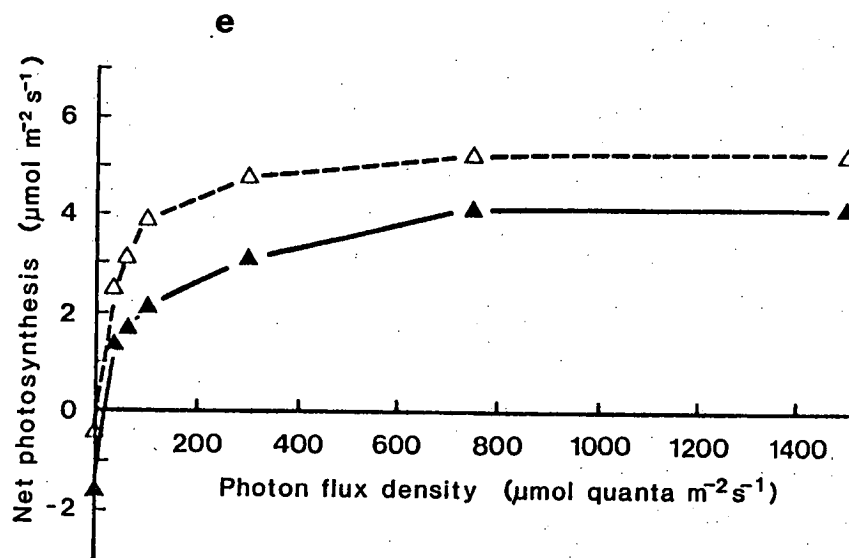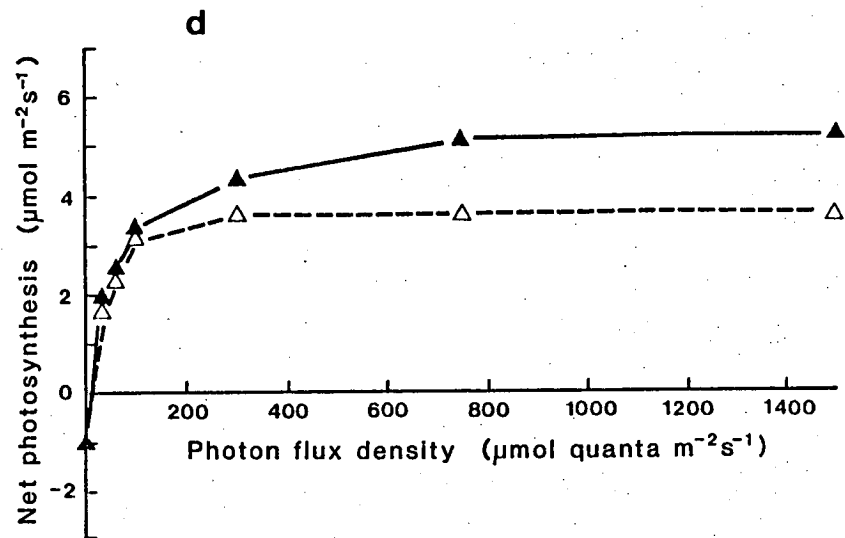
Fig. 6.2   Light-dependence curves of photosynthesis of
seedlings grown outdoors under a woodland canopy. Each
point is the mean of 5 replicates. The largest standard
error is shown on each curve, where it is greater than
0.25.

N. cunninghamii: ▲
A. moschatum: ●
E. lucida: ■
P. aspleniifolius: o
A. selaginoides: △

Fig. 6.3   Relative growth rates of seedlings grown under
four light intensities in a controlled environment growth
cabinet.   Each point is the mean of 5-10 replicates
(all standard errors are < 0.25).

N. cunninghamii: ▲
A. moschatum: ●
E. lucida: ■
P. aspleniifolius: o
A. selaginoides :   △
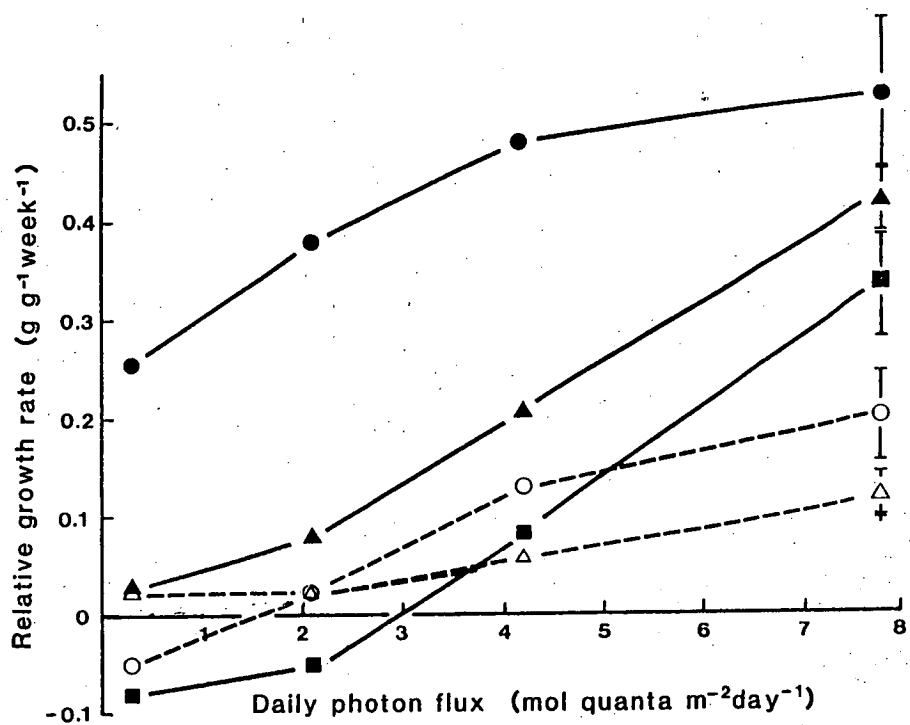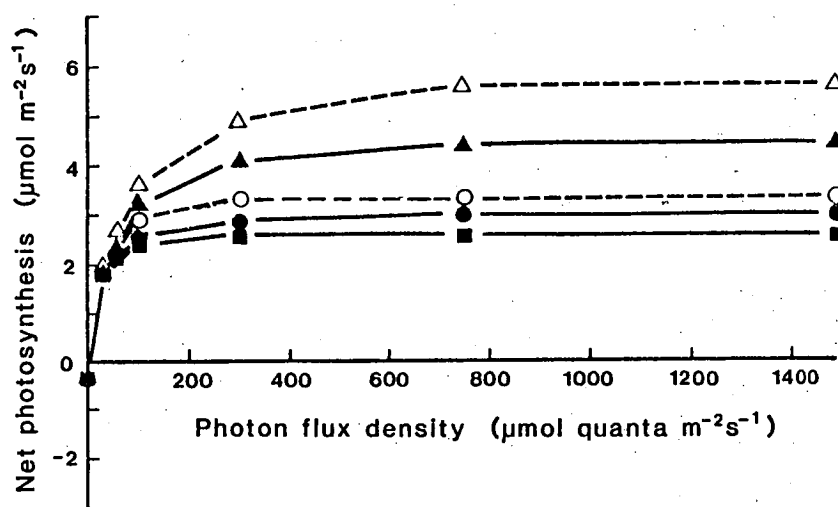
Table 6.1   Leaf characteristics and details from the light-dependence curves. Each value is the mean of 5-8 replicates, with standard errors where appropriate.

Species	Growth light regime	Specific leaf area $(m^2g^{-1}x10^{-3})$	Chlorophyll $(mg\ m^{-2})$	$(mg\ g^{-1})$[1]	Dark respiration rate $(\mu mol\ m^{-2}s^{-1})$	Light compensation point $(\mu mol\ quanta\ m^{-2}s^{-1})$	Maximum rate of photosynthesis $(\mu mol\ g^{-1}leaf\ dry\ weight\ s^{-1}\ x10^{-4})$
N. cunninghamii	sun	131 + 7	383 + 24	50	1.73 + 0.12	27 + 3	8.10 + 0.61
	shade	149 + 8	406 + 15	60	1.05 + 0.12	17 + 2	4.96 + 0.31
	shade-house	139 + 8	540 + 11	75	0.36 + 0.03	6 + 1	6.10 + 0.51
E. lucida	sun	104 + 5	429 + 23	45	2.03 + 0.20	30 + 1	7.09 + 1.02
	shade	185 + 9	381 + 22	70	0.83 + 0.20	15 + 3	4.92 + 0.40
	shade-house	144 + 12	453 + 11	65	0.45 + 0.06	8 + 1	3.70 + 0.38
A. moschatum	sun	132 + 5	298 + 29	39	1.60 + 0.16	21 + 1	5.17 + 0.63
	shade	229 + 7	537 + 31	123	0.41 + 0.16	5 + 2	9.63 + 0.70
	shade-house	172 + 10	380 + 20	65	0.42 + 0.06	7 + 1	4.91 + 0.40
P. aspleniifolius	sun	41 + 4	484 + 47	20	0.87 + 0.15	11 + 2	2.01 + 0.17
	shade	115 + 6	618 + 54	71	0.92 + 0.16	13 + 2	4.24 + 0.32
	shade-house	106 + 2	555 + 40	58	0.41 + 0.05	7 + 1	3.75 + 0.35
A. selaginoides	sun[2]	24			1.61	20	1.07
	shade	52 + 3			0.48 + 0.06	6 + 1	2.75 + 0.45
	shade-house	38 + 1			0.80 + 0.15	9 + 1	2.30 + 0.09

[1] Calculated from the SLA
[2] Measurements are from only one plant

plants were small and thickened. Subsequently the results of these species grown in full sunlight may not reflect field performance under cooler and more variable temperatures.

The growth rate study (Fig. 6.3) indicates that A. moschatum has a significantly higher relative growth rate (RGR) at the low daily photon fluxes (DPFs) than the other species, but at 7.78 mol quanta m^{-2} day^{-1} does not differ significantly from the RGR of N. cunninghamii at the 95% level. There is no significant difference between the RGR of species other than A. moschatum at the low DPF (0.26 and 2.07 mol quanta m^{-2} day^{-1}). At higher DPF levels N. cunninghamii is significantly higher (p<0.05) than the RGR of A. selaginoides (4.40 and 7.78 mol quanta m^{-2} day^{-1}), and P. aspleniifolius (7.78 mol quanta m^{-2} day^{-1}). The RGR of N. cunninghamii does not differ significantly from the RGR of E. lucida at the 95% level at any of the light levels.

Discussion

A. moschatum has a low LCP in shade-raised plants and has the limited capacity to acclimate photosynthetically to high PFDs that is typical of shade-plants as described by Boardman (1977) and Bjorkman (1981). A. moschatum is clearly superior to the other species only when grown in heavy shade (lower DRR and LCP than all species except A. selaginoides, and a higher P_{max} on a leaf dry weight basis and higher RGR than all species). In the shadehouse-raised plants, the P_{max} of A. moschatum does not differ from N. cunninghamii, E. lucida or P. aspleniifolius on either a leaf area or dry weight basis. This suggests that the light environment of the shadehouse was higher than the light saturation point of A. moschatum. In contrast, the responses of shadehouse-raised E. lucida and P. aspleniifolius were most similar to results of shade-raised plants, and the response of shadehouse-raised N. cunninghamii plants was intermediate between sun and shade-raised plants. In N.cunninghamii, E. lucida and P. aspleniifolius the DRR and LCP was lower in

shadehouse-raised plants than sun-raised plants. It is not certain whether this is due entirely to characteristics of the light environment (variability and intensity of light) or is affected by the different temperature and humidity conditions in the shadehouse during growth. The greater shade-tolerance of A. moschatum suggests that it would regenerate under denser canopies than the other species. However predictions and explanations of natural regeneration patterns based on these results are limited by the effect of other environmental factors on establishment and growth. This is particularly evident in the case of A. moschatum which regenerates within the rainforest primarily by basal sprouts from established stems (Chapter 2). While vegetative reproduction may further facilitate establishment under low light conditions due to the absence of the stresses commonly experienced during seedling establishment, it potentially limits its spread through the rainforest.

N. cunninghamii, E. lucida and P. aspleniifolius do not separate clearly from one another on most of the major features of the sun- and shade-raised plants. However N. cunninghamii has a higher P_{max} on both a leaf area and leaf dry weight basis in shadehouse-raised plants than E. lucida and P. aspleniifolius. In addition, while the RGR of N. cunninghamii does not separate from any species other than A. moschatum in the lowest light conditions, at more moderate levels of shade (7.78 mol quanta m^{-2} day^{-1}) its RGR exceeds that of P. aspleniifolius and A. selaginoides. These features are consistent with the clustering of seedlings of N. cunninghamii and E. lucida in canopy gaps, with E. lucida seedlings more highly clustered (due possibly to higher light requirements) than those of N. cunninghamii (Chapter 2).

Although P. aspleniifolius has its highest P_{max} on a leaf area basis when grown under high PFDs, the low SLA in the high light-high temperature conditions experienced there reduced the P_{max} on a dry weight basis. However, these consistently high temperatures are not a feature of natural

conditions in Tasmanian rainforest habitats and the
thickened leaves of plants growing in full sunlight in the
glasshouse are not characteristic of plants growing in full
sunlight on lowland sites in the field. Therefore under the
temperature regime occurring in the field, high light
intensities are probably optimal for growth of P.
aspleniifolius. The reasons for its failure to regenerate in
closed forests is not clear from comparisons of the
instantaneous LCPs with N. cunninghamii and E. lucida,
although its regeneration appears to be strongly linked to
light conditions (Chapter 2). Both gymnosperms have a low
P_{max} on a leaf dry weight basis due to lower SLA values than
the other species grown in these experimental conditions.
These species also have a relatively low leaf area ratio
(Chapter 9). These features would be expected to have an
impact on the dynamics of P. aspleniifolius where it
establishes under an open canopy and is competing with the
species with inherently higher growth rates (N. cunninghamii
and E. lucida, Chapter 9) and therefore may be overtopped
and shaded. Similarly, the failure of A. selaginoides to
regenerate in small canopy gaps where N. cunninghamii is
establishing from seed, the relationship between seedling
establishment and canopy opening, and the frequent
establishment of this species on exposed sites (in contrast
with the shade-tolerant A. moschatum) (Chapter 2) suggest
that it is a light-demanding species relative to all species
except P. aspleniifolius. The three-dimensional leaf
arrangement of A. selaginoides within the leaf chamber used
in infra-red gas analysis, and the poor growth of this
species under conditions which are considerably different
from the climate of its natural habitat, limits direct
comparison with the other species and the extrapolation from
experimental conditions to field situations. Although A.
selaginoides has a low instantaneous LCP, the results of the
growth rate experiment showed that under the experimental
conditions, its growth LCP is not significantly different
from that of N. cunninghamii, E. lucida and P.

aspleniifolius, and at more moderate levels of shade it has a lower growth rate than these species. Further study of responses to light and interactions with temperature are necessary to clarify the shade-tolerance of A. selaginoides relative to N. cunninghamii, E. lucida and P. aspleniifolius. As with P. aspleniifolius, where A. selaginoides establishes in a canopy gap, it may be overtopped and subjected to shading by seedlings of faster-growing species. The data presented by Ogden (1978) at Mt Anne indicated that very few A. selaginoides were establishing in the forest and that the individuals that did establish successfully in the more recent past died before reaching the canopy. Together with the correlations between seedling establishment and canopy opening shown in Chapter 2, this suggests that regeneration is dependent on a relatively high light environment. The effect of a low growth rate in A. selaginoides in its establishment in canopy gaps must be exacerbated by the infrequent seed production in A. selaginoides so that establishment in gaps may occur well after establishment by other species.

Explanations and predictions of successional trends in mesic forest on equable sites are usually correlated with the comparative shade-tolerance of the canopy species, with the most shade-tolerant canopy species dominating old, undisturbed forests (Jones 1945; Forcier 1975; Williamson 1975; Connell & Slatyer 1977; Noble & Slatyer 1978). This contrasts with the observations in Tasmania of rainforest dominated by N. cunninghamii which is regenerating continuously, even when it is co-occurring with the more shade-tolerant A. moschatum (Chapter 2). The Tasmanian rainforest also contrasts with the Nothofagus-dominated rainforests of Chile and New Zealand. Studies in these areas suggest that when Nothofagus co-occurs with shade-tolerant rainforest trees, it fails to regenerate sufficiently to maintain its dominance unless there is exogenous disturbance (Veblen & Ashton 1978; Veblen et al. 1980, 1981; Wardle 1983, 1984). Clearly factors other than shade-tolerance are

important in determining the dominant status of N. cunninghamii in Tasmania, at least with respect to A. moschatum. Shade-intolerant trees commonly have an advantage in reproductive strategies (Forcier 1975; Williamson 1975), microsite preferences (Billings 1938; Bormann 1953; Veblen et al. 1981) which facilitate early dominance on a disturbed site. Read (1985) suggested that the dominance by N. cunninghamii is explicable if these advantages operate at a small scale of disturbance such as canopy gaps created by the death of an old tree. The reproduction of the shade-tolerant A. moschatum almost entirely by stem sprouts within the rainforest (Chapter 2) is sufficient to explain the ability of shade-intolerant species such as N. cunninghamii and E. lucida to regenerate succesfully in canopy gaps.

Chapter 7   Responses to temperature.

Introduction

Photosynthetic responses to temperature directly affect plant growth rate and therefore affect a plant's competitive ability in a particular climatic temperature regime. Similarly, frost damage is a drain on dry matter accumulation and reduces net annual growth. Plant death may occur at extreme low temperatures. Therefore photosynthetic responses to temperature and frost resistance may partially explain patterns of regeneration and species distribution with respect to altitude and latitude. There are several notable features of the distribution of Tasmanian rainforest canopy species with respect to altitude and latitude:

1. N. cunninghamii has a wide altitudinal distribution. In Tasmania it occurs from sea-level to 1260 m a.s.l., and in Victoria occurs to 1570 m a.s.l. (Howard & Ashton 1973). It spans approximately 7° latitude.

2. A. moschatum has a latitudinal range of 12°, extending from southern Tasmania to the northern tablelands of N.S.W. (Floyd 1978). It is not as common at high altitudes as N. cunninghamii (Table 7.1), occurring to 1375 m a.s.l. in Victoria (Howard & Ashton 1973), and to 1120 m a.s.l. in Tasmania (Table 7.1).

3. A. selaginoides is most common at altitudes above 600 m, in Tasmania (Table 7.1).

4. A. selaginoides, P. aspleniifolius, and E. lucida are endemic to Tasmania.

In addition to these distribution patterns, in Chapter 2 the tendency for gap regeneration of E. lucida and N. cunninghamii was noted, with a larger gap requirement for regeneration of P. aspleniifolius and A. selaginoides. The importance of initial floristic composition after site disturbance was also suggested as a potentially important determinant of canopy composition over long periods of time. Therefore comparative responses to extreme environments such

Table 7.1   Species distributions with respect to altitude in Tasmania.
The quantitative data used is only from study sites (167) which contain N. cunninghamii, and therefore is particularly limited at the higher altitudes, where A. selaginoides may occur in the absence of N. cunninghamii. The data is expressed as the percentage of sites of an altitude class which contain the particular species, with the number of sites in brackets. Stars (*) indicate altitude classes where a species has been recorded, but not included in the quantitative data because co-occurring species have not been noted. Data is from Busby (1984), Kirkpatrick (pers. comm.), Brown (pers. comm.), and Chapter 2 of this thesis.

Species	Altitude (m a.s.l.)													
	0-100 (24)	-200 (11)	-300 (7)	-400 (20)	-500 (15)	-600 (19)	-700 (14)	-800 (17)	-900 (10)	-1000 (18)	-1100 (9)	-1200 (2)	-1300 (1)	-1400
A. moschatum	29	64	71	100	80	88	64	56	50	33				
E. lucida	67	73	71	80	33	42	36	41	10	6				
P. aspleniifolius	58	100	86	65	20	63	86	88	40	50	*	*		
A. selaginoides	*		*		13	42	43	41	50	50	44	50	*	*

as high and low temperatures are relevant to survival on exposed sites, and competitiveness with co-occurring species.

In this chapter two responses to temperature are examined:

1. Photosynthetic response to temperatures of 7-35°C.
2. Frost resistance.

These responses are discussed in relation to the distribution of the species and their regeneration strategies.

Part A. Photosynthetic responses to temperature

Materials and methods

1. Photosynthetic responses to temperature
of plants grown in natural fluctuating temperatures

Plant growth regime

Seedlings of A. moschatum, E. lucida and N. cunninghamii (Nc700) were grown from seed collected from 700 m, and A. selaginoides and N. cunninghamii (Nc980) from seed collected at 980 m at Mt Field (42°41´S 146°40´E). Cotyledonary seedlings of P. aspleniifolius were collected from 700 m at Mt Field. All seedlings were planted in sandy loam containing slow release fertiliser in June 1982 and were grown in a shadehouse until February 1984. The mean monthly maximum and minimum temperatures during the 1983-84 growing period are shown in table 7.2. The foliage produced during the growing period was typical of mature plants. Only foliage which expanded during the conditioning period was used in the experiment. Photosynthesis was measured in individual leaves of A. moschatum, E. lucida and phylloclades of P. aspleniifolius. Terminal shoots of N. cunninghamii and A. selaginoides were used due to the small size of individual leaves.

Measurements

An open gas exchange system incorporating a
Grubb-Parsons SB2 infra-red gas analyser was used to measure
the net rate of CO_2 assimilation at selected temperatures.
Humidified air (317-340 μl l^{-1} CO_2) was pumped through a
leaf chamber of cross-sectional area 10 cm ^{2} at a flow rate
of 0.4 l min^{-1} and moisture was removed from the sample and
reference lines prior to analysis. The quantum flux density
was constant at 900 μmol quanta m^{-2} s^{-1} This was above the
light saturation points of all the species. Leaf temperature
was measured by a thermocouple in contact with the underside
of the leaf and was recorded continuously on chart. The
temperature of the leaf was controlled by heating or cooling
the air passing through the leaf chamber, and a
water/glycerol mixture circulating through chambers above
and below the leaf chamber. The lowest temperature that
could be consistently obtained using this method was $7^{O}C$.
Measurements were commenced at $20^{O}C$ and the temperature
reduced at a rate of 0.5 to $0.1^{O}C$ min^{-1} in increments of
$2-3^{O}C$ to $7^{O}C$, then warmed to $20^{O}C$ and raised in $2-3^{O}C$
increments to $35^{O}C$. This was found to be the most efficient
method in terms of rapidity of plant response and recovery,
and in temperature control of the leaf chamber. The slowest
rate of temperature change occurred at the lowest
temperatures. Plant responses were recorded continuously on
chart and values were measured after responses had
stabilised. Plant responses were detected within one minute
of the change in temperature and stabilised within five
minutes of temperature stabilisation. Each
temperature-dependence curve took two to three hours to
complete and no deterioration in plant response was observed
independent of changing temperature. Plants recovered to
their maximum response after the low and high temperature
treatments, given sufficient time.

2. Photosynthetic responses to temperature
of plants grown at 25°C and at 12°C

Plant growth regime

Seedlings of all species were grown under natural light conditions in the glasshouse from the time of their germination or transplanting from the field. The origins of the seed and seedlings are the same as in Experiment 1, except that N. cunninghamii seedlings from 980 m were not used in this experiment. Five seedlings of each species were transferred in November 1984 to a controlled environment growth cabinet at 25°C and light intensity of 150 to 190 µmol quanta $m^{-2}s^{-1}$ over a 16 hour photoperiod. The light intensity was the highest available that could provide even light and temperature for all plants and was close to the light saturation point of A. moschatum and approximately half that of the other species. Leaf temperature varied by less than 0.5°C irrespective of distance from the light source.

Temperature-dependence curves were measured every 2-3 days on two leaves from one plant of each species to determine when plants were fully acclimated to conditions in the growth cabinets. Most acclimation occurred within 5 days and was complete after 11 days. Temperature-dependence curves were measured on foliage from each of the five plants of each species in the method described in Part 1. The cabinet temperature was then reduced to 12°C. Temperature-dependence curves were measured after 2, 5, 8 and 11 days on two leaves of one plant of each species. Most acclimation had occurred within 5 days but plants were left for 14 days before taking the full measurements. Temperature-dependence curves were measured as described previously. In each case the leaves selected for measurement had developed during the spring flush in the glasshouse 8-10 weeks prior to the conditioning treatment. The relatively slow growth rate of these species prevented comparative studies of leaves which developed in the conditioning

temperature regime (12°C or 25°C). However, since these species produce leaves only in spring and summer, the ability of mature leaves to acclimate to the prevailing temperature is considered to be the most ecologically significant response.

Results

The relative photosynthesis (% of the maximum rate of net photosynthesis) of the two provenances of N. cunninghamii were identical in response to temperatures $\leq 27^{\circ}$C but Nc700 has a significantly higher ($p < 0.05$) relative photosynthesis at temperatures greater than 29°C (Fig. 7.1). The absolute rates of photosynthesis were higher in Nc980 plants than Nc700 except at the highest temperatures (Fig. 7.1), but these differences were not significant ($p < 0.05$). Due to the differences in these provenances, Nc700 is compared with A. moschatum, E. lucida and P. aspleniifolius which originated from the same elevation, and Nc980 is compared with A. selaginoides (from the same seed collection site). Nc700 has the broadest response curve of the rainforest species (Fig. 7.2a) with ≥ 90% of the maximum rate of net photosynthesis (P_{max}) from $12.0-31.0^{\circ}$C, a range of 19.0°C. Its relative photosynthesis is significantly higher than E. lucida, P. aspleniifolius and A. moschatum at 35°C and than P. aspleniifolius and A. moschatum at 7°C ($p < 0.05$). P. aspleniifolius exhibits ≥ 90% of its P_{max} over a range of 16.5°C ($12.0-28.5^{\circ}$C). E. lucida and A. moschatum have the narrowest temperature curves, with ≥ 90% of their P_{max} over 13.2°C ($13.0-26.2^{\circ}$C) in E. lucida and 12.5°C ($15.5-28.0^{\circ}$C) in A. moschatum, which also has the highest temperature requirement for maximum photosynthesis ($21-25^{\circ}$C). Nc980, with 90% of its P_{max} over 17.2°C ($11.8-29.0^{\circ}$C), does not have such a broad response curve as Nc700 due to the reduced rate of photosynthesis at high temperatures (Fig. 7.1). However it is broader than that of A. selaginoides which has ≥ 90% of its P_{max} over a range of 15.5°C ($10.5-26.0^{\circ}$C) and

is the most photosynthetically tolerant species of the lower temperatures and least tolerant of the higher temperatures (differences significant at the 95% level).

Only A. moschatum showed a significantly higher P_{max} (p<0.05) in the seedlings acclimated to 25°C (Fig. 7.3b). In all other species there was no significant effect of the temperature regimes on the P_{max} (Fig. 7.3). All species showed some acclimation to the temperature regime, either in a shift of the optimum temperature or in the shape of the curve (or both). N. cunninghamii, A. selaginoides and P. asplenifolius showed a significant increase (p<0.05) in relative photosynthesis at temperatures below their optimum, when acclimated to 12°C from 25°C, with a shift in optimum temperatures for photosynthesis of 1-3°C. The response to temperatures above their optimum was not significantly different (p<0.05) between the two temperature regimes. A. moschatum and E. lucida did not show any significant increase in relative photosynthesis at temperatures below their optimum, when acclimated to 12°C but significant differences (p<0.05) were recorded at temperatures above their optimum, between the two temperature regimes (Fig. 7.3). Some of the same trends are observed between species as recorded from plants grown under natural fluctuating temperatures, namely, the broad response curves of P. aspleniifolius and N. cunninghamii and the narrow response curve of A. moschatum when these plants have acclimated to 12°C. However in plants acclimated to 12°C there was no superiority of A. selaginoides and N. cunninghamii at low temperatures, as recorded under natural fluctuating temperatures, and with the exception of the higher relative rate of photosynthesis of P. aspleniifolius, there were no significant differences among species at 9°C. In plants acclimated to 25°, A. selaginoides and A. moschatum showed the greatest relative decrease of the species in net photosynthesis at high temperatures, and P. aspleniifolius and E. lucida showed the greatest tolerance of the higher temperatures (Figs. 7.3 & 7.4). N. cunninghamii had a narrow

Fig. 7.1   The photosynthetic response to incident
temperature of two altitudinal provenances of
N. cunninghamii from Mt Field, raised outdoors under a
woodland canopy.
a. Relative photosynthesis: the net rate of photosynthesis
expressed as a percentage of the maximum rate of
photosynthesis.
b. Net rate of photosynthesis.
Each value is the mean of five replicates with standard
errors shown when they are $\geq$ 3% or 0.3 μmol $CO_2m^{-2}s^{-1}$.

700 m provenance: ●
980 m provenance: ○
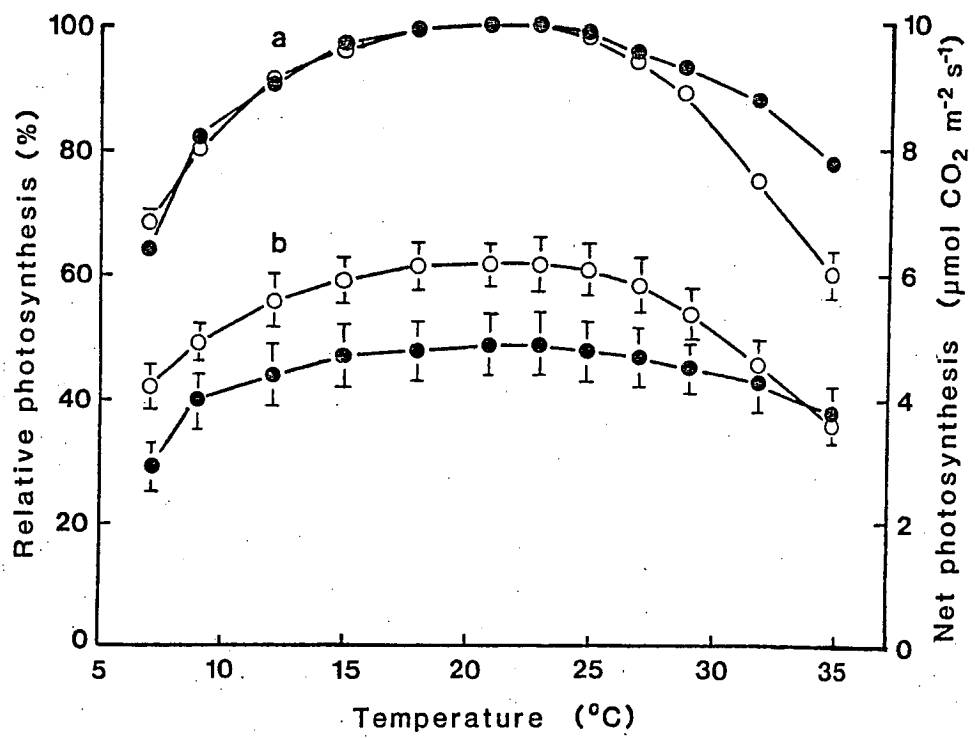
Fig. 7.2   The photosynthetic response to incident
temperature of plants raised outdoors under a woodland
canopy. The net rate of photosynthesis is expressed as a
percentage of the maximum rate of photosynthesis.

a. Plants from 700 m a.s.l.
b. Plants from 980 m a.s.l.

N. cunninghamii: ●

E. lucida: □

A. moschatum: ▲

P. aspleniifolius: △
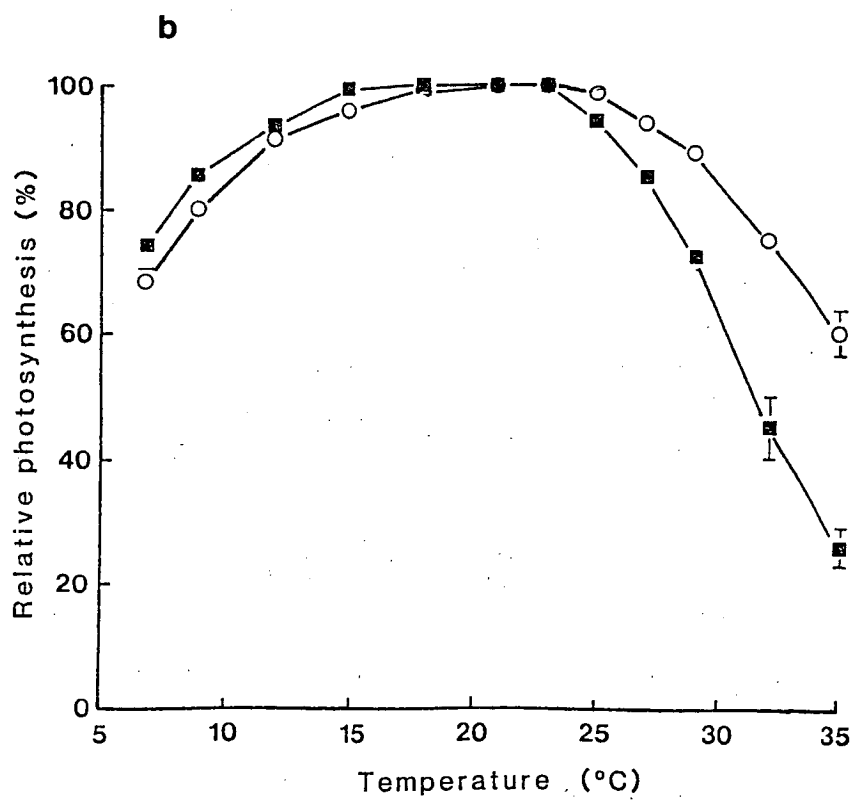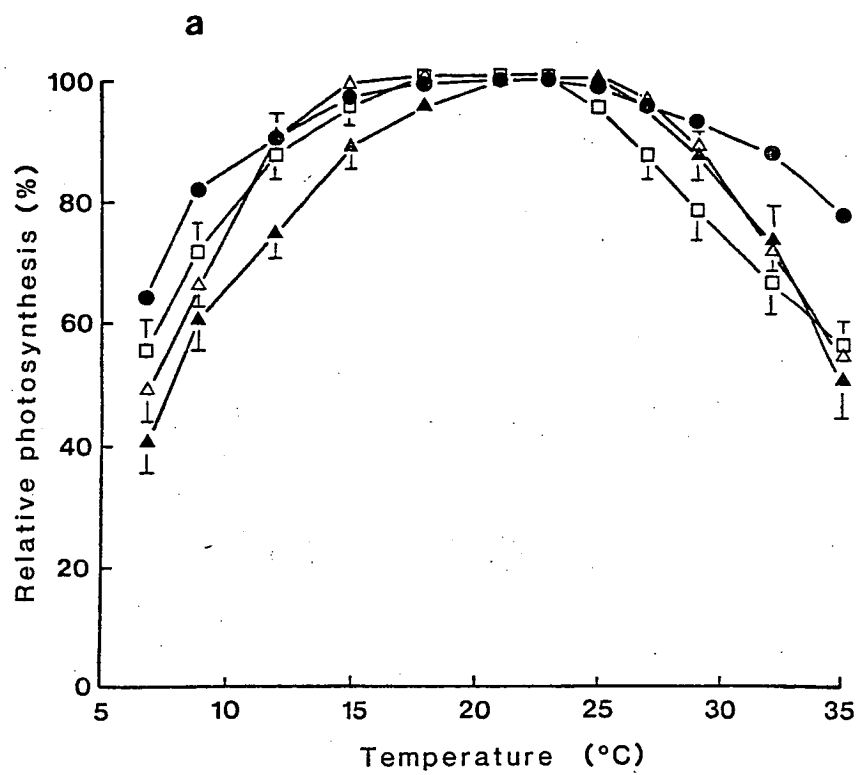
A. selaginoides: ■

Fig. 7.3   The photosynthetic responses to incident and
growth temperatures of plants from Mt Field raised in
controlled environment growth cabinets at 12°C (△)
and 25°C (▲).

a. N. cunninghamii
b. A. moschatum
c. A. selaginoides
d. E. lucida
e. P. aspleniifolius.

Net rate of photosynthesis: ----
Relative photosynthesis: ——

a Relative photosynthesis (%) / Net photosynthesis (µmol CO_2 m^{-2} s^{-1}) vs Temperature (°C)

b Relative photosynthesis (%) / Net photosynthesis (µmol CO_2 m^{-2} s^{-1}) vs Temperature (°C)

c Relative photosynthesis (%) / Net photosynthesis (µmol CO_2 m^{-2} s^{-1}) vs Temperature (°C)

d Relative photosynthesis (%) / Net photosynthesis (µmol CO_2 m^{-2} s^{-1}) vs Temperature (°C)

e Relative photosynthesis (%) / Net photosynthesis (µmol CO_2 m^{-2} s^{-1}) vs Temperature (°C)

Fig. 7.4   The photosynthetic response to incident and
growth temperature regimes of plants from Mt Field, raised
in controlled environment growth cabinets at
a. 25°C
b. 12^{0}C

N. cunninghamii: ●

E. lucida: ■

A. moschatum: ▲

P. aspleniifolius: □

A. selaginoides: △

This data is shown in Fig. 7.3 with standard errors.
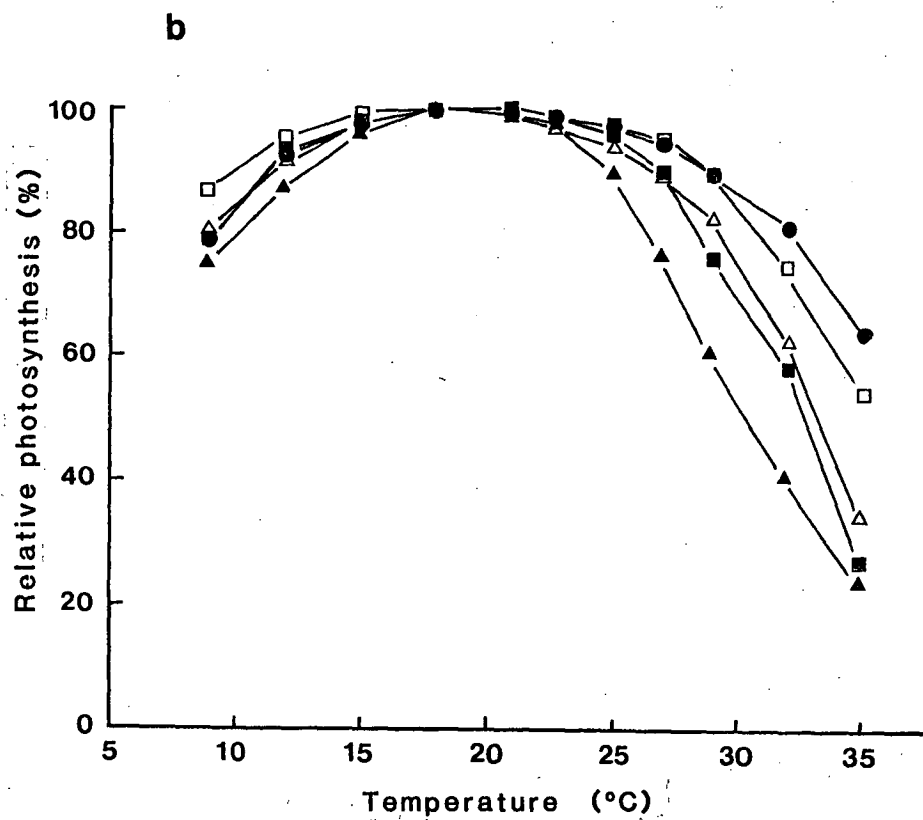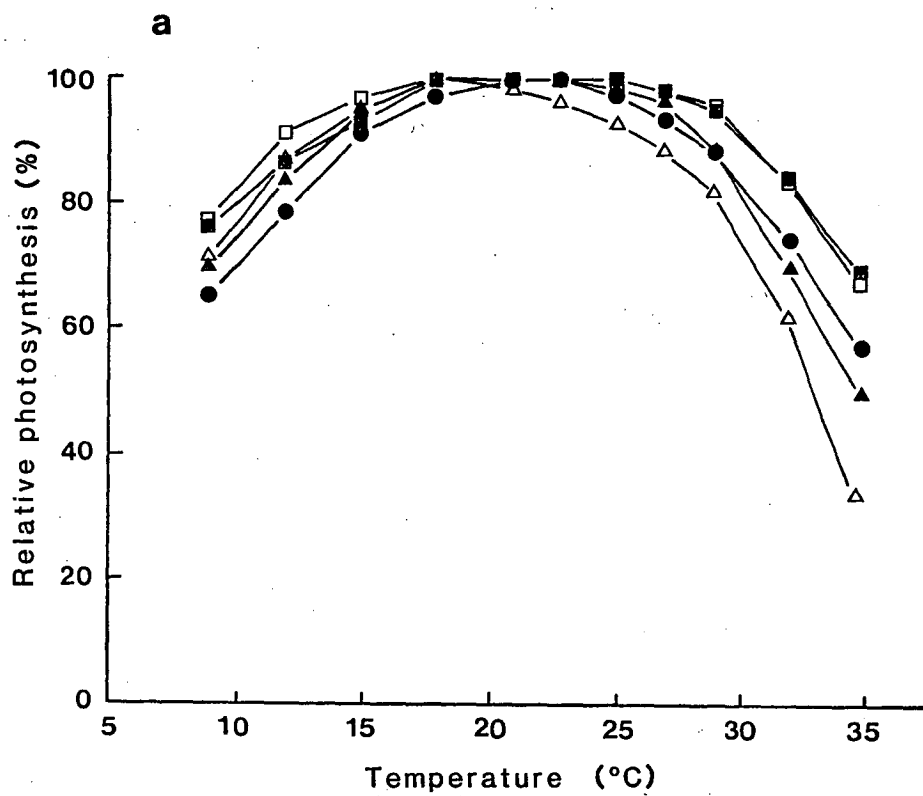
response curve, unlike the curves in plants acclimated to 12°C, or grown under a natural temperature regime. It was the only species which had its broadest response when grown under natural fluctuating temperatures.

Part 2. Frost resistance

Materials and methods

The use of conductivity as a measure
of tissue damage

The estimation of tissue damage resulting from exposure to controlled freezing temperatures by measuring the conductivity of exosmosed electrolytes was first used by Dexter et al. (1930). This method is based on observations that exosmosis increases with increasing tissue damage. The measure obtained cannot be used as a direct measure of the percentage of killed cells since exosmosis may occur in injured cells which have suffered reversible damage (Palta et al. 1977). However, studies comparing the results obtained using this technique with results from whole plants have indicated reliability of the conductivity method in predicting frost injury (Dexter et al. 1930; Wilner 1960; Aronsson & Eliasson 1970).

The advantages of this technique over studies of whole plants are:

1. It greatly reduces the problem of vertical and horizontal temperature gradients in frost chambers since the tissue samples are small and consequently may be positioned at the same vertical level and spread over a smaller area than whole plants.

2. Results are obtained within a few days.

3. The number of plants required may be small, depending on the size of the plant, since tissue samples for many temperature treatments may be taken from a single plant.

4. Results are easily quantified.

In the studies of frost resistance of alfalfa varieties by Dexter et al. (1930, 1932) the specific conductivities of samples of identical weight were used for comparisons. Later studies (Wilner 1960; van den Driessche 1976) expressed the conductivity after freezing as a percentage of the conductivity of heat-killed cells. This ratio eliminates any variation of conductivity due to variation in tissue mass. Flint et al. (1967) noted that conductivity values of unfrozen tissues may vary among species, and within species growing under different conditions. They suggested the use of an index of injury which is weighted by the control value so that the index = 0 in unfrozen tissue and = 100 in fully damaged tissue. Hence it eliminates differences due to changes (and inherent differences) in "leakiness" of unfrozen (control) tissues and allows direct comparisons between species. The index of injury, I_T

$$=100(R_t - R_o)/(1-R_o); \quad R_t = L_t/L_k; \quad R_o = L_o/L_d$$

where:

I_t is the index of injury resulting from exposure to temperature t.

R_t is the fractional release of total electrolytes from the sample exposed to temperature t.

R_o is the fractional release of electrolytes from an unfrozen sample.

L_t is the specific conductance of leachate from a sample frozen at temperature t.

L_k is the specific conductance of leachate from a sample frozen at temperature t and then heat-killed.

L_o is the specific conductance of leachate from an unfrozen sample.

L_d is the specific conductance from an unfrozen sample and then heat-killed.

Determination of frost resistance
using the conductivity method

Six discs (6 mm diameter) were punched from leaves or

phylloclades (all from one leaf where possible) of five
plants of N. cunninghamii, A. moschatum, E. lucida and P.
aspleniifolius. The small size of A. selaginoides leaves not leaves
made the use of discs impossible. Individual leaves of A.
selaginoides were cut at the base.

Each sample of six discs (or leaves) was placed in a 20
ml glass vial. Small excised samples tend to supercool more
than intact tissue (Burke et al. 1976) and therefore 0.1 ml
distilled water and a few grains of $AgNo_3$ was added to
promote freezing (a method devised by P. Hallam, C.S.I.R.O.
Hobart). The vials were then placed on a reflective
aluminium tray 5 cm above the floor of a frost chamber (50 x
52 x 75 cm interior) cooled from a coil at the top of the
chamber with the controlling temperature sensor positioned 1
cm above the tray and the chamber temperature recorded on
chart. The chamber was cooled at its maximum rate
(1.0°C/min) to 2.0°C then at 0.2°C/min to the set
temperature. The lag of tissue temperature is shown in
Figure 7.5. Tissue temperature varied within ± 0.2°C of the
set chamber temperature, within the horizontal spread of
vials across the chamber. The set temperature was maintained
for 90 minutes followed by thawing at approximately 0.2°C
min^{-1} to 2.0°C. Frost injury was measured in samples exposed
to 0.5, 1.5, 3 and 5 hours of frost temperatures in
preliminary experiments. No significant difference occurred
at the 95% level of significance. This indicates that the
longer period of exposure to frosting temperatures at the
low temperatures due to the longer cooling and thawing
period does not have a significant effect on the final frost
injury, i.e. the final injury is temperature-determined, and
not influenced by the duration of exposure to frost
temperatures.

The vials were removed from the chamber and 8 ml of
distilled water was added to each vial which was then capped
and shaken for 24 hours at room temperature. Figure 7.7
shows the relationship between the conductivity of the
sample solution and the incubation period. Conductivity of

Fig. 7.5   The rate of change of tissue temperature in freezing experiments. The tissue (at room temperature) was placed in the freezing chamber at 5.5°C, with the chamber temperature decreasing at 1.0°C min^{-1}.

At 1.5°C chamber temperature ($\blacktriangle_1$), the rate of cooling was changed to 0.2°C min^{-1}. After 90 minutes exposure to the set temperature ($\blacktriangle_2$), the refrigeration was turned off, and the chamber allowed to warm at 0.2°C min^{-1} to 2.0°C.

Chamber temperature: ——
Tissue temperature: – – –

Fig. 7.6   The effect of leaf perimeter to area ratio on the relative conductivity of control (unfrozen) tissue of A. moschatum. Both the slope and intercept are highly significant (p<0.001), indicating the leakage of solutes from undamaged cells as well as from the cut edges of the tissue samples.

$$y = 0.0566 + 0.3168x$$

$$F = 840.69 \qquad p < 0.001$$
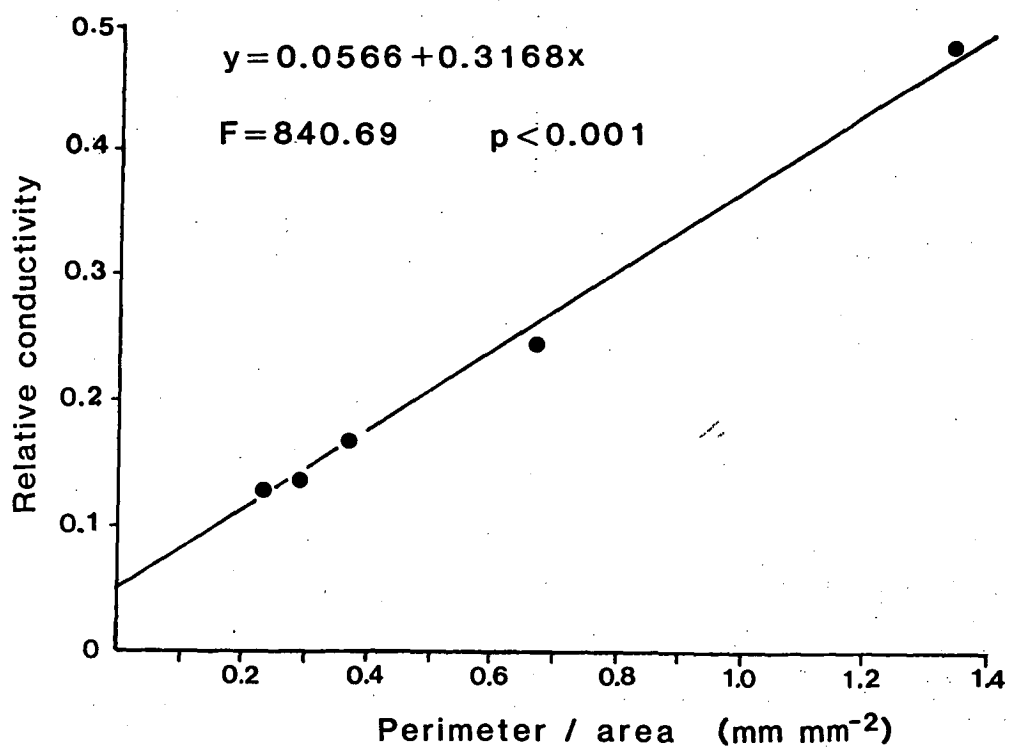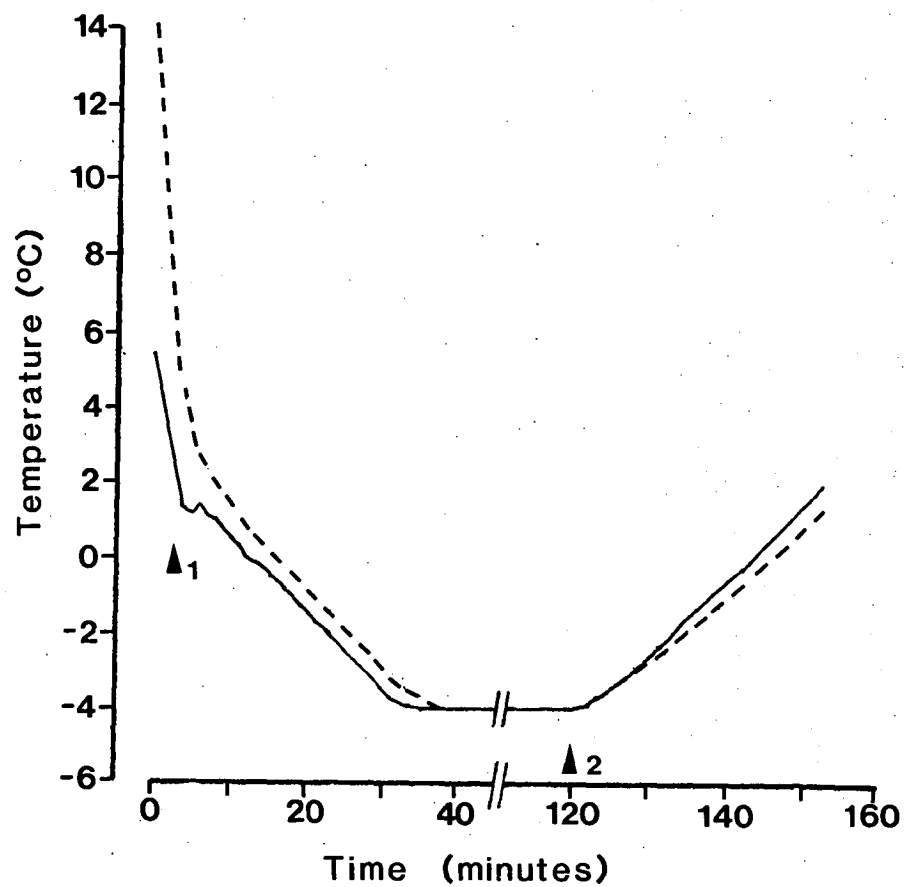
Fig. 7.7   The effect of the duration of the initial
incubation period on the measured relative conductivity of
tissue frozen to -20°C, and unfrozen (control)
tissue. The points on each curve represent the means of

five replicates. The specific conductivity of the five
replicates was measured at intervals of 2-8 hours and the
relative conductivity was calculated using a final
incubation period (after heat-killing the tissue) of 24
hours. The results of N. cunninghamii (●) and
A. moschatum (▲) are shown. Results of the other species
fall within this range.

Fig. 7.8   Differences in the frost resistance of
altitudinal provenances of N. cunninghamii.
a. Seedlings raised in the glasshouse.
b. Seedlings raised outside.
Measurements were taken in July 1984.

N. cunninghamii from 700 m a.s.l.:   ●
N. cunninghamii from 980 m a.s.l.:   O
A. selaginoides from 980 m a.s.l.:   □
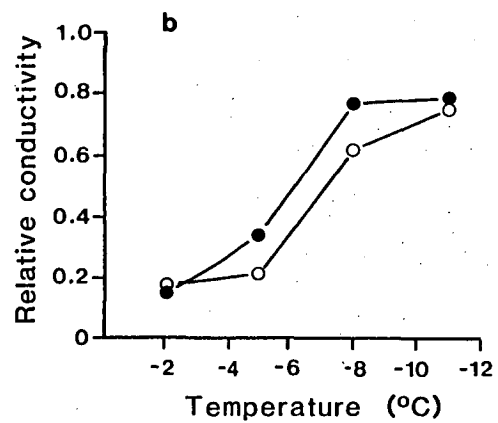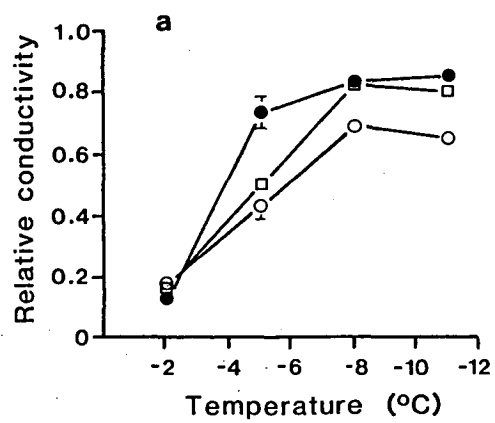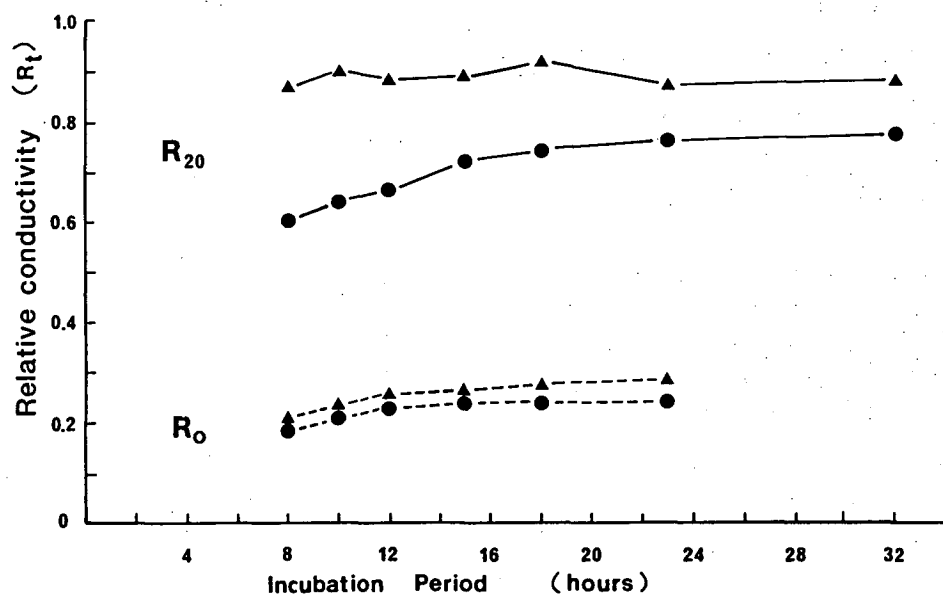
the solution (L_t) was measured with a Radiometer Copenhagen
CDM 3 conductivity meter with a Type PP1042 RF probe.
Samples were then placed in a bath of boiling water for ten
minutes. Preliminary experiments showed that conductivity of
the samples was the same after 5, 10, 15 and 20 minutes in
the boiling water. The vials were again shaken for 24 hours
and the conductivity of the solution measured (L_k).

Control tissues were treated in the same way but without
exposure to low temperatures. Figure 7.6 indicates that the
control value of relative conductivity (R_o) results from
leakage from injured cells in the cut perimeter of the
sample and also from solute leaking from undamaged tissue.

The mean relative conductivity (R_t) was calculated for
each treatment of each species. Where the mean control
values of the species or treatments being compared showed
significant difference (at the 95% level), e.g. among
different species, the index of injury (I_t) was used for
comparison, but since this is a single value calculated from
the means of the R_t and the R_o there is no simple way of
calculating the error of the value.

Comparisons of several methods of
determining comparative frost resistance

Frosts of sufficient severity to distinguish
differential frost resistance among the species may be
infrequent (no data is available) and have not occurred
within the last four years at study sites at Mt Field.
Therefore it has not been possible to test this experimental
method of determining frost resistance with field
observations. Results obtained using this method were
compared, however, with results from the experimental
exposure of whole seedlings to frost temperatures, and with
results from the exposure of small foliage branches to frost
temperatures:

1. The frost resistance of three-month-old seedlings raised
in the glasshouse was determined using a) the conductivity

method and b) by exposing whole seedlings to freezing temperatures. Seedlings of N. cunninghamii, E. lucida, A. moschatum and P. aspleniifolius were grown from seed collected at 700 m at Mt Field. A. selaginoides was grown from seed collected at 980 m at Mt Field. Each seedling was planted in sandy loam soil in a 3 cm diameter plastic pot. Seedling size among the species varied from 2 cm in the slow-growing A. selaginoides to 4 cm in N. cunninghamii and E. lucida. Five seedlings of each species were placed in an alternating arrangement on the floor of the frost chamber and exposed to freezing temperatures (-2, -5, -8 and -11°C) in the same manner as described in the conductivity experiments. Each treatment of seedlings was returned to the glasshouse after the frost treatment, and seedling were observed regularly over several weeks until signs of damage were visible. The quantity of damage (browning of the foliage) was estimated visually. On the day following the whole plant experiments, frost resistance was determined using the conductivity method as described earlier. Five replicate seedlings were used (once only) for each temperature treatment, with only one disc or segment being taken from each leaf. The method used was the same as that described earlier.

2. Results obtained using the conductivity method were compared in August 1984 and September 1985 with results from experiments using small branches of foliage collected from Mt Field in a similar method to that described by Sakai & Wardle (1978) and Sakai et al. (1981), but using naturally hardened plant material. Branches 10-15 cm long, from the same large branch used for sampling for the conductivity method, were laid on a plastic mesh support 5 cm above the base of the frost chamber. The freezing treatments were the same as described above. After thawing was complete, the branches were placed in plastic bags with their stems in water. Foliage tissue damage was assessed visually after 3-5 days by comparison with unfrosted shoots kept in the same conditions.

The results of these experiments indicated the same order of frost resistance among the species irrespective of method, but often with different absolute values (see Results section). Since relative values are of greater interest than absolute values in these experiments, and because of the advantages of the conductivity method mentioned earlier, the following experiments determine frost resistance using the conductivity method.

Comparative frost resistance and hardening of plants grown in the glasshouse

The experimental plants were either grown from seed (N. cunninghamii, A. moschatum, E. lucida and A. selaginoides) or transplanted as cotyledonary seedlings (P. aspleniifolius) from Mt Field National Park (42°41´S 146°40´E). N. cunninghamii, E. lucida, A. moschatum and P. aspleniifolius were collected (seed or seedling) at 700 m elevation. A. selaginoides seed was collected at 980 m elevation. Plants were grown in sandy loam soil, with slow-release fertiliser, and watered daily. All plants were 26 months old (30-70mm high) at the start of the experiment and the tissue used was produced during the preceding growing season. These plants were producing adult foliage. All plants had been in the glasshouse for at least six months prior to the start of the experiment. The mean daily maximum temperature for the preceding 4 weeks was 23.4°C and the mean daily minimum temperature was 15.4°C, with an absolute minimum temperature of 13.2°C. Frost damage was measured in these unhardened plants at -1, -2, -4, -5, and -8°C and they were then placed in a hardening regime of 4°C night temperature in a cold storage room with an 8-hour photoperiod in a glasshouse of mean maximum temperature over the next 39 days of 25.5°C. Frost damage to temperatures of -2, -5, -8, -11 and -14°C was measured after 3, 9 18, 25 and 39 nights in the hardening regime.

The frost resistance of N. cunninghamii was also
compared in two altitudinal provenances - 700 m (as above)
and 980 m (the site from which A. selaginoides seed was
collected), in unhardened seedlings (as above) and seedlings
which were hardened naturally during the 1985 Hobart winter
and measured in July. The mean daily maximum temperatures
for the four weeks prior to measurement was 12.4°C, with a
mean daily minimum temperature of 4.9°C, and an absolute
minimum temperature of 2.8°C.

Comparative frost resistance
of plants in the field

The method described above was used to test the frost
resistance of adult foliage from trees growing at 980 m (A.
moschatum, P. aspleniifolius, N. cunninghamii and A.
selaginoides) and 700 m (A. moschatum, P. aspleniifolius, E.
lucida and N. cunninghamii) at Mt Field National Park. Frost
resistance was measured once per month from August 1984 to
September 1985 on foliage from exposed branches, such as on
road edges. The foliage used was produced during the growing
seasons 1982-83 and 1983-84 and was collected from five
trees of each species at each of the two sites.
Maximum-minimum thermometers were placed at each site and
read monthly at the time of foliage collection. In January
and August 1985, foliage from two-year old seedlings was
tested for frost resistance - A. selaginoides and N.
cunninghamii from the 980 m site (seedlings of P.
aspleniifolius and A. moschatum were not found at this site
although they occurred there as adults), and N.
cunninghamii, A. moschatum, E. lucida and P. aspleniifolius
from the 700 m site. The small size of the seedlings meant
that a whole seedling was used for each replicate in each
treatment (five seedlings per treatment). Seasonal changes
in the frost resistance of seedlings at Mt Field could not
be monitored due to insufficient seedlings to meet the
requirements of such an experiment.

Foliage was transported to Hobart in plastic bags
containing moist tissue paper, packed in an
expanded-polystyrene box containing a sealed ice block. The
foliage was stored in Hobart at 5^OC. The frost treatments
were completed within 36 hours from the time of collection.
Preliminary experiments showed that there there was no
change in frost resistance of the detached shoots over 48
hours under these storage conditions.

Results

Comparison of methods of determination
of frost resistance

The values of frost damage occurring in seedlings as
determined by the conductivity method are similar to the
values obtained by exposing whole seedlings to low
temperatures and estimating the damage visually at the
higher temperature treatments (Table 7.3). The higher values
of damage at the lower temperatures using the whole plant
method are probably an indication that severe tissue damage
leads to organ (and plant) death.

Figure 7.11 shows the relative frost resistance of the
naturally hardened plants from Mt Field using two methods of
determination. The order of frost resistance determined does
not vary between methods. However, the absolute values of
foliage frost damage are quite different. In general,
greater leaf frost damage is recorded using the disc method
at a given temperature. It is uncertain which of these
methods gives the more accurate indication of the absolute
frost resistance of these species, since severe frosts have
not been recorded during this period of study and
consequently field results are not available. Sakai, & Wardle
(1981) recorded a foliage frost resistance (lowest
temperature at which little or no damage occurred) of -10^OC
for P. aspleniifolius and -17^OC for A. selaginoides.
Although the latter value is similar to that obtained for A.

selaginoides in this study, the value for P. aspleniifolius obtained by Sakai & Wardle is lower than obtained in this experiment. This may be due to differences in provenances or to differences between the hardening regimes, and differences in the freezing treatments.

Comparative frost resistance of plants
raised in the glasshouse

The relationship between frost injury and temperature in unhardened seedlings is logarithmic, with little damage at temperatures close to $0^{\circ}C$, and an increasing rate of damage with decreasing temperatures until maximum damage occurs at approximately -5--$8^{\circ}C$ (Fig. 7.9). Frost injury of >10% occurred in unhardened foliage of A. moschatum and P. aspleniifolius at $-4^{\circ}C$ but in the other species frost injury did not occur below above $-5^{\circ}C$ (Fig. 7.9a). The order of frost resistance in the unhardened seedlings is A. moschatum < P. aspleniifolius < (E. lucida and N. cunninghamii) < A. selaginoides. Measurement of frost resistance of unhardened N. cunninghamii grown from seed collected from the 980 m site (Nc980) indicates that it has a greater frost resistance than both Nc700 and A. selaginoides (grown from seed collected from the 980 m site) (Fig. 7.8a). This provenance variation indicates that A. selaginoides should be compared only with provenances growing on the same site. The provenance variation in species other than N. cunninghamii is not known.

All species except P. aspleniifolius had responded to the hardening regime by Day 3 with a significant reduction of R_{-5}, and in N. cunninghamii and A. selaginoides a significant reduction of R_{-8} had also occurred (p<0.05) (Fig. 7.10). R_{-5} was at its minimum value by Day 10 in A. moschatum and by Day 18 in all other species. N. cunninghamii showed significant hardening (at the 95% level) to all the frosting temperatures. A. selaginoides showed hardening to $-8^{\circ}C$, and E. lucida and P. aspleniifolius

Table 7.2   Mean daily maximum and minimum temperatures in the shadehouse during the 1983-84 growing season.

| | Month | | | | | |
	September	October	November	December	January	February
Maximum	13.1	15.1	18.9	21.1	19.7	20.2
Minimum	8.3	11.4	12.2	14.5	12.9	13.9

Table 7.3   Comparisons of the frost resistance (% damage) of unhardened three-month-old seedlings determined by the conductivity method (C) with the frost resistance determined by freezing whole plants (W). The values are calculated from five replicates. The P. aspleniifolius seedlings bear true leaves (no phylloclades).

| | Method | Freezing temperature (^{O}C) | | | |
		-2	-5	-8	-11
N. cunninghamii	C	0	14	71	85
	W	0	23	100	100
A. moschatum	C	0	75	96	97
	W	0	86	100	100
E. lucida	C	0	21	74	84
	W	0	32	100	100
P. aspleniifolius	C	0	52	92	91
	W	0	63	100	100
A. selaginoides	C	0	49	83	87
	W	0	41	100	100

Fig. 7.9   Frost resistance of seedlings grown in the glasshouse.

a. Unhardened seedlings.

b. The same seedlings grown for 39 days with 4°C night temperatures (16 hours).

N. cunninghamii (700 m):   ●

A. moschatum (700 m):   ▲

E. lucida (700 m):   ■

P. aspleniifolius (700 m):   ◆

A. selaginoides (980 m):   □
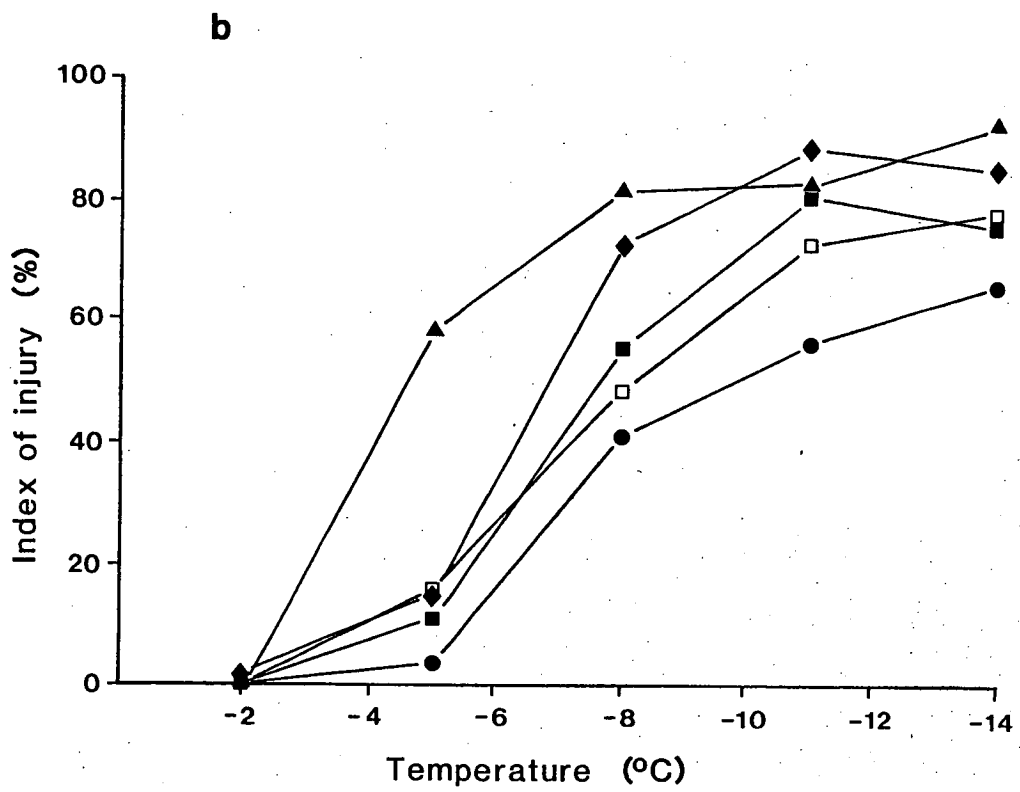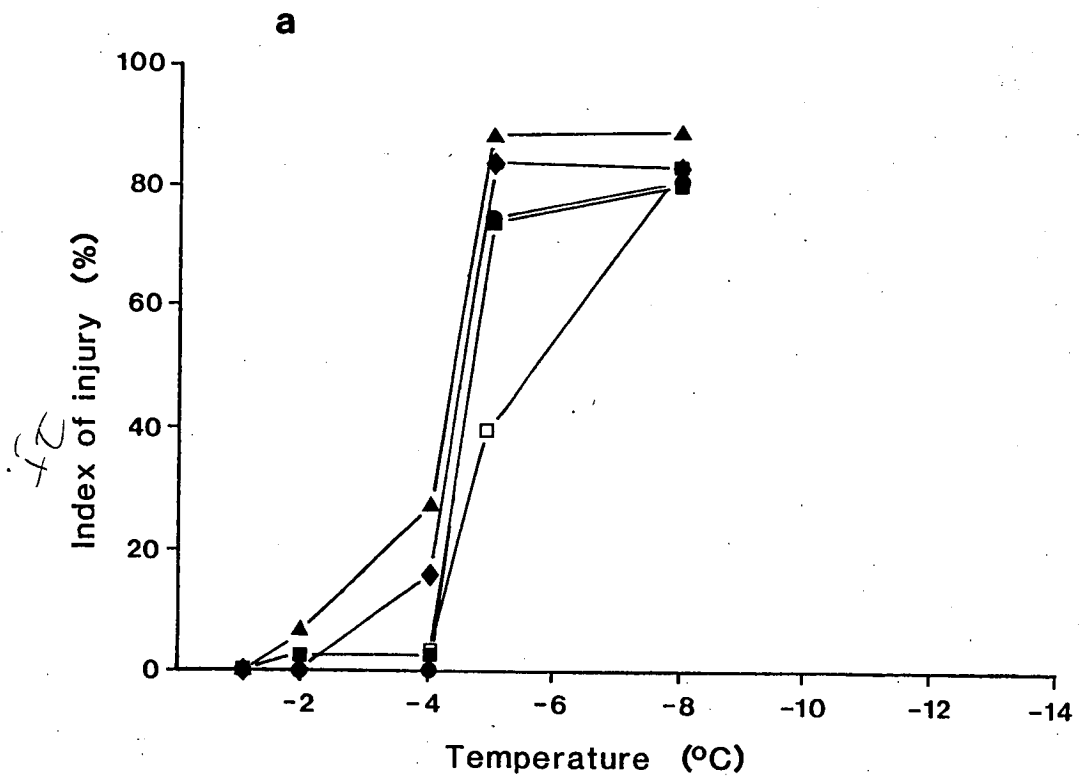
Fig. 7.10   Changes in frost resistance during the
hardening regime. Each point is the mean of five replicates
with standard errors shown where they are $\geq$ 0.03.

a. <u>N. cunninghamii</u> (700 m)

b. <u>A. moschatum</u> (700 m)

c. <u>P. aspleniifolius</u> (700 m)

d. <u>E. lucida</u> (700 m)

e. <u>A. selaginoides</u> (980 m)

R_{-2}:   ■

R_{-5}:   o

R_{-8}:   ▲

R_{-11}:   □

R_{-14}:   ●
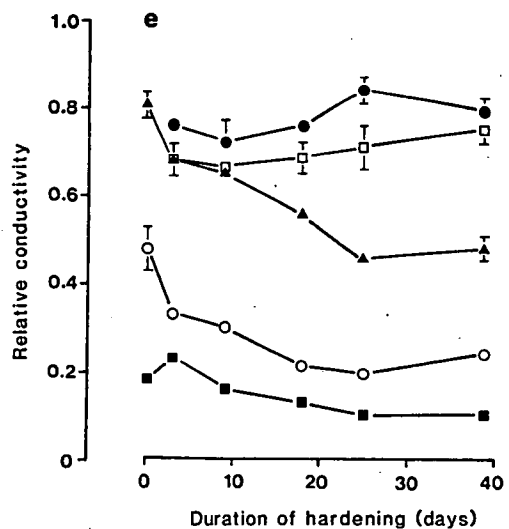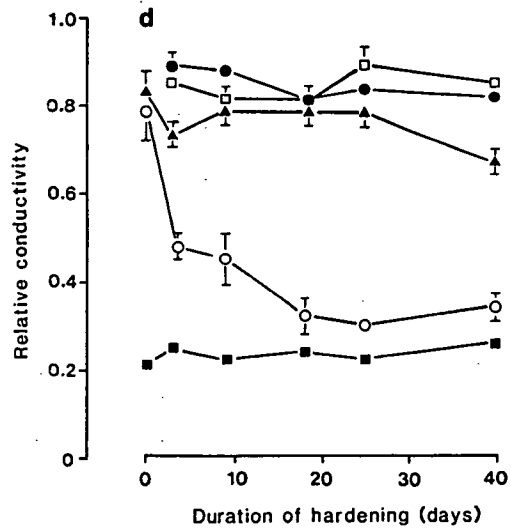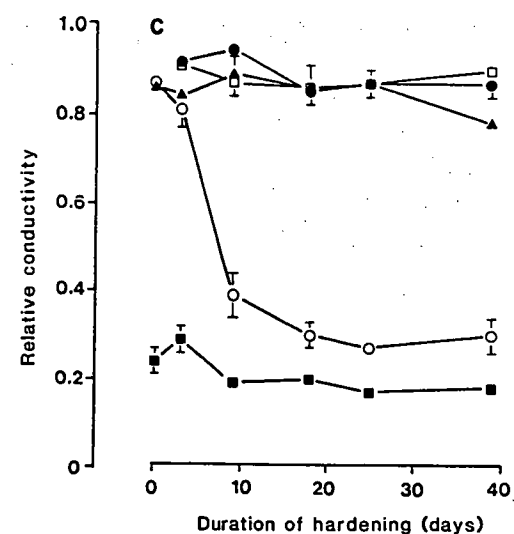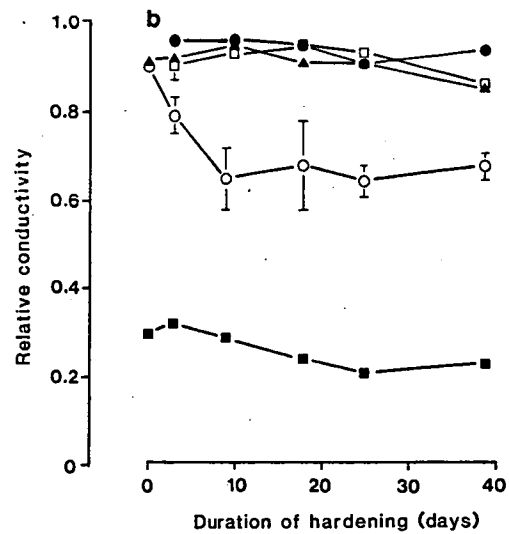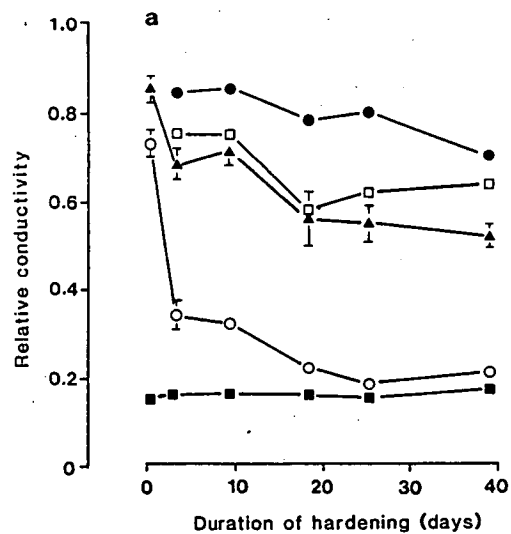
Fig. 7.11   A comparison of the frost resistance of adult
foliage from trees at Mt Field as determined by the
conductivity method (- - - -) and visual assessment of damage
to foliage (———). Each point is the mean of five
replicates with standard errors shown where they are $\geq$ 3%.
a. Foliage collected from 700 m a.s.l.
b. Foliage collected from 980 m a.s.l.

N. cunninghamii: ●
A. moschatum: ▲
E. lucida: ■
P. aspleniifolius: ◆
A. selaginoides: □
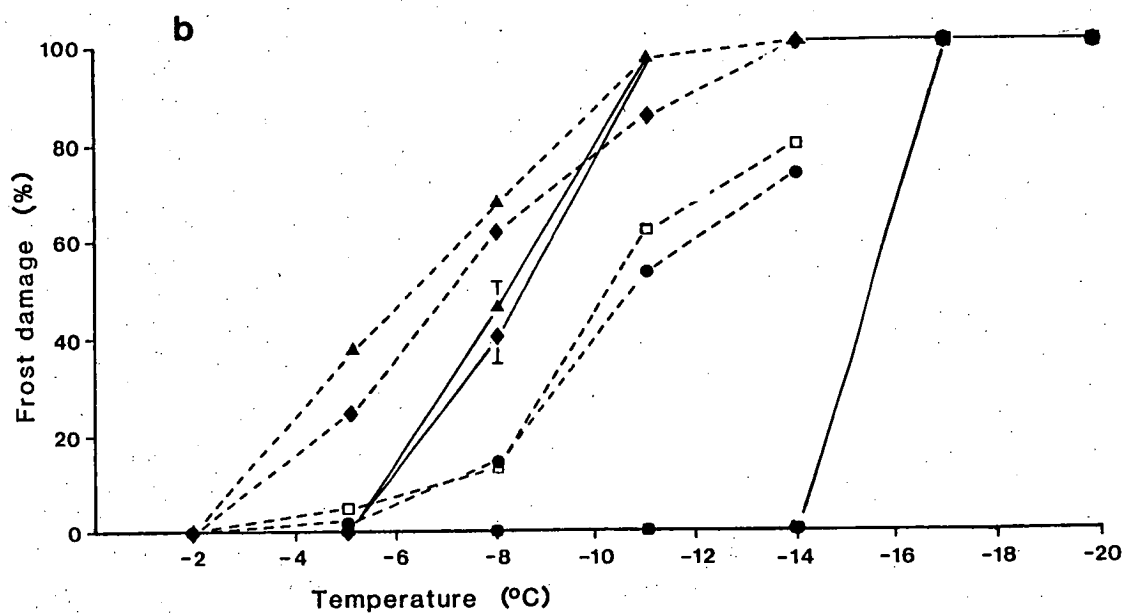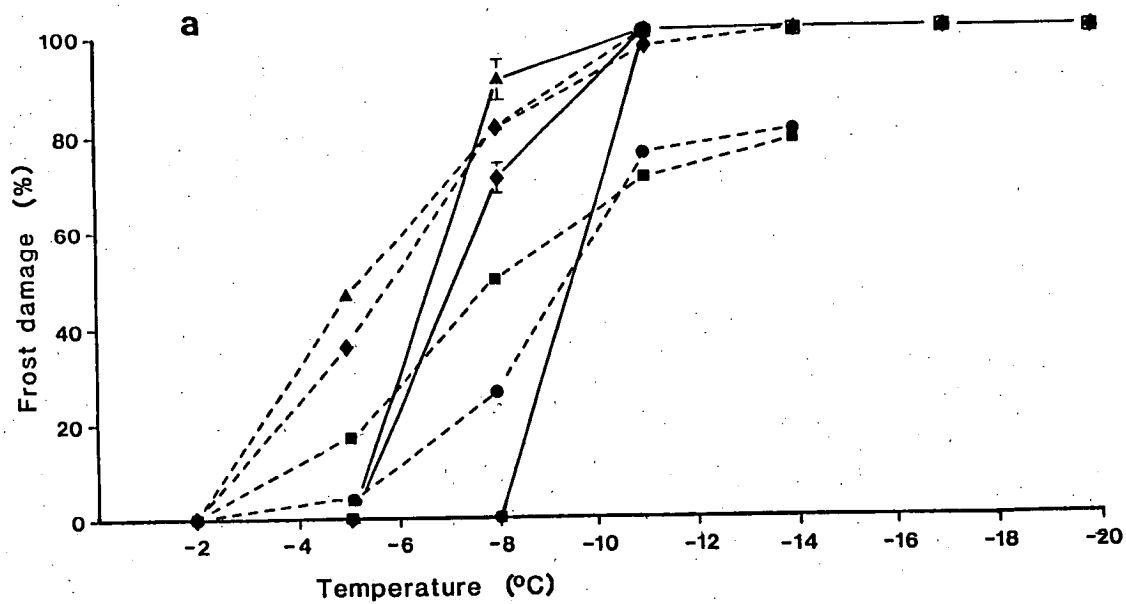
showed significant hardening only to -5°C. None of the
species showed significant difference between R$_{-2}$ and R$_0$.
The decline in R$_{-2}$ in <u>A. moschatum</u>, <u>P. aspleniifolius</u> and <u>A.</u>
<u>selaginoides</u> is caused by a small decline in the control
value (not shown) as the plant hardened. By Day 39, the
order of frost resistance was <u>A. moschatum</u> < <u>P.</u>
<u>aspleniifolius</u> < <u>E. lucida</u> < <u>A. selaginoides</u> < <u>N.</u>
<u>cunninghamii</u> (Fig. 7.9b).

The comparative frost resistance
of plants in the field

Foliage collected in the first monthly sampling (August
1984) was exposed to temperatures down to -20°C. The more
frost sensitive species recorded significant damage at -5°C
and all species from both sampling sites appeared to reach a
maximum level of injury by -17°C, with the level of injury
plateauing at or above this temperature (Fig. 7.12). The
maximum damage experienced by each species correlated with
the frost resistance of that species, i.e. the more
frost-sensitive species had higher maximum values of damage.
This trend was less clear in summer, when the index of
injury appeared to be gradually approaching 100% at low
frost temperatures (Fig. 7.13).

The order of frost resistance in mature plants in the
field was <u>A. moschatum</u> < <u>P. aspleniifolius</u> < <u>E. lucida</u> < <u>N.</u>
<u>cunninghamii</u> at 700 m elevation (Figs 7.12a & 7.13a), and <u>A.</u>
<u>moschatum</u> < <u>P. aspleniifolius</u> < <u>A. selaginoides</u> < <u>N.</u>
<u>cunninghamii</u> at 980 m elevation (Figs 7.12b & 7.13b). This
order remained generally consistent throughout the year,
although sometimes the difference between adjacent species
was small. This order is identical to that obtained in
plants artificially hardened (Fig. 7.9b), and also to the
unhardened plants if Nc980 is compared with <u>A. selaginoides</u>
rather than with Nc700 (Figs 7.8a & 7.9a).

The seasonal changes in frost resistance are shown in
detail in Figures 7.14 & 7.15. The monthly measurements of

trees at Mt Field commenced in August 1984, and some
dehardening had already occurred by the September
measurement in all species at both sites and continued, with
maximum sensitivity to most frost temperatures occurring in
December to February. In general, resistance to the lower
freezing temperatures decreased first and increased last. A.
moschatum and P. aspleniifolius from the low elevation
(Am700 and Pa700) and A. moschatum from the high elevation
(Am980) showed relatively little change in sensitivity to
-14°C throughout the year and Am700 showed little change in
sensitivity to -11°C. Foliage collected from 980 m exhibited
a greater degree of hardening than that of the same species
from the low elevation (Figs 7.12 & 7.13). This correlates
with the temperature differences between the sites in terms
of monthly maximum and minimum temperatures (Fig. 7.16),
although some genetic differences may also occur between the
populations, as indicated between the two populations of N.
cunninghamii in glasshouse experiments (Fig. 7.8). A.
selaginoides has a clear peak in sensitivity in December,
with hardening occurring by the January measurement (Fig.
7.15d). It is already fully hardened to -5°C by March. E.
lucida reaches a plateau in R_{-5} and R_{-8} in October with
relatively little change in sensitivity until April-May
(Fig. 7.14d). For other species, there is more than one
peak. These peaks are most frequent in the "sensitive" range
with high standard errors where samples are intermediate in
hardiness, and to some degree are artifacts of the error.
However the majority of troughs show correspondence among
species (notably the most frost-sensitive species) and
provenances, e.g. R_{-5} in November (Pa700, Am700) and April
(Pa700, Am700, Pa980, Am980). There is no clear trend of
temperature changes in the climatic data that account for
these sharp variations between monthly samples, but the data
collected at the sample sites shows only monthly maximum and
minimum temperatures (Fig. 7.16a), and the temperatures
experienced at Strathgordon (Fig. 7.16b) may not be
sufficiently similar to those at Mt Field to allow

extrapolation.

The R_{-2} values of Am700, Am980, Pa700, Pa980, El700 and Nc980 in January and February (and December in Pa700 and Pa980) are significantly different from the R_0 values. This temperature is ~~below~~ above the freezing temperature of the tissues although freezing may occur in the disc edges. The damage is unlikely to be caused by desiccation, since A. moschatum is relatively tolerant of desiccation (Chapter 8), but shows the most damage at -2°C.

The conductivity of killed tissue (L_D) per tissue dry weight varies seasonally in Am700, Pa700, and Am980, and to a lesser degree in As980 (Fig. 7.17). Pa 980, Nc700, Nc980 and El700 did not show any clear seasonal trends in conductivity per dry weight (Fig. 7.17). The peak values were recorded in October for As980 and Am980, and in November for Pa700. In Am700 there is a peak in October-November 1984, followed by a decline reaching a minimum value in January 1985, followed by a general increase to September. There does not seem to be any relationship between the seasonal solute levels and seasonal patterns of frost resistance.

The relative frost resistance of seedlings does not correlate exactly with frost resistance of mature foliage. Seedlings examined in January showed similar injury among species at -5°C but at -8°C and -11°C species separated out, with the order of frost resistance, Am700 < As980 < (El700 and Pa700) < (Nc700 and Nc980) (Fig. 7.18a). The major difference in these results compared with mature foliage measured in January, is the frost sensitivity of A. selaginoides seedlings. This was also observed in young unhardened seedlings raised in the glasshouse (Table 7.3) but was not observed in the older seedlings raised in the glasshouse (Fig. 7.9) and is probably due to the difference in seedling age, with the foliage of older seedlings being more typical of mature plants. In July (1985) the order of frost resistance of seedlings in the field was Am700 < (El700 and Pa700) < Nc700 < As980 < Nc980, with the greatest

Fig. 7.12   Frost resistance measured in adult foliage
from trees at Mt Field in August 1984.
Each point is calculated from five replicates.
a. Foliage collected at 700 m a.s.l..
b. Foliage collected at 980 m a.s.l..

N. cunninghamii: ●
A. moschatum: ▲
P. aspleniifolius: ◆
E. lucida: ■
A. selaginoides: □

a

b
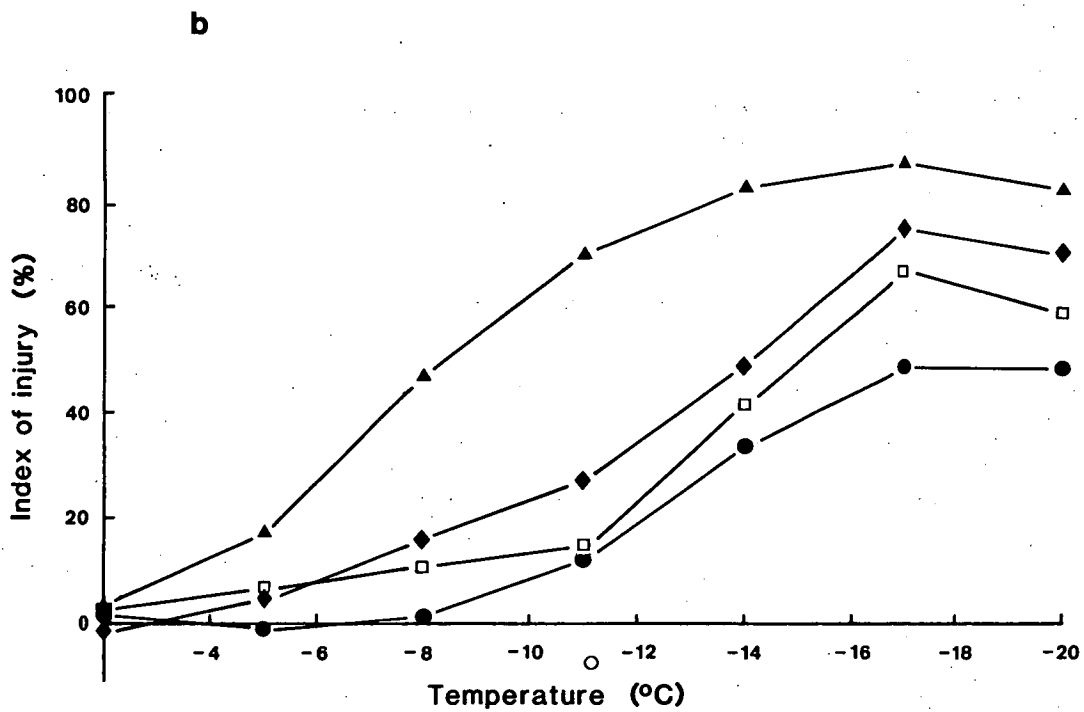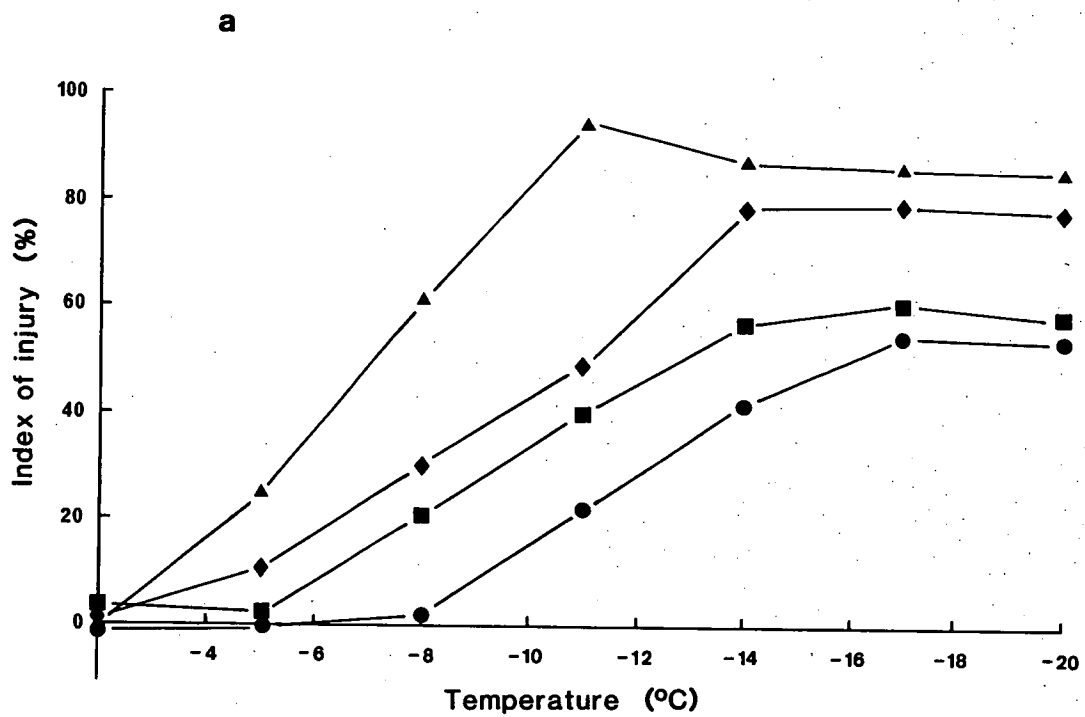
Fig. 7.13   Frost resistance measured in adult foliage
from trees at Mt Field in January 1985.
Each point is calculated from five replicates.
a. Foliage collected at 700 m a.s.l..
b. Foliage collected at 980 m a.s.l..

N. cunninghamii: ●

A. moschatum: ▲

P. aspleniifolius: ◆

E. lucida: ■

A. selaginoides: □
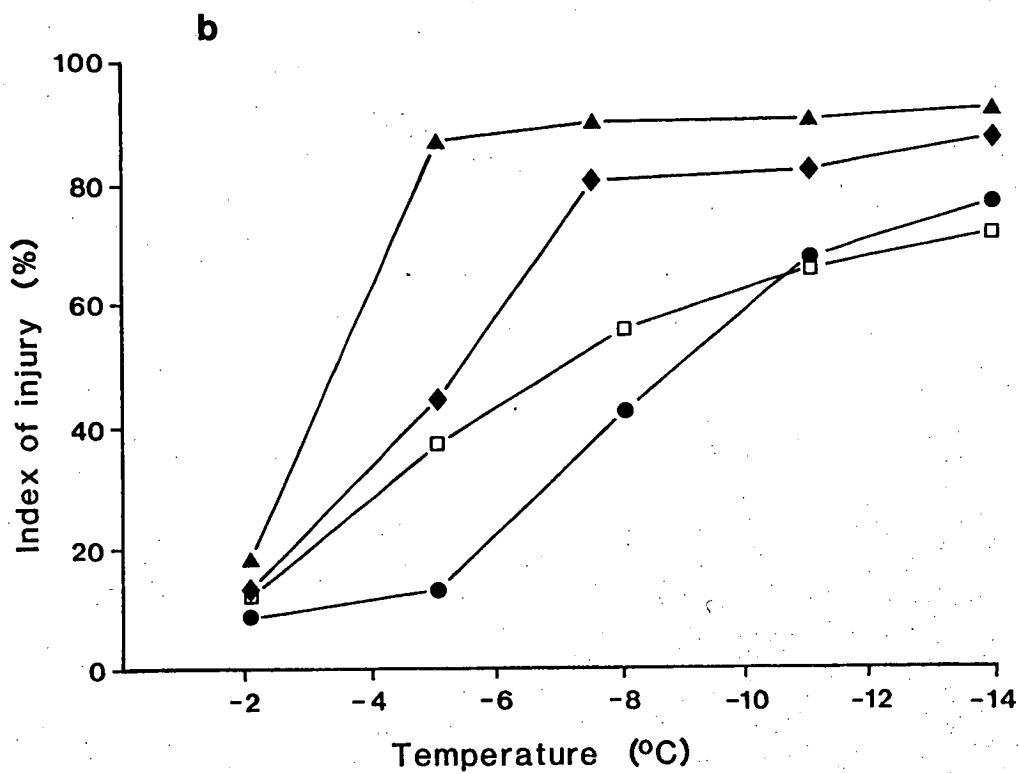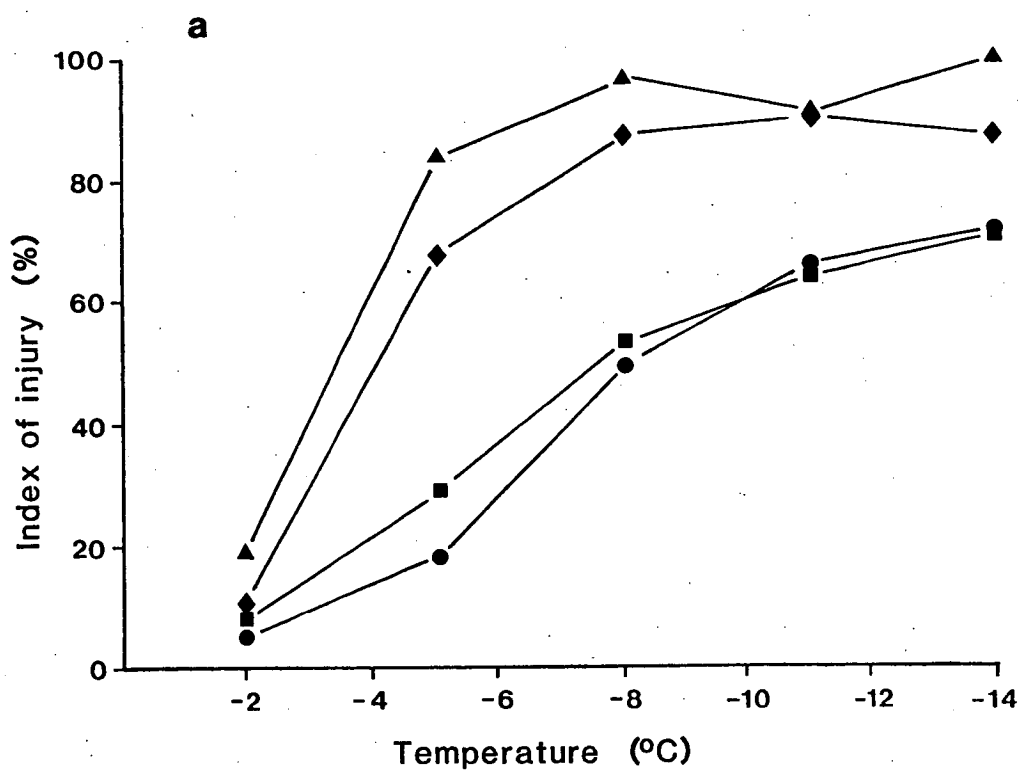
Fig. 7.14 Seasonal changes in frost resistance measured
in adult foliage from trees growing at 700 m a.s.l. at
Mt Field. Each point is the mean of five replicates,
with standard errors shown where they are $\geq$ 0.03.
a. <u>N. cunninghamii</u>
b. <u>A. moschatum</u>
c. <u>P. aspleniifolius</u>
d. <u>E. lucida</u>.

R_0: △
R_{-2}: ■
R_{-5}: ○
R_{-8}: ▲
R_{-11}: □
R_{-14}: ●

a

Relative conductivity vs Month

A S O N D J F M A M J J A S
1984   1985
Month

b

Relative conductivity vs Month

A S O N D J F M A M J J A S
1984   1985
Month

c

Relative conductivity vs Month

A S O N D J F M A M J J A S
1984   1985
Month

d

Relative conductivity vs Month

A S O N D J F M A M J J A S
1984   1985
Month
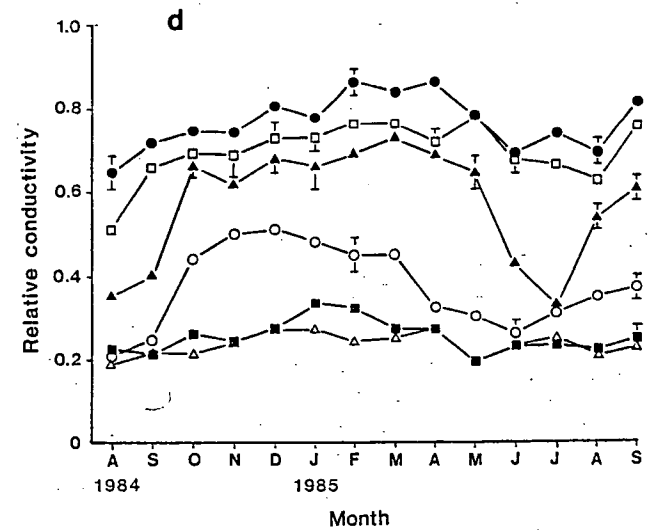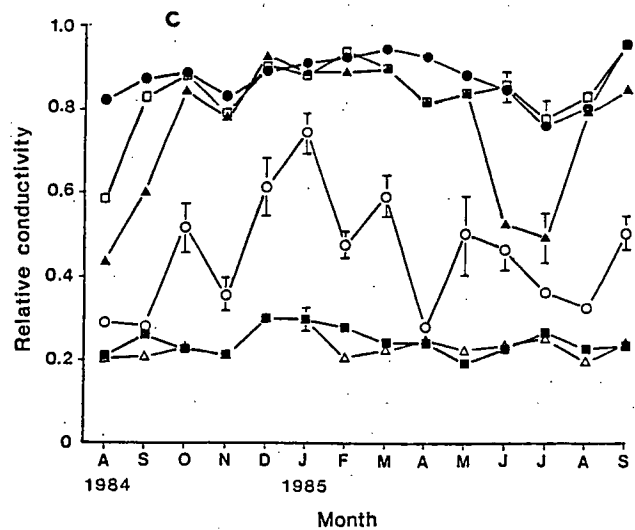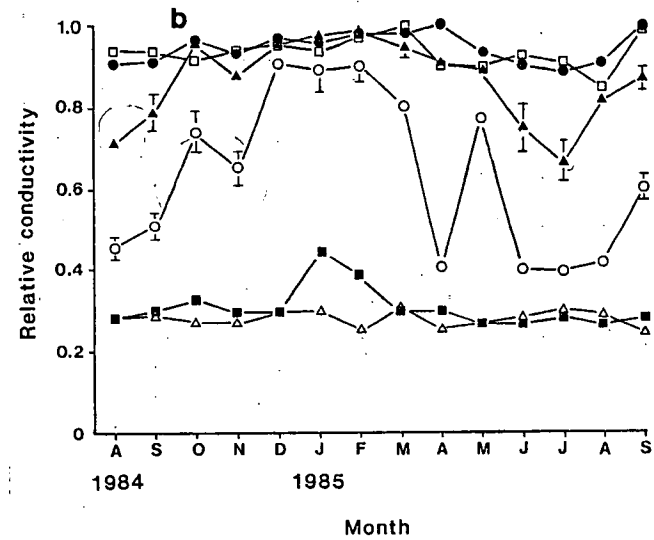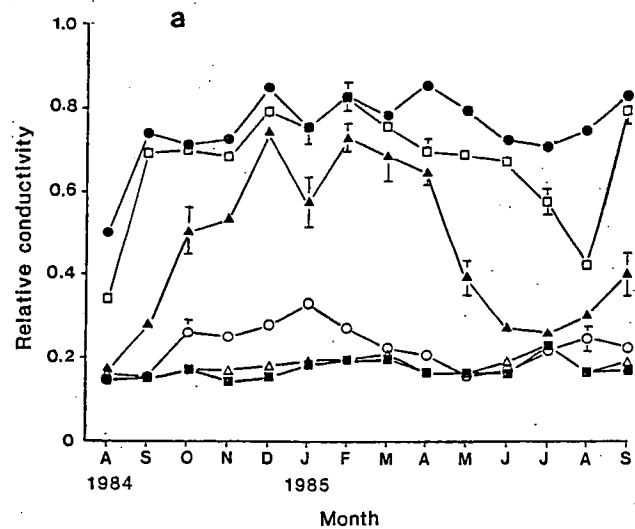
Fig. 7.15   Seasonal changes in frost resistance measured
in adult foliage from trees growing at 980 m a.s.l. at
Mt Field. Each point is the mean of five replicates,
with standard errors shown where they are $\geq$ 0.03.

a. <u>N. cunninghamii</u>
b. <u>A. moschatum</u>
c. <u>P. aspleniifolius</u>
d. <u>A. selaginoides</u>.

R_0:   △
R_{-2}:   ■
R_{-5}:   ○
R_{-8}:   ▲
R_{-11}:   □
R_{-14}:   ●
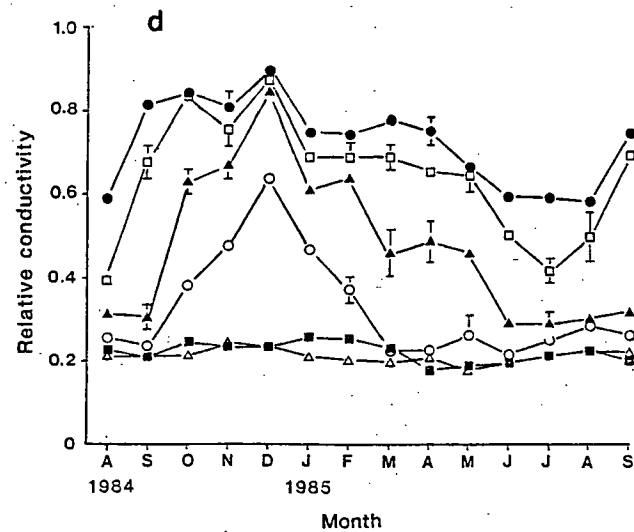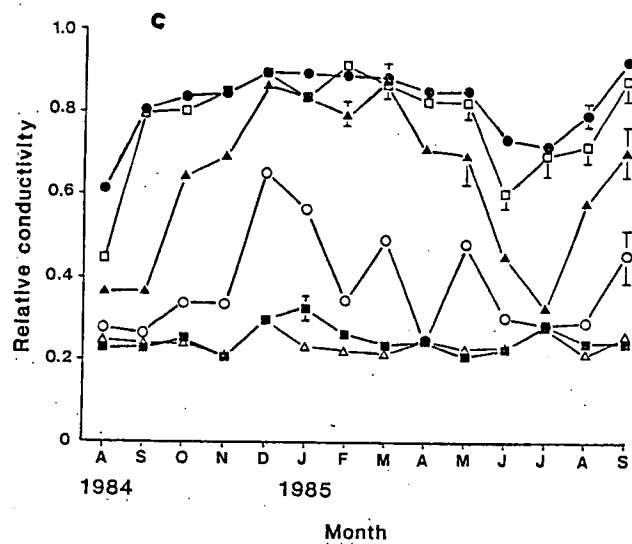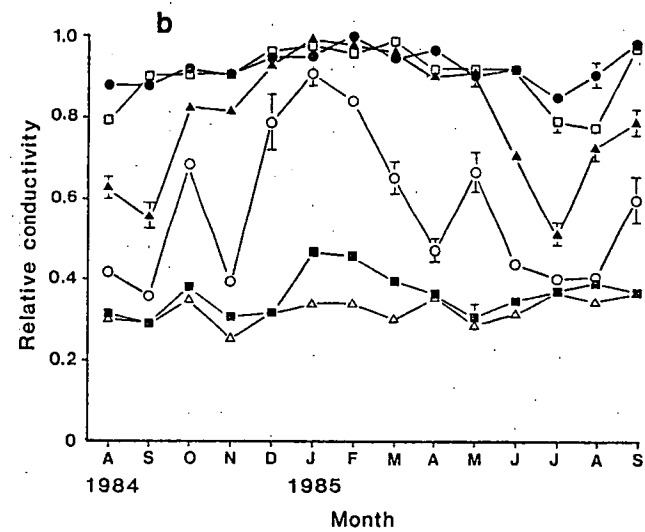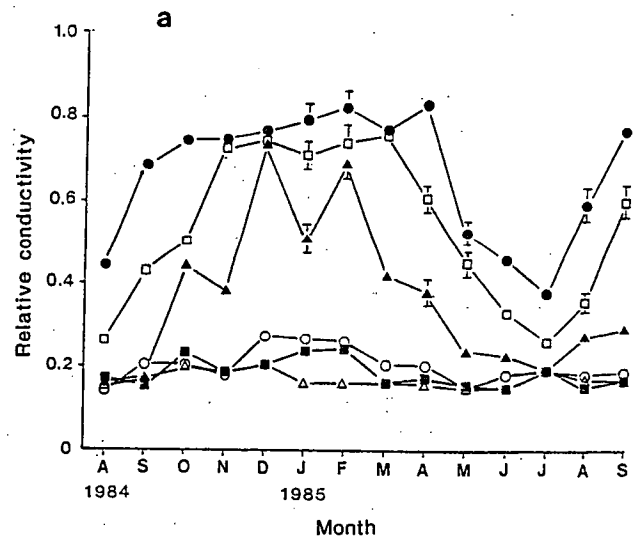
Fig. 7.16   Seasonal temperature characteristics.

a. From maximum-minimum thermometers at 700 m a.s.l. (△)
and 980 m a.s.l. (▲), at Mt Field.

Monthly maximum (——), monthly minimum (– – –).

b. From Bureau of Meteorology records for Strathgordon,
the closest station at which records are kept year-round.

Mean monthly maximum (—▲—), and minimum (--▲--).

Mean maximum (—△—) and minimum (--△--) for the seven
days prior to sampling.
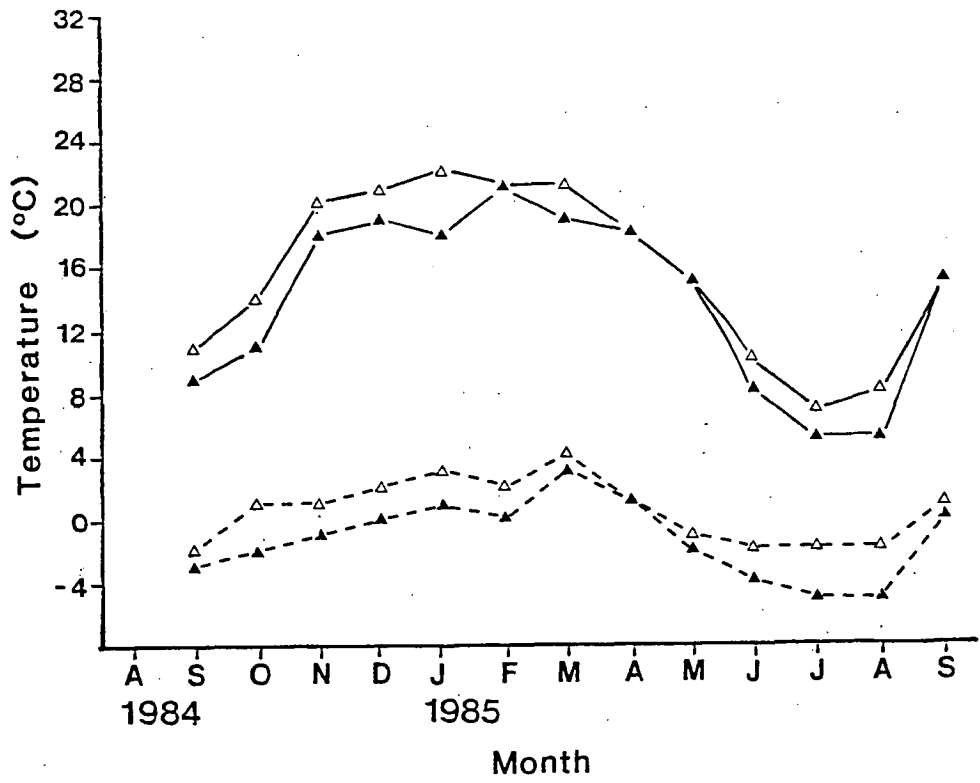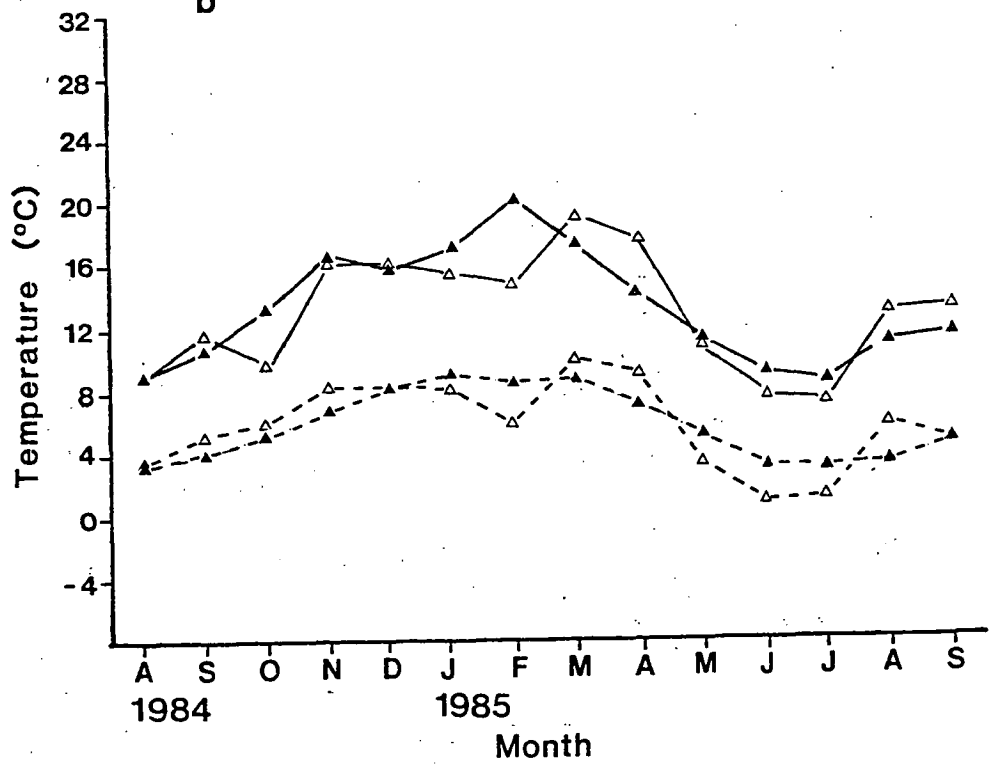
Fig. 7.17   Seasonal changes at Mt Field in the mean
conductivity of killed tissue (in 8 ml of water) (L_d)
expressed on the basis of the dry weight of the sample.
Standard errors are shown where they $\geq$ 0.3.
a. Samples from 700 m
b. Samples from 980 m

N. cunninghamii: ●
A. moschatum: ▲
E. lucida: ■
P. aspleniifolius: ◆
A. selaginoides: □

a

b
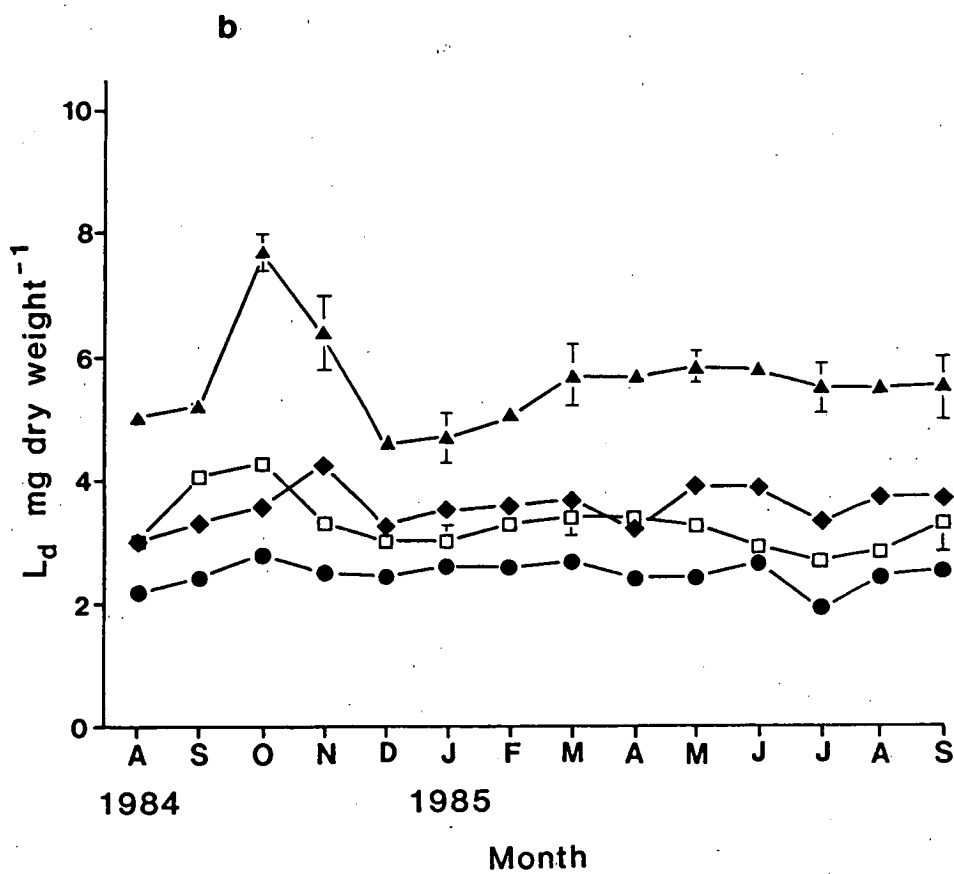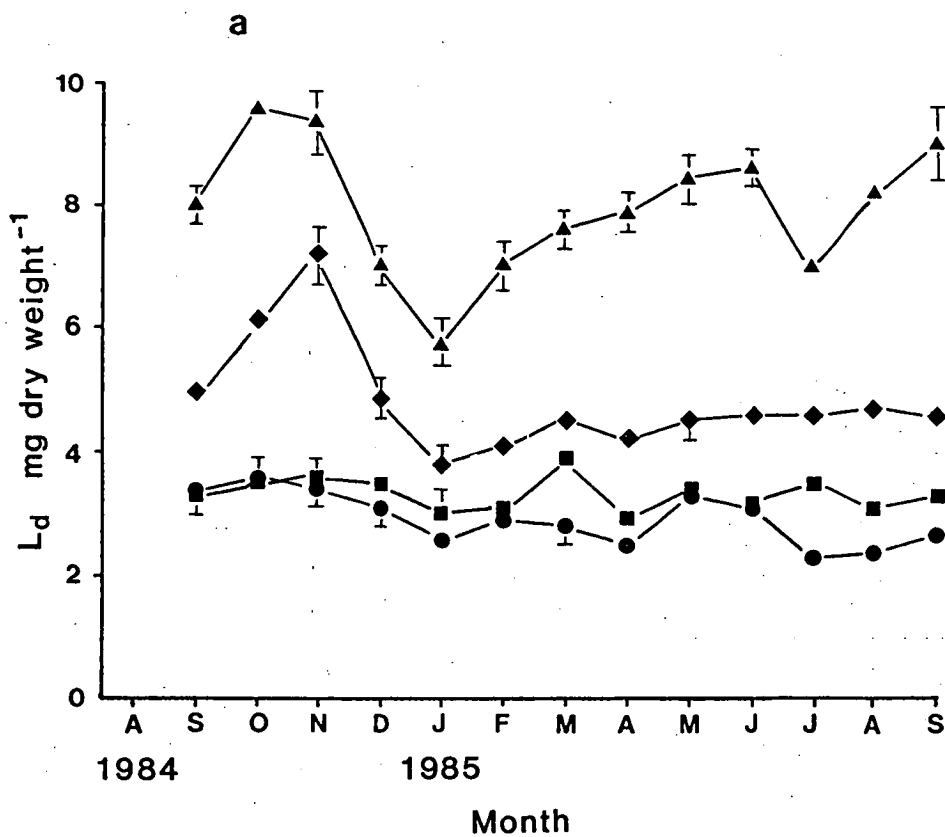
Fig. 7.18   Frost resistance of two-year-old seedlings.
Each point is calculated from five replicates.
a. January 1985
b. July 1985.

N. cunninghamii from 700 m: —●— ; 980 m:--○--
A. moschatum from 700 m: —▲—
E. lucida from 700 m: —■—
P. aspleniifolius from 700 m: —◆—
A. selaginoides from 980 m: --□--
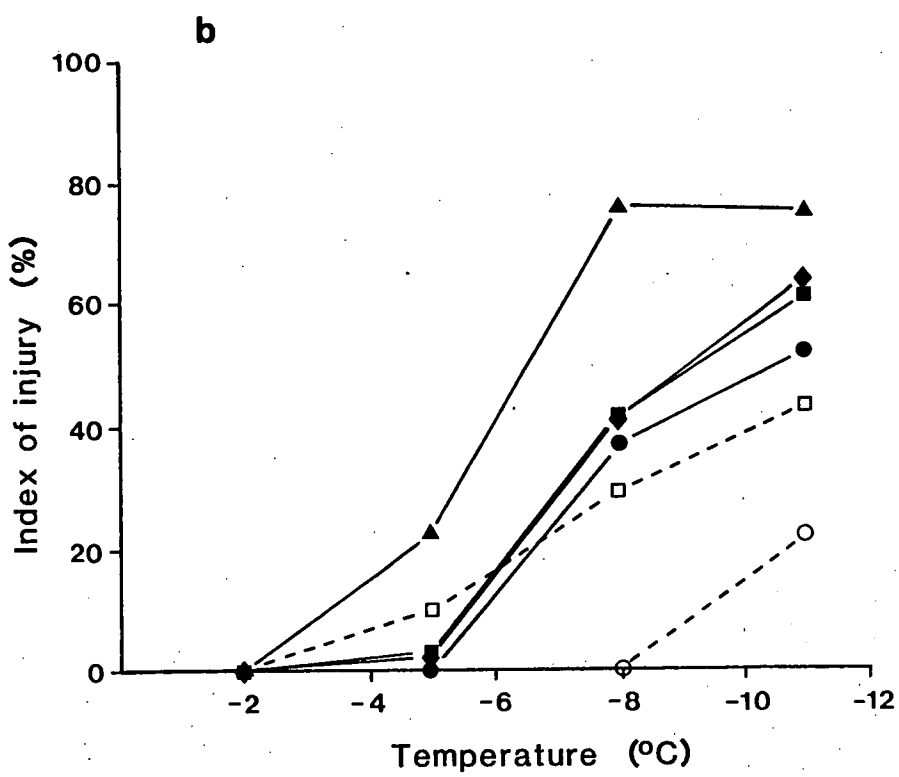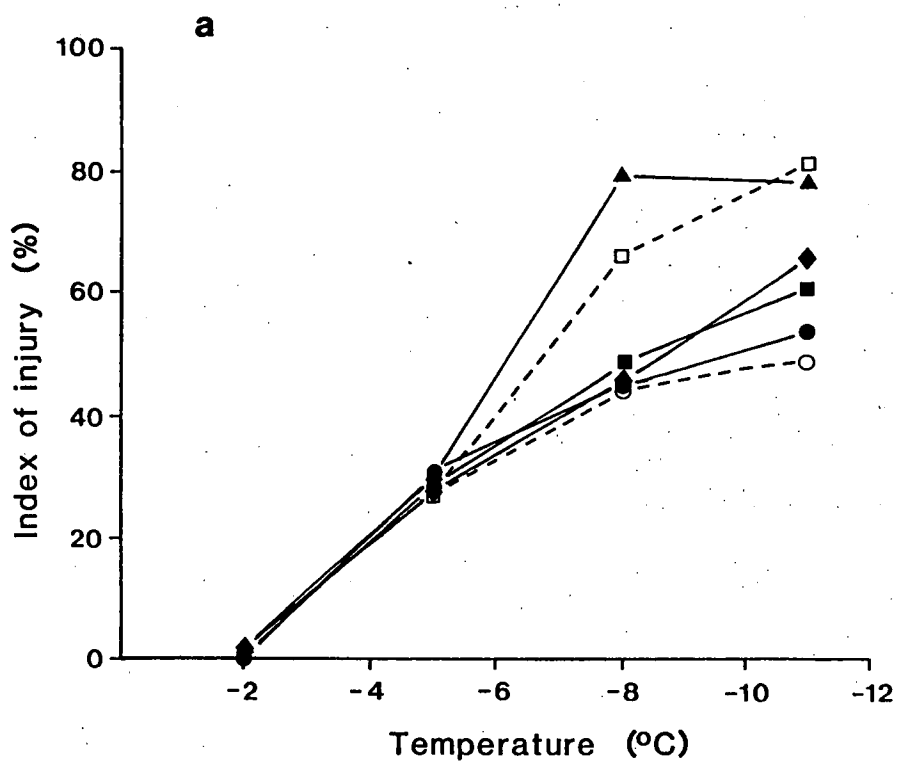
Fig. 7.19   Frost resistance of seedling (o) and adult
(●) foliage for each species measured in July 1985.

a. <u>N. cunninghamii</u> from 700 m.

b. <u>N. cunninghamii</u> from 980 m.

c. <u>A. moschatum</u> from 700 m.

d. <u>P. aspleniifolius</u> from 700 m.

e. <u>E. lucida</u> from 700 m.

f. <u>A. selaginoides</u> from 980 m.
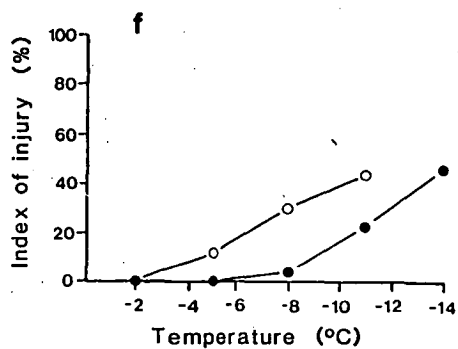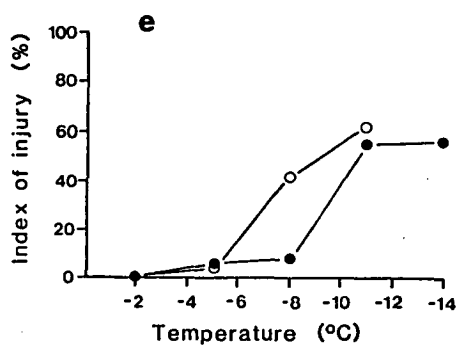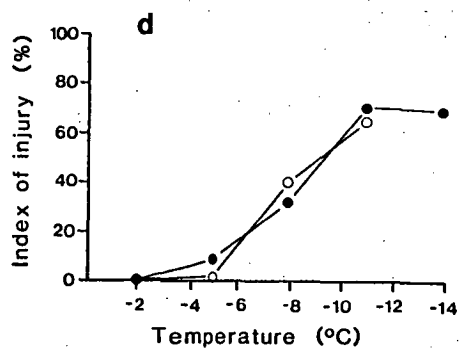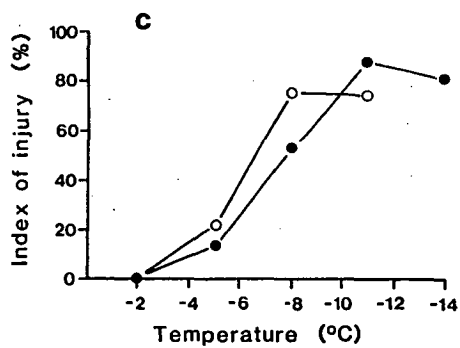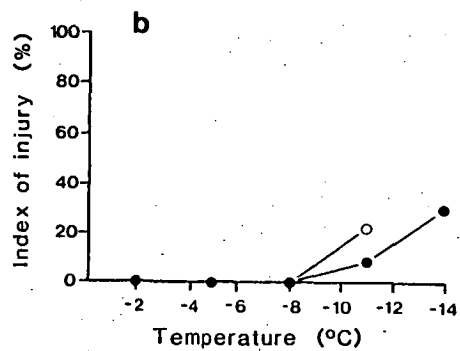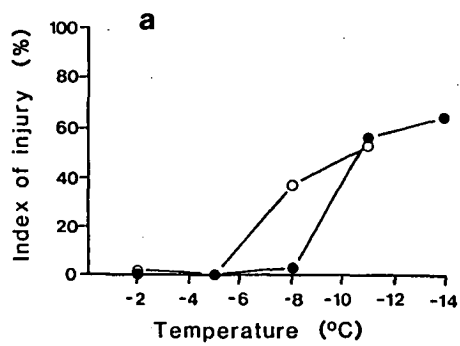
degree of hardening occurring in Nc980 and As980 (Fig. 7.18b). In all species except P. aspleniifolius, frost resistance is lower in seedling foliage than mature foliage in plants examined in July (Fig. 7.19). In P. aspleniifolius, phylloclades are the predominant form of foliage in the mature plant, compared with leaves in the young seedling, and therefore the foliage varied in type as well as ontogeny. The seedling measurements taken in January were at a different time of the month than the measurements of the mature plants and therefore cannot be strictly compared.

Discussion

Although a general trend of frost resistance in the order A. moschatum < P. aspleniifolius < E. lucida < A. selaginoides < N. cunninghamii was observed, there are several diversions from this pattern, e.g. the low frost resistance of A. selaginoides seedlings at Mt Field in January, and the very similar frost resistance of adult foliage of N. cunninghamii and A. selaginoides recorded during some winter months at Mt Field. Adult foliage of A. selaginoides from Mt Field also shows a greater degree of dehardening in summer than N. cunninghamii from the same altitude, although in winter there is relatively little difference in the frost resistance of these two species. These species were sampled at only the lower end of the altitudinal range of A. selaginoides, so it is possible that A. selaginoides has provenances at higher altitudes or on more exposed sites that may exceed N. cunninghamii in winter frost resistance, or that it is able to harden more than N. cunninghamii under more severe low temperatures than were experienced during the observation period.

The photosynthetic responses to temperature are similar to those obtained in other studies of plants from cool temperate environments, in the optima recorded and in the breadth of the temperature-dependence curves. Berry &

Björkman (1980) noted that even cold-adapted plants from
extreme environments may not reach their temperature optimum
until 15-20°C and may have a broad temperature-dependence
curve. The impact of the growth light regime on the
photosynthetic responses to temperature is uncertain in
these species. However, even with these restricted results,
there are distinct correlations between these responses and
the altitudinal distributions of the species (Table 7.1).
Photosynthetic responses to temperature and frost resistance
potentially determine the habitat and regeneration niche of
species by directly affecting survival, and by indirectly
affecting survival by carbon balance and the competitive
force of the species relative to other species in its
establishment environment. There is no attempt to
distinguish between these features in this discussion, and
it is acknowledged that the effect of temperature on
reproductive capacity of a species is also important.
However, the "susceptibilities" do indicate the environment
of which the plant is tolerant and therefore to which it is
adapted (Grime 1965).

The photosynthetic responses of N. cunninghamii after a
conditioning regime of constant temperature do not indicate
any consistent pattern of superior photosynthetic tolerance
to changing temperatures that might be expected from its
broad altitudinal distribution. However, N. cunninghamii
seedlings which are acclimated to natural fluctuating
temperatures are relatively tolerant of instantaneous
changes in temperature. While this suggests that fluctuating
temperatures are important in the temperature tolerance of
N. cunninghamii, other factors such as the light conditions
of the conditioning regime may have an interacting effect on
the photosynthetic responses to temperature. N. cunninghamii
is consistently the most frost resistant species, in both
the hardened and unhardened state, and at both the seedling
and adult stage. This is consistent with the broad
altitudinal distribution of this species and with its
ability to establish and grow competitively on exposed sites

such as those created by disturbance. There is no evidence
of reduced photosynthetic capacity at high temperatures
relative to A. moschatum that can easily explain the absence
of N. cunninghamii from the northern distributional range of
A. moschatum e.g. Errinundra Plateau, Clyde Mt. and
Barrington Tops. Differences between the climate of these
sites and sites where N. cunninghamii does occur are not
well described and may involve other features than
temperature. If temperature differences between these sites
are significant, it is probably more relevant to compare the
temperature responses of N. cunninghamii with the
temperature response of northern species which occupy a
similar regeneration niche, e.g. Nothofagus moorei and
Eucryphia moorei, than with the shade-tolerant A.
moschatum.

The sensitivity of A. moschatum to low temperatures in
terms of a relatively high temperature required for maximum
photosynthesis, a low rate of net photosynthesis at
instantaneous low temperatures, limited acclimation to low
temperatures, and the relatively high frost sensitivity of
seedling and adult foliage in both hardened and unhardened
state, is consistent with its relative infrequency at high
altitudes (Table 7.1) and its infrequent establishment on
exposed sites (Chapter 2). It is also consistent with the
shade-tolerance and typical absence of this species from the
upppermost region of the forest canopy (Chapter 2). A.
moschatum has a narrow photosynthetic temperature optimum,
and this lies within the optimal temperature range of the
other species, with the exception of A. selaginoides with
which it overlaps. Therefore its wide latitudinal range
(northwards) relative to the other lowland Tasmanian
rainforest canopy species is not simply explained by
temperature optima, and may relate to interacting components
of the climate, competitive ability with respect to species
of similar regeneration niche, or as Howard & Ashton (1973)
suggested, to historical factors such as superior dispersal
and the consequent ability to cross dry corridors.

P. aspleniifolius has a photosynthetic tolerance of
temperature that is similar to that of E. lucida, yet
seedlings from 700 m at Mt Field of P. aspleniifolius are
frost sensitive relative to E. lucida. However no
comparative measurements of these species have been made of
plants from higher altitudes, and it is possible that the
comparative reponses of these two species may reverse at
higher altitudes. P. aspleniifolius occurs at high altitudes
more often than E. lucida (Table 7.1). There is no clear
evidence from these results to explain the absence of these
two species from Victorian rainforest in terms of their
tolerance of the temperature regime.

A. selaginoides has the lowest temperature optimum and
shows relatively little decline in the net rate of
photosynthesis at low temperatures. It has the greatest
sensitivity to high instantaneous temperatures, even after a
conditioning regime of 25°C. These responses are consistent
with its current distribution predominantly above 600 m
(Table 7.1). However the current distribution has also been
related to the incidence of fire and logging (Kirkpatrick
1977a, 1977b) and therefore its infrequency on lowland sites
may reflect greater accessibility to some degree, as well as
a climatic influence on fire frequency. Although adult
foliage of A. selaginoides also has a high frost resistance,
surpassed only by N. cunninghamii in this study, its
seedlings are relatively frost sensitive in summer. This may
explain in part at least the observation by Kirkpatrick &
Harwood (1980) that A. selaginoides required nurse plants
for establishment after fire at Mt Bobs. The dehardening of
A. selaginoides seedling and adult foliage might also be
expected to affect its growth in areas experiencing late and
early frosts, relative to N. cunninghamii, but no relevant
field data is available.

Chapter 8   Plant resistance to water deficit stress

Introduction

Plant responses to low water availability vary widely among species from different habitats (Levitt 1980). Variation also occurs among species of different successional status from the same habitat, with early successional plants commonly better adapted to withstanding water (deficit) stress than late successional plants typical of mature forest (Bazzaz 1979). This indicates the possible importance of differential resistance to water stress in determining the distribution of rainforest species, particularly in areas of marginal rainfall, by its effect on both their habitat and regeneration niches. Three particular aspects of their distribution and regeneration are of interest and may be related to differential resistance to water stress:

1. The occurrence of A. moschatum in gullies in sclerophyll forest in the absence of other rainforest canopy species (Jackson 1983).

2. The low incidence of A. moschatum regeneration from seed within rainforest (Chapter 2).

3. The particularly high seedling numbers of N. cunninghamii, P. aspleniifolius and E. lucida on many disturbed sites (where there is an abundant seed source) such as road edges and burnt forest.

In this chapter, responses to water availability are examined in N. cunninghamii, A. moschatum, E. lucida, P. aspleniifolius and A. selaginoides, and the results are discussed in terms of the habitat and regeneration niches of the species.

Materials and methods

1. Tolerance of water deficit (drought) stress in detached foliage.

In this experiment, leaf tissue was dehydrated in micro-desiccators and the tissue damage resulting from the particular level of dehydration is determined by measurement of the electroconductivity of exosmosed solutes.

Leaves (phylloclades in P. aspleniifolius) were collected in March 1985 from three year-old plants growing outdoors in a shadehouse under a canopy of approximately 60% cover formed by eucalypt forest. The leaves selected had been produced in the previous growing season, i.e. were approximately 15 months old. Leaves were taken from three plants of each species. Discs of 6 mm diameter were cut from the leaves, and (keeping discs from each plant separate) were floated on distilled water for one hour at $18^{O}C$. This was sufficient time for the tissue to reach full turgor. One disc was taken from each plant of a particular species to give an experimental unit of three discs. Each unit was weighed to give the turgid weight (TW). Units were then placed in micro-dessicators in which the discs were laid on fine nylon mesh 8 mm above the surface of salt solutions of known water potentials as described by Slatyer (1958). These were placed under fluorescent and incandescent lights (55 μmol quanta $m^{-2}s^{-1}$) at $22^{O}C$. Discs were removed from the micro-desiccators after 3-12 hours. Equilibration of the tissue with the vapour over the solution was not always achieved prior to disc removal, and was not considered important since the objective was to provide a slow dehydration of tissue that enabled a reliable correlation between tissue water status and damage, rather than a measure of tissue water potential.

Each unit of tissue was weighed immediately after removal from the micro-desiccator to give the fresh weight (FW) and placed into a glass vial containing 8.0 ml of distilled water. The relative conductivity of each tissue unit was measured using the method described in Chapter 7. The tissue units were then dried at $90^{O}C$ for 24 hours and dry weight (DW) measured. There was no difference in the

turgid weight:dry weight ratio of discs dried immediately after cutting and discs dried after dehydration and conductivity measurements. The relative water content, RWC, (= relative turgidity) was calculated as

$$\frac{FW - DW}{TW - DW} \times 100 \qquad \text{(Weatherley 1950)}$$

The conductivity method of measuring tissue damage has been widely used to measure damage resulting from freezing stress but has not to my knowledge been used to measure tissue damage caused by dehydration. The method is based on the exosmosis of solutes from damaged cells and therefore should be widely applicable as a measure of any stress affecting membrane permeability. This method has not been tested against other methods used in the determination of tissue damage from dehydration. Visual methods of assessment of damage as used by Ashton et al. (1975) were of no value due to the lack of any visual change which could be accurately quantified. The major change in appearance was shrivelling of the tissue. Controls necessary for the calculation of the index of injury, I_{RT}, consisted of five replicates of units of three hydrated discs, one disc from each plant, which were each placed in vials containing 8.0 ml of distilled water, with the measurement of relative conductivity as described in Chapter 7.

2. Avoidance of water deficit stress -
the relationship between plant
RWC and water potential.

In this experiment, the relationship between plant RWC and water potential was measured across a range of soil water deficits.

Seed of A. moschatum, N. cunninghamii, E. lucida and A. selaginoides from Mt Field (42°41$^{\prime}$S 146°40$^{\prime}$E) was germinated and the seedlings of these plants and P. aspleniifolius cotyledonary seedlings collected from Mt Field (at the seed collection site) were transplanted into sandy loam soil in 3

cm diameter black plastic pots. Twenty seedlings of each
species were grown for 17 weeks in the glasshouse, watered
once per day. The seedlings were then watered, allowed to
drain for one hour, and then the pots were wrapped in
plastic to enclose the pot and the soil surface, with the
shoot protruding. This ensured a slow rate of water loss
from the soil with the rate dependent on evapotranspiration
from the plants. At intervals over the next two months,
plants were selected from each species, a shoot section was
cut and the shoot water potential was measured using a
Scholander pressure bomb. Leaf discs, or leaf sections in
the case of A. selaginoides and P. aspleniifolius, were cut
for the measurement of RWC. Measurements were made at dawn,
when plant water status was relatively steady.

This experiment was repeated using three-year-old plants
with adult foliage. Five plants of each species which had
been grown in sandy loam soil and watered daily, were
prepared as described above. Five lateral shoots were
removed at intervals over the following six weeks from each
plant and the shoot water potential and RWC was measured.

3. Avoidance of water deficit stress -
The rate of water loss from detached foliage.

Detached leaves of N. cunninghamii, E. lucida and A.
moschatum, and phylloclades of P. aspleniifolius, were
allowed to dehydrate and diffusive conductance at the leaf
surface and RWC were measured at regular time intervals. A.
selaginoides was not included in this experiment because its
leaf and shoot morphology prevents accurate measurement of
diffusive conductance using a porometer. Consequently the
experiment was repeated using foliage weight changes to
indicate rates of water loss.
a. Ten leaves were taken in December 1983 from each of three
three-year-old seedlings grown outdoors in a shade-house for
18 months. The leaves chosen were approximately one-year-old
(previous season's growth). These were placed with petioles

in water under shade at room temperature for two hours to
ensure full turgor, and then, still in water, were placed in
a controlled environment growth cabinet at 25°C at a light
intensity of 150 umol quanta $m^{-2}s^{-1}$ and relative humidity of
38% until the stomata were fully open. The leaves were then
placed at random, stomatal surface facing downwards, on a
fine nylon mesh stretched over a wire frame in the same
growth cabinet. At half to one-hourly intervals, diffusive
conductance was measured using a Li-Cor Li-700 Transient
Porometer and discs were taken from the leaf for measurement
of RWC, from one leaf from each replicate plant. These
values were also recorded from a sample of leaves
immediately on removal from water (time = 0).

b. One leaf of N. cunninghamii, A. moschatum, E. lucida and
P. asplenifolius (phylloclade) and one shoot section 3 cm
long of A. selaginoides was taken in September 1984 from
each of five three-year-old seedlings grown outdoors in a
shade-house for 24 months. The leaves chosen were
approximately one-year-old (previous season's growth). The
foliage was placed with petioles or stems in water in shade
at room temperature for two hours and subsequently under a
light intensity of 150 umol quanta $m^{-2}s^{-1}$ at 20°C and 32%
relative humidity in a controlled environment growth cabinet
until the stomata were fully open. The foliage was then
removed from the water, weighed (turgid weight), and placed
at random on a fine nylon mesh stretched over a wire frame
in the growth cabinet with the stomatal surface facing
downwards, except for A. selaginoides which was laid
horizontally. All samples were weighed at 13 minute
intervals for the first hour and at 15 to 20 minute
intervals for the next two hours. All foliage was then dried
at 90°C for 24 hours and weighed. Transpiration was
calculated as

$$\frac{W_1 - W_2}{W1} \cdot hour^{-1}$$

where W_2 is the current weight of the foliage and W_1 is the
weight of the foliage at its previous measurement. The

transpiration and RWC values of the five replicates were
averaged for each species.

Results

Tolerance of water deficit stress

Tissue damage, as determined by the exosmosis of
solutes, responds exponentially to decreasing tissue RWC
(Fig. 8.1). A. moschatum has a greater tolerance of
decreasing tissue water content than the other species, with
no significant damage occurring to 60% RWC (Fig. 8.1a).
There was no clear difference in tolerance of water deficit
among the other species (Fig. 8.1).

Avoidance of water stress

The relationship between RWC and shoot water potential
in seedlings exposed to decreasing soil water content varied
among the species. N. cunninghamii seedlings developed a
relatively low shoot water potential with small changes in
relative water content (Fig. 8.2b). A. selaginoides required
a much larger decrease in RWC to effect the same decrease in
shoot water potential (Fig. 8.2b). A. moschatum, E. lucida
and P. asplenifolius were intermediate between the former
species in their response and could not be separated (Fig.
8.2). A notable feature of this experiment was the failure
to record live N. cunninghamii seedlings with RWCs below 65%
(Fig. 8.2b). Seedlings of A. moschatum were alive to 35%
RWC, P. aspleniifolius and E. lucida were alive down to
40-45% RWC, and live A. selaginoides seedlings were recorded
to RWCs down to 52% (Fig. 8.2). Attempts were made to
measure seedlings with lower water contents but in each case
the seedlings died (8-15 for each species) prior to
measurement. Similar results were obtained from the
three-year-old seedlings with adult foliage except that P.
aspleniifolius was intermediate between E. lucida/A.

Fig. 8.1   Tissue damage resulting from dehydration of
foliage discs or segments in microdesiccators. The
index of injury is calculated from the conductivity of
exosmosed solutes from damaged tissue (see Chapter 7).

a. A. moschatum
b. N. cunninghamii
c. E. lucida
d. P. aspleniifolius
e. A. selaginoides.
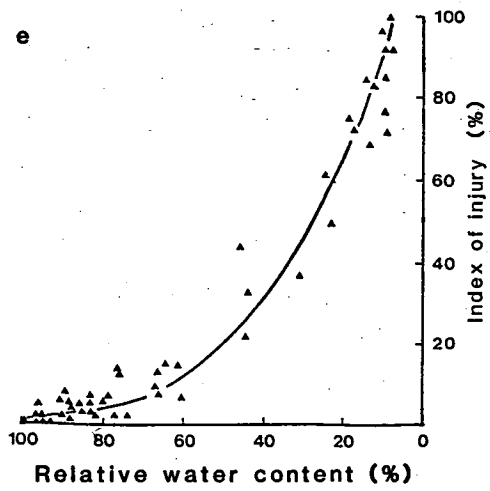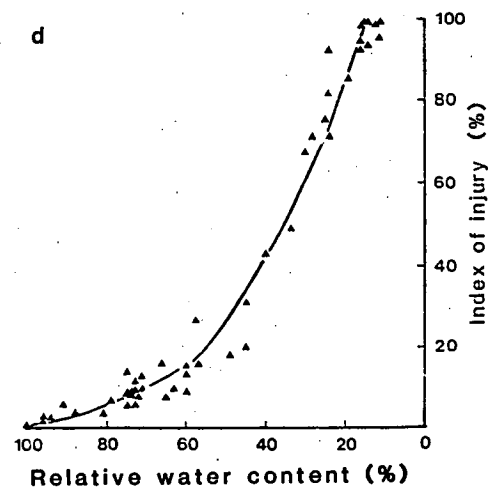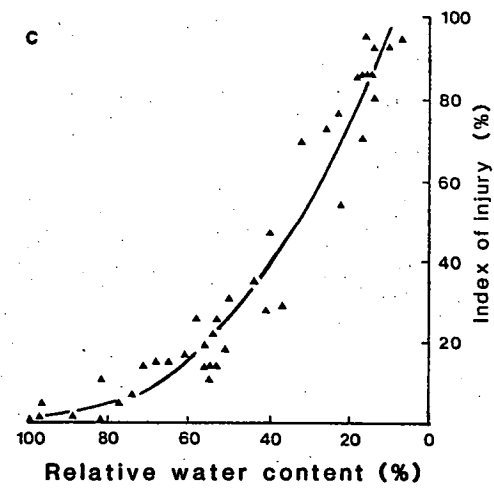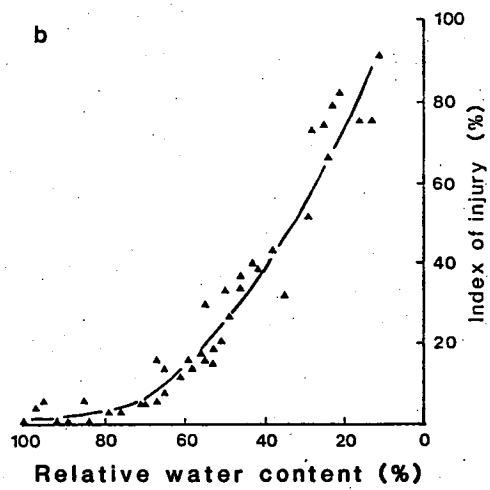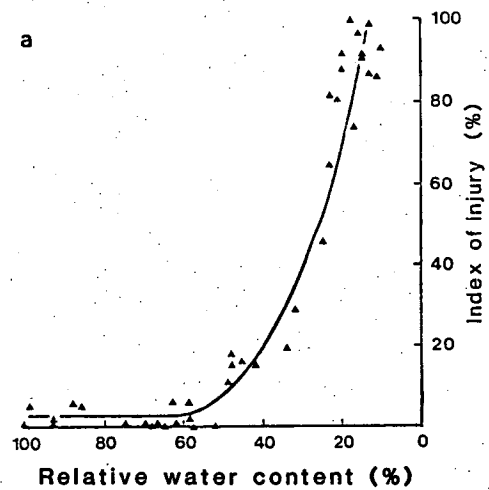
Fig. 8.2   The relationship between relative water
content and water potential in six-month-old seedlings
exposed to slow droughting.

a. <u>P. aspleniifolius</u>:   ▽

    <u>E. lucida</u>:   ■

b. <u>N. cunninghamii</u>:   ●

    <u>A. moschatum</u>:   ▼

    <u>A. selaginoides</u>:   □

a

Relative water content (%)

Shoot water potential (-MPa)

b

Relative water content (%)

Shoot water potential (-MPa)
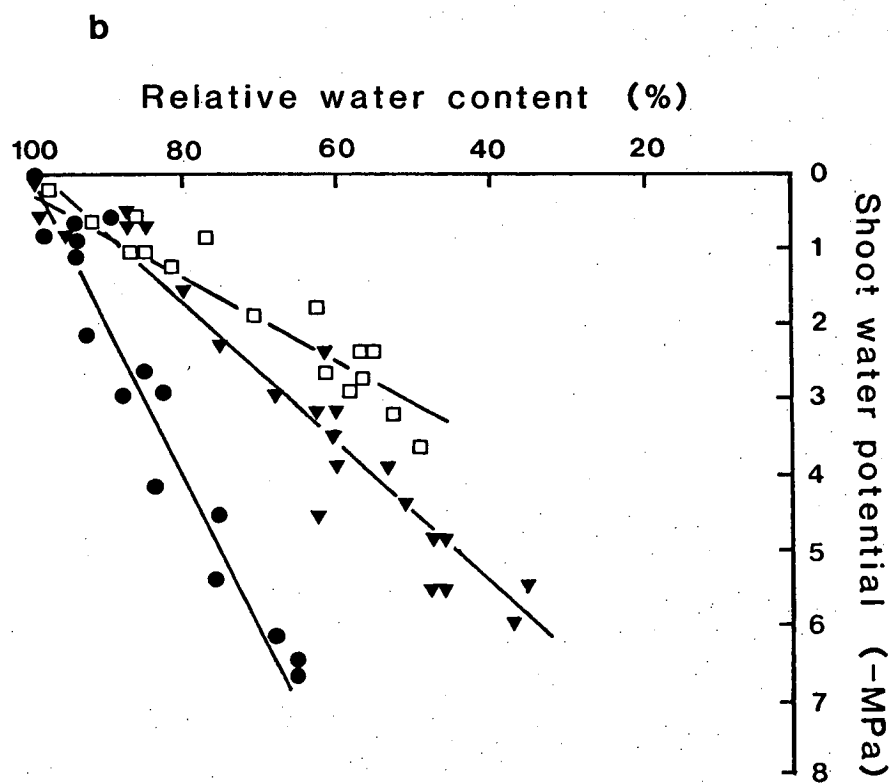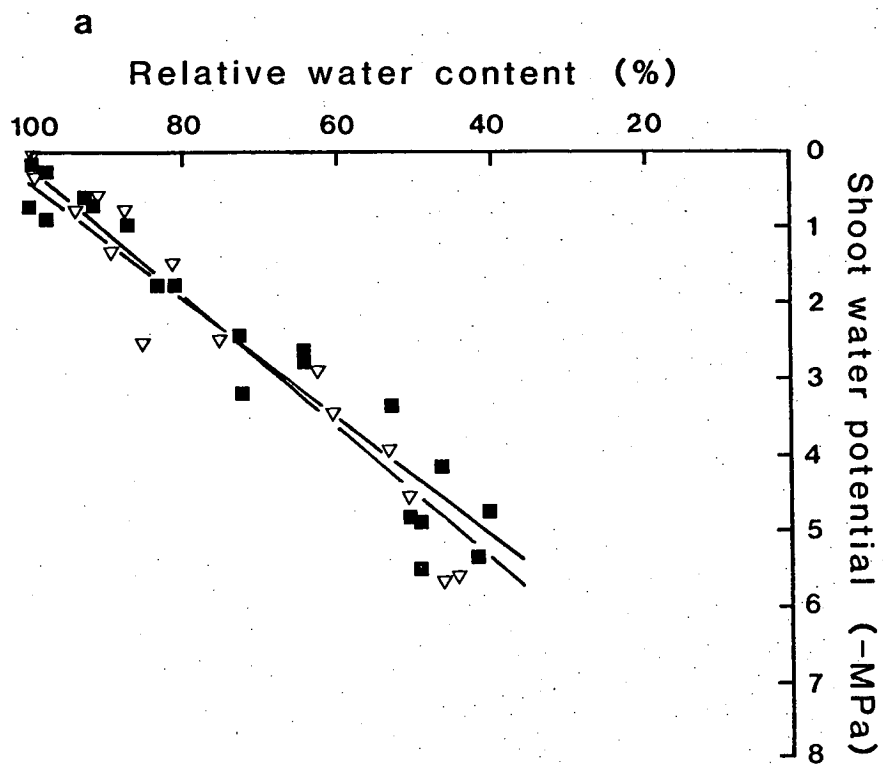
Fig. 8.3   The relationship between relative water
content and water potential in three-year-old seedlings
exposed to slow droughting.

a. P. aspleniifolius: Δ

    E. lucida: ■

b. N. cunninghamii: ●

    A. moschatum: ▲

    A. selaginoides: □

a

Relative water content (%)

Shoot water potential (-MPa)

b

Relative water content (%)

Shoot water potential (-MPa)
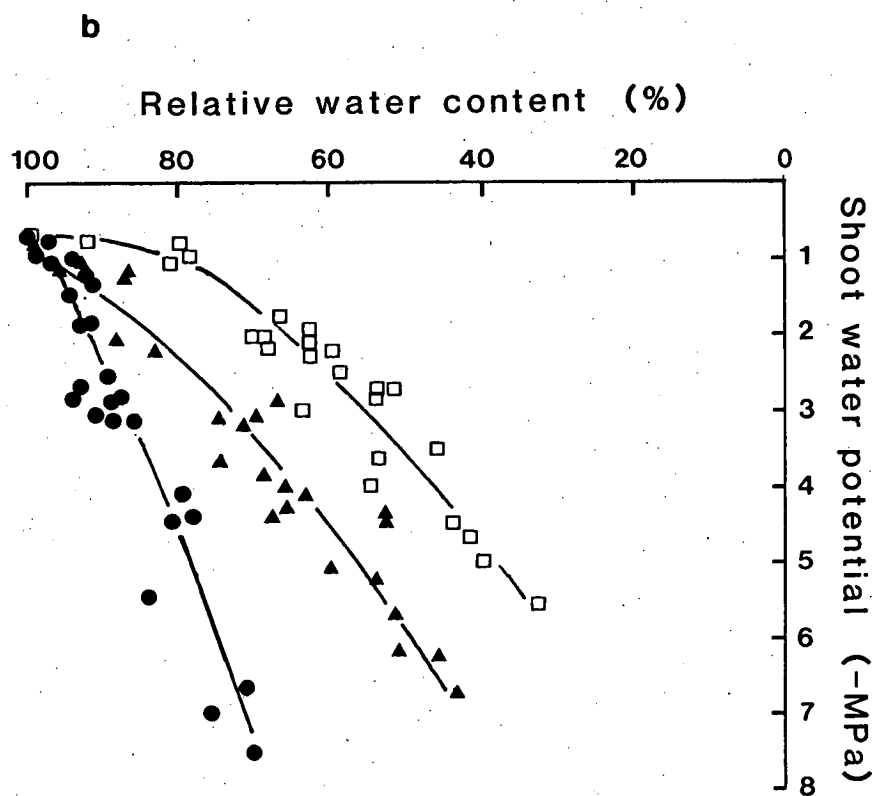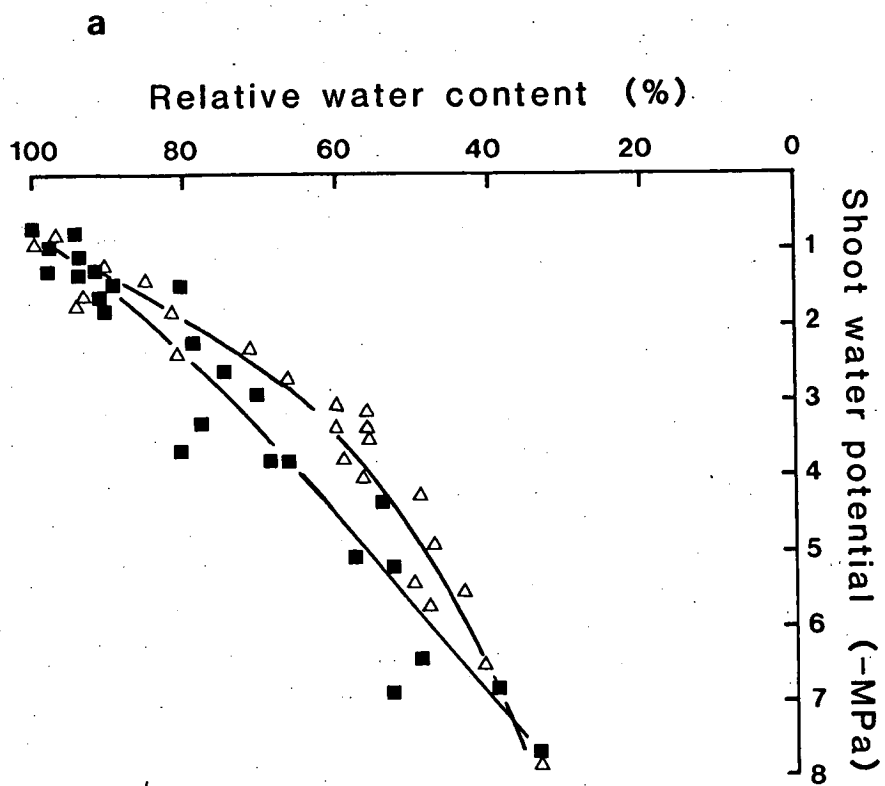
moschatum and A. selaginoides in its response curve (Fig. 8.3). The critical RWCs at which plant death occurred could not be accurately determined because of the small number of plants. However, plants which developed water potentials of -5.5--7.8 MPa, were rewatered and examined for signs of recovery. The only species which showed any leaf recovery was A. moschatum, although one or two seedlings of all species developed new shoots from axillary buds.

In both experiments examining water loss from detached foliage, the loss of RWC over the measurement period was in the order A. moschatum < P. aspleniifolius < E. lucida < N. cunninghamii (Fig. 8.4a&b). Although the order was constant, the actual values showed some variation beween experiments due probably to differences in the cabinet conditions and the season of sampling, and possibly to differences in the technique of determining RWC (whole leaf vs discs). A. selaginoides showed a water loss intermediate between that of E. lucida and N. cunninghamii over the measurement period (Fig. 8.4b). The differences in RWC among species during dehydration are consistent with differences in the critical values of RWC at which stomatal closure occurs, although in field situations, differences among species in boundary layer resistance due to differences in leaf arrangement may be of considerable importance. In figure 8.5a the commencement of stomatal closure is indicated by the sharp decrease in diffusive conductance, with cuticular conductance indicated by the asymptotic section of the curve following the x-axis. The maximum values of leaf diffusive conductance (of water vapour) fall within the range reported by Korner et al. (1979). The sensitivity of stomatal response to decreasing RWC is in the order, A. moschatum > P. asplenifolius > E. lucida > N. cunninghamii, with the latter species showing little stomatal response to decreasing RWC until 85% RWC (Fig. 8.5a). Stomata of A. moschatum are closed at 93% RWC and further conductance remains low (<0.01 cm s^{-1}), P. aspleniifolius at 91%, E. lucida at 87% and N. cunninghamii at 79%. In Figure 8.5b,

Fig. 8.4   Changes in the relative water content of
  dehydrating detached foliage.

a. Detached leaves and phylloclades were placed in a
controlled environment growth cabinet at 25 ^{O}C
and 38% relative humidity. Relative water content was
measured by the disc flotation method. Each point is
the mean of three replicates, with standard errors
shown where $\geq$3%.
b. Detached leaves and phylloclades were placed in a
controlled environment growth cabinet at 20°C
and 32% relative humidity. The relative water content
was measured by periodic weighing of whole leaves.
Each point is the mean of five replicates, with
standard errors shown where $\geq$3%.

N. cunninghamii: ●
A. moschatum: ▲
E. lucida: ▪
P. aspleniifolius: ◆
A selaginoides: □
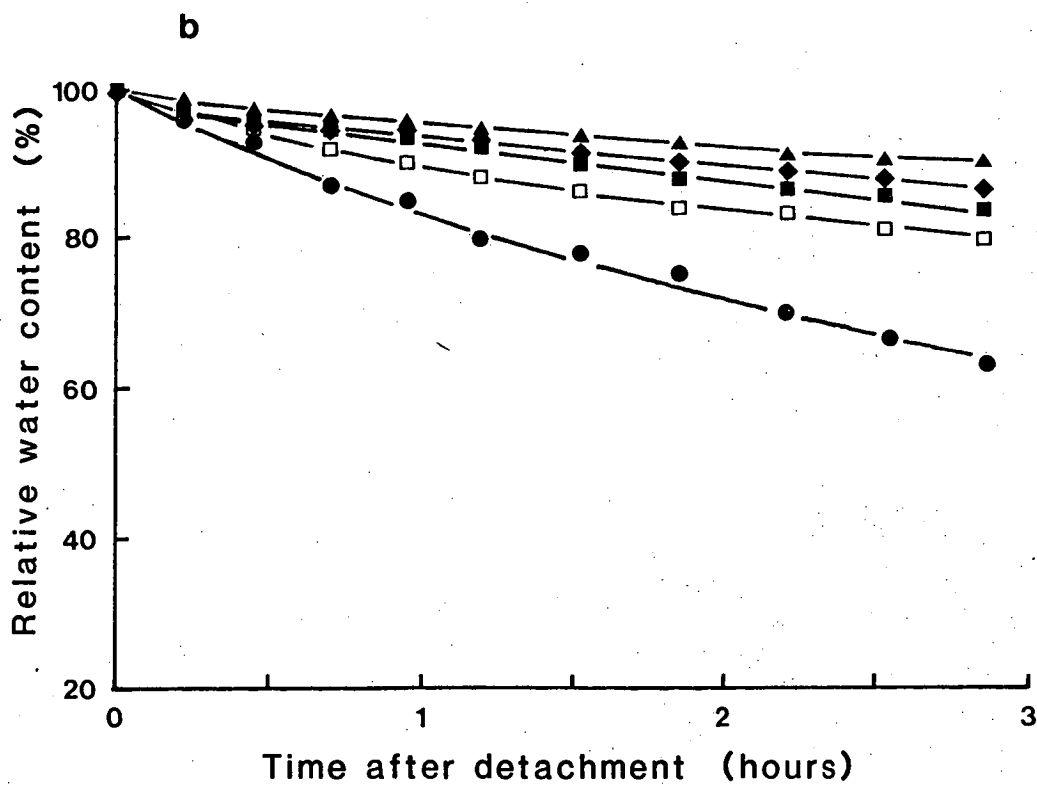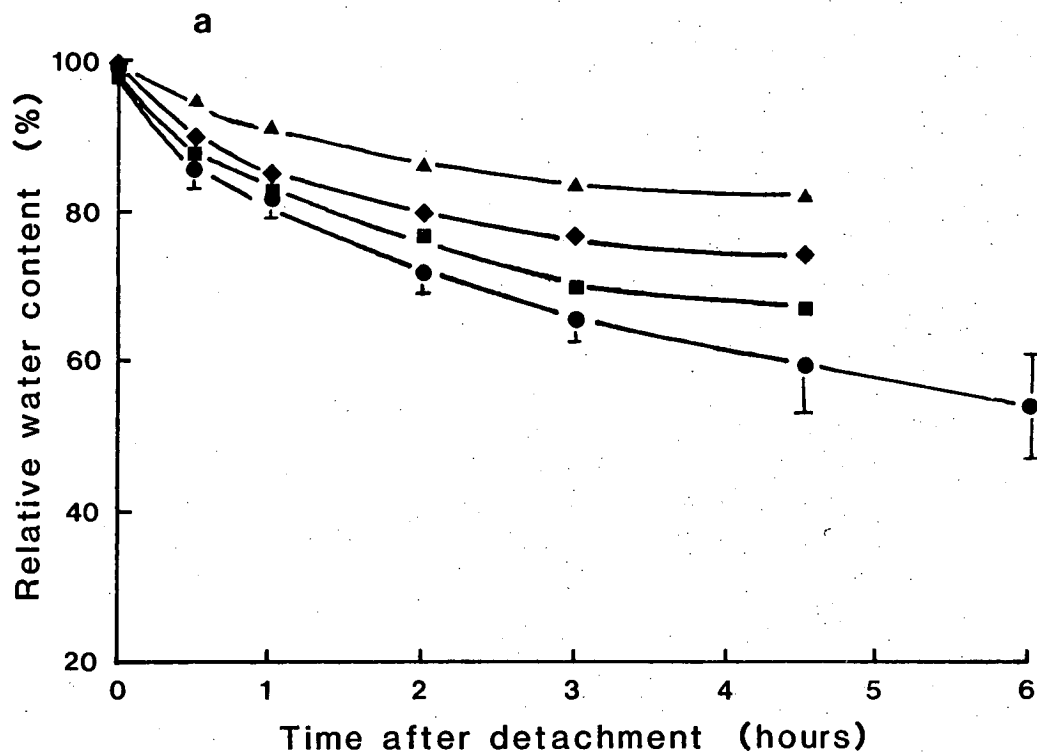
Fig. 8.5　The relationship between water loss and relative water content in dehydrating detached leaves.

a. Desiccating conditions as described in Fig. 8.4a. The relative water content was measured by the disc flotation method. Diffusive conductance was measured with a transient porometer.

b. Desiccating conditions as described in Fig. 8.4b. The relative water content was measured by periodic weighing of whole leaves. The transpiration rate was calculated as

$$\frac{w_1 - w_2}{w_1} \cdot \frac{1}{time}$$

where w_2 is the current leaf weight and w_1 is the leaf weight at the previous weighing. Each point is the mean of five replicates.

N. cunninghamii:　●
A. moschatum:　▲
E. lucida:　■
P. aspleniifolius:　△
A. selaginoides:　□

a

Diffusive conductance (cm s^{-1})

Relative water content (%)

b

Transpiration (mg g fresh weight^{-1} hour^{-1})

Relative water content (%)
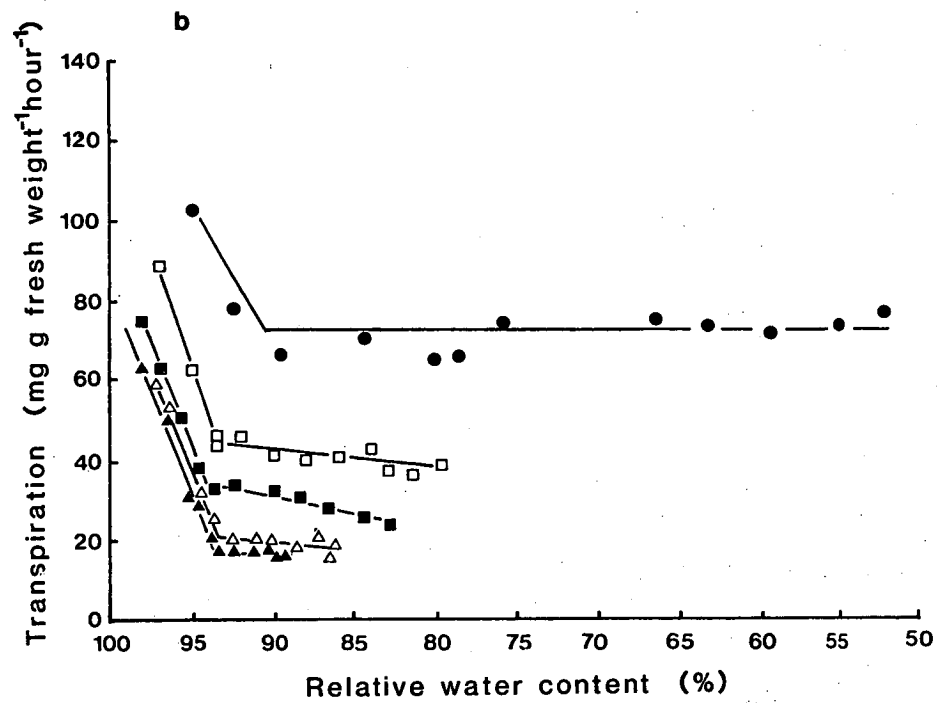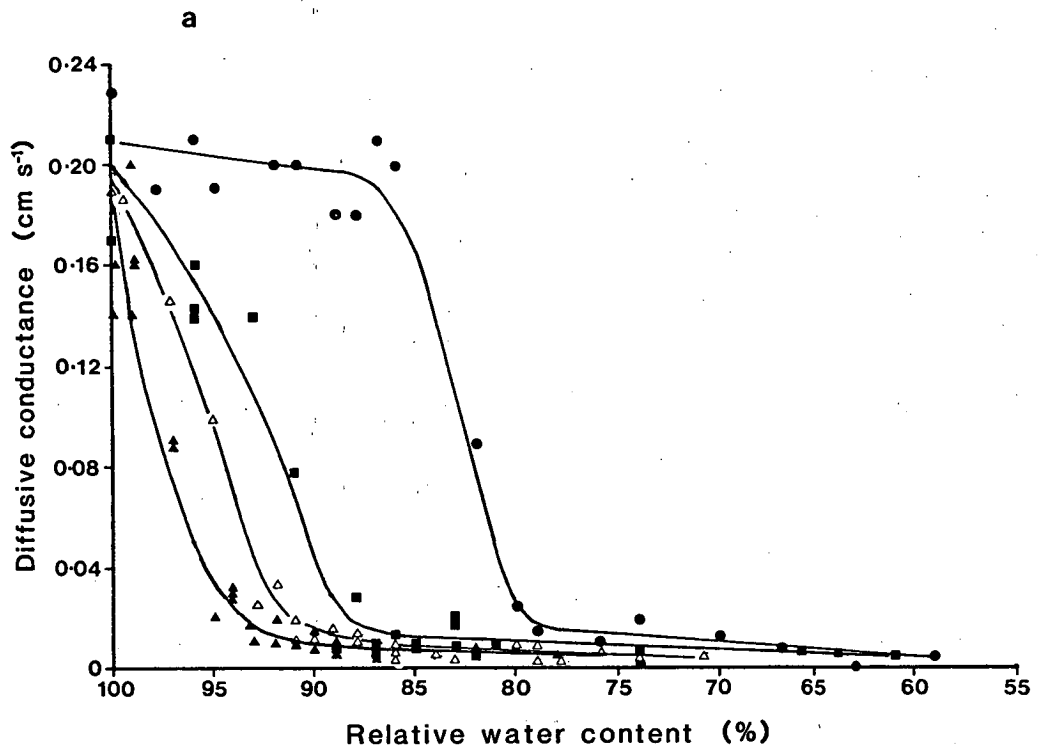
the onset of stomatal closure is indicated by the sharp decrease in transpiration, with cuticular transpiration indicated by the asymptotic section of the curve following the x-axis. The onset of stomatal closure is not apparent due to the rapidity of the response and there is relatively little difference among A. moschatum, E. lucida, P. aspleniifolius and A. selaginoides in the value of RWC at which stomata are closed (93-94%). The stomata of N. cunninghamii are not closed until reaching a RWC of 90%. There are however significant differences (at the 95% level) in the rate of cuticular water loss, in the order, A. moschatum and P. asplenifolius > E. lucida > A. selaginoides > N. cunninghamii.

Discussion

Resistance to water deficit stress has often been defined in terms of the ability of a plant to survive in spite of low tissue water potentials but that there is evidence that the development of low water potentials at relatively high levels of RWC should be regarded as an adaptive response to water stress by slowing the approach of relative water contents to critical levels at which tissue damage occurs (e.g. Weatherley & Slatyer 1957; Jarvis & Jarvis 1963; Hsiao 1973; Hsiao et al. 1976). Relationships between RWC and water potential have been used to assess aspects of drought resistance among some Australian tree species (Slatyer 1961; Connor & Tunstall 1968; Ashton et al. 1975). The data shown in Table 8.1 does not show the reduced water stress avoidance in rainforest species that might be expected, and in fact, N. cunninghamii has the greatest capacity to decrease its water potential for a small decrease in RWC of the species listed. This is also true of the rainforest species when they are compared with species typical of more arid vegetation, such as Acacia aneura and Acacia harpophylla (Connor & Tunstall 1968).

The response shown by N. cunninghamii indicates the

Table 8.1   Characteristics of leaf desorption curves of Australian
forest and woodland trees.

Species	Relative water content (%) at -2.0 MPa	Water potential (MPa) at 50% relative water content
N. cunninghamii	90	-10.2
A. moschatum	76	-4.4
P. aspleniifolius	79	-4.6
E. lucida	79	-4.3
A. selaginoides	68	-3.1
Casuarina stricta[1]	80	-3.3
Eucalyptus goniocalyx[1]	81	-3.3
E. radiata[1]	77	-3.3
E. obliqua[1]	64	-2.4

[1] Ashton et al. (1975), using a pressure bomb for the determination of
water potential and the floating disc method for determination of
relative water content.

greatest development of low water potentials at decreasing levels of RWC of the rainforest species. There is no evidence of lower dehydration tolerance in N. cunninghamii relative to the other species (except A. moschatum), and therefore no evidence that the low water potentials are an indication of greater dehydration strain. At moderate levels of water stress, this response may be effective in balancing water uptake with water loss, and thereby maintaining photosynthesis and growth (Jarvis & Jarvis 1963; Levitt 1980). In addition, the low critical level of RWC at which stomatal closure occurs in N. cunninghamii permits gas exchange to continue at low water deficits. This behaviour is characteristic of "water spenders" (Levitt 1980). These results are in agreement with the critical RWC (causing plant death) of approximately 70% recorded by Howard (1973c) in five-month-old seedlings of N. cunninghamii raised in glasshouse conditions. Howard also noted a slow decrease in RWC in droughted seedlings at levels below 80% and suggested that the seedlings were effective in reducing water loss by transpiration, although the current experiments indicate that the critical RWC for stomatal closure (conversion to "water saver") in N. cunninghamii is lower than in the other rainforest species, and is therefore probably less able to avoid severe water stress. Similar responses have been described in several eucalypt species which are typical of moist forests and are characterised by low values of RWC at which stomatal closure occurs but which have an ability to maintain a relatively high water status by access to deep soil water (summarised by Florence 1981). However these species are confined to sites where they can reliably maintain water uptake during the dry months, and are susceptible to infrequent severe droughts on the more marginal sites (Ashton et al. 1975).

The three-year-old N. cunninghamii seedlings failed to survive RWCs of less than 70%, even though the tolerance of decreasing leaf RWCs is similar to that of other species (except A. moschatum) (Fig. 8.1). This suggests that the

further decrease of shoot water potentials under severe water stress is of no advantage and, as suggested by Jarvis & Jarvis (1963), may cause detrimental direct effects on physiological processes causing plant death. The results of the determination of leaf tissue tolerance to decreasing RWC conflict with the measured relationships between RWC and shoot water potential in 1) the low levels of damage occurring at RWCs close to the critical values (for plant death), and 2) the similar tolerance of N. cunninghamii, E. lucida, P. aspleniifolius and A. selaginoides to decreasing RWCs (Fig. 8.1), although N. cunninghamii seedlings are killed at higher levels of RWC than the other three species. For example, the N. cunninghamii seedlings did not recover after rewatering, with leaf RWCs of 60-75% (Fig. 8.3). This corresponds to an injury of less than 20% (from Fig. 8.1). Similarly, A. moschatum and E. lucida seedlings did not recover from leaf RWCs of approximately 50%, corresponding to an injury of less than 10%, and of approximately 25% respectively. It is not clear whether this reflects inadequacy of the technique for measuring tissue damage (visual assessment as used by Ashton et al. (1975) in eucalypts was not successful) or some difference in the relationships between RWC and shoot water potential between the two experiments, such that the low water potentials developing over weeks may involve osmotic adjustment to the slow tissue dehydration which does not occur in detached tissue exposed to rapid dehydration.

A. moschatum has the highest critical point of RWC for stomatal closure, thereby avoiding low levels of RWC at which damage occurs, but in doing so, must reduce gas exchange and therefore photosynthesis, even at relatively high levels of RWC, and probably at higher levels of soil water content than N. cunninghamii due to the ability of the latter to decrease its tissue water potential at high levels of RWC. A. moschatum also has a greater leaf tissue tolerance of dehydration than the other species. The combination of this high dehydration tolerance, the high

avoidance of water stress by early stomatal closure (with respect to RWC), and survival of seedlings at lower levels of RWC than N. cunninghamii (at least), indicates that this species may be less competitive than N. cunninghamii in terms of growth rate and extraction of water from the soil at low levels of water stress, but may be more effective in both avoiding and tolerating more severe levels of water stress than N. cunninghamii.

P. aspleniifolius and E. lucida are largely inseparable in their responses, although P. aspleniifolius had achieved stomatal closure at a higher RWC than E. lucida in leaves dehydrated at 25°C, and had higher RWCs after both experiments on water loss from detached leaves. A. selaginoides shows a low resistance to water deficit stress, with the lowest development of low water potentials in relation to decreases in RWC, a high critical RWC (for death) (exceeded only by N. cunninghamii), and a low cuticular resistance to water loss (exceeded only by N. cunninghamii).

There are no published accounts of drought damage of rainforest trees in Tasmania. It is not clear to what extent this reflects lack of observation, or a substantiation of Jackson's hypothesis that rainforest in Tasmania is not currently limited directly by rainfall, at least in the lowlands, due to the interactions between rainfall and the incidence of fire. These experiments indicate a clear trend of physiological drought resistance in the order of A. moschatum > (P. aspleniifolius and E. lucida) > A. selaginoides. The superior resistance of A. moschatum to severe water stress predicts its occurrence in areas of marginal rainfall with respect to rainforest distribution. This is consistent with the occurrence of A. moschatum in narrow gully corridors in sclerophyll forest in eastern Tasmania, in the absence of other rainforest canopy species although other factors such as superior seed dispersal and differential survival of fire may also be important. The physiological drought resistance of E. lucida and P.

aspleniifolius is higher than that of A. selaginoides and this may account in part for the more restricted distribution of A. selaginoides, and for the observation by Kirkpatrick & Harwood (1980) that A. selaginoides required a nurse crop of other species for seedling establishment after fire at Mt Bobs.

The physiological response of N. cunninghamii recorded in the current experiments contrasts with those of the other species in that it can avoid moderate stress by lowering its water potential but that its low critical relative turgor for stomatal closure, and the high critical value of relative turgor at which death occurs probably renders it susceptible to severe water stress. It is not certain to what extent the development of low water potentials can protect N. cunninghamii from water loss in severe drought in field situations. Howard (1973c) observed deaths of N. cunninghamii of all ages in the 1967 drought in Victoria and suggested that adults are susceptible to severe drought throughout their lifespan, with severe droughts occurring once or twice per century. Its widespread distribution in Tasmanian rainforest and mixed forest relative to rainforest species other than the occasional outliers of A. moschatum, suggests that either rainforest species limits (lowland at least) in Tasmania are rarely determined directly by rainfall, as mentioned earlier, or that morphological features such as boundary-layer resistance of the crown, root depth, and root-shoot ratio may have a positive effect on the avoidance of water stress in N. cunninghamii. Some caution must be applied to the interpretation of this data with respect to field situations due to its restricted nature, particularly with respect to growth conditions. Field data relating to the measurement of environmental water deficits and plant responses may clarify some of these points.

These physiological responses to water stress are also important in young seedlings when root penetration of the substrate is poor and therefore prone to dehydration. Water

stress may be severe on exposed sites after disturbances such as fire or logging, and protected microsites such as fallen logs may be important in providing safe-sites from high evaporative and heat loads for seedling establishment. Water stress may also be an important determinant of seedling substrate preference. The most common substrates are exposed soil, moss, rotting logs and occasionally the trunks of tree ferns. Seedlings rarely establish on litter-covered soil. This may in part be due to rapid drying of litter and the difficulty of reaching stable moisture levels, but may also be affected by the frequency of browsing insects and pathogens, and potentially by leaf and litter leachates. Growth rates may have a significant impact on the survival of small seedlings, allowing root penetration prior to the warm, dry summer weather. The high frequency of establishment of N. cunninghamii seedlings on disturbed sites where there is a seed source indicates that its drought avoidance strategies (inluding growth rate and morphological features such as root absorbing area) are in general sufficient for regeneration after disturbance. The infrequency of A. moschatum establishment from seed within the rainforest is unlikely to be directly related to its physiological responses to water stress, given its drought resistance relative to the other species. However its slow growth rate relative to N. cunninghamii and E. lucida (Chapter 9) under exposed conditions may lead to seedling death due to slow root penetration of the substrate.

Chapter 9   Growth rates

Introduction

The importance of high plant growth rates have been
recognised in the outcome of interspecific competition
(Grime 1979). Inherent low growth rates have been recognised
as a feature of plants growing in severe environments, even
to the extent of suggesting that they may confer an
advantage in the tolerance of severe environments (Parsons
1968; Grime 1979). Differences in canopy composition in
Tasmanian lowland rainforest have often been attributed to
site soil quality, with N. cunninghamii and A. moschatum
dominating rainforest on fertile, well-drained soils, and E.
lucida and P. aspleniifolius and the smaller trees such as
Anodopetalum biglandulosum, Anopterus glandulosus and
Cenarrhenes nitida increasing in importance with decreasing
soil quality (Gilbert 1959; Jackson 1965,1968,1983;
Kirkpatrick 1977). The tree diversity increases on poor
soils and the canopy is short and staggered. On the poorest
soils however, the tree diversity may be low with P.
aspleniifolius dominating the canopy (Jackson 1983).

In this chapter, growth rates are examined under
relatively optimal conditions (moist, mild temperature and
in fertile, well-drained soils) and under more limiting
conditions, particularly with regard to soil quality. The
latter is of particular interest in determining whether
there is a trend in growth rates that can explain the
reported trend of canopy composition with respect to soil
quality. Similarly, changes in species composition such as
the infrequency of A. selaginoides at lower altitudes, may
also be caused by differences in growth rates under
different climatic conditions.

Materials and methods

1. Pot growth rate trials

Seed of <u>N. cunninghamii</u>, <u>A. moschatum</u>, <u>E. lucida</u> and <u>A. selaginoides</u> was germinated in the glasshouse in May 1982 and the seedlings transplanted into sandy loam soil containing slow release fertiliser in 5 cm diameter plastic pots. After four weeks from the date of germination of the seedlings used, the seedlings were placed outside the glasshouse in full sunlight. The seedlings were watered twice daily, as well as being exposed to the natural rainfall. Seedlings were repotted as necessary due to increases in size. At approximately four week intervals, five seedlings of each species were harvested and height and dry weight were measured. The final harvest was taken at 224 days after germination.

Further trials were conducted to compare the growth rates of the canopy species under a natural canopy vs exposed conditions. A trial was also set up at the same time to examine the growth rates within the glasshouse which appeared to be a more optimal environment based on observations of seedling growth. <u>N. cunninghamii</u>, <u>A. moschatum</u>, <u>E. lucida</u> and <u>A. selaginoides</u> were established from seed collected from Mt Field, the former three species at 700 m elevation, and the latter species at 980 m elevation. <u>P. aspleniifolius</u> seedlings (approximately 3 months old) were collected from 700 m at Mt Field. Seedlings of all species were transplanted into 5 cm diameter pots of sandy loam containing slow release fertiliser. Four weeks after transplanting (September), ten seedlings of each species were harvested, and fifteen seedlings of each species were placed in the three growth treatments:
a. In the glasshouse, unshaded, watered daily.
b. Outdoors in full sunlight, watered at dawn and late afternoon each day, as well as by natural rainfall.
c. Outdoors under a woodland canopy (60% canopy cover as determined from hemispherical photograph), watered three times per week, as well as by natural rainfall.
The growth conditions of each site are summarised in Table

Table 9.1   Mean monthly maximum and minimum temperatures
(^{O}C) of the seedling growth regimes .

| | | Month | | | | | |
		Sep	Oct	Nov	Dec	Jan	Feb
Glasshouse:	max	28.0	28.8	23.5	26.5	26.4	24.0
	min	17.7	17.0	16.1	15.7	15.8	15.0
Outside:	max	17.0	18.6	21.8	19.5	20.0	21.3
	min	9.2	8.8	11.3	10.1	12.7	12.2
Shadehouse	max	13.2	15.3	16.2	15.2	16.3	15.8
	min	9.3	10.2	11.3	11.6	11.4	10.4

9.1. The seedlings were arranged systematically in each treatment (alternated) to avoid local effects of shading or temperature. The seedlings in the glasshouse required transplanting to larger pots in December. After 171 days, (February) all seedlings were harvested. At each harvest seedling height, dry weight and leaf area were measured. Dry weight was partitioned into leaf, stem and root in N. cunninghamii, A. moschatum, A. selaginoides and E. lucida. Partitioning of the shoot into stem and leaf was not consistently possible in P. aspleniifolius due to the production of phylloclades in seedlings greater than approximately 5 cm high.

2. Growth rates of lowland species with respect to nutrient concentration.

In this experiment growth rates are examined in seedlings of N. cunninghamii, A. moschatum, E. lucida and P. aspleniifolius grown in vermiculite fertilised with nutrient solution of different concentrations.

Seedlings of these species, at the 2-6 leaf stage (two-three years old), were collected from Frodsham's Pass (42°50'S 146°23'E) in September 1983. The seedlings were planted in vermiculite in 5 cm diameter plastic pots. These pots were nutriented with 25% Hoaglands solution twice weekly and watered every other day for four weeks to allow establishment. At the end of this period, when the roots were clearly growing, 10 seedling of each species were harvested and dry weights measured. Ten seedlings of each species were then placed in each of four nutrienting regimes:

a. 100 ml of 25% Hoaglands solution, twice weekly, with watering every other day.

b. 100 ml of 15% Hoaglands solution, twice weekly , with watering every other day.

c. 100 ml of 5% Hoaglands solution, twice weekly, with watering every other day.

d. No nutrients applied, with watering every day.
The seedlings were positioned alternately within a treatment
and treatments were rotated weekly to avoid local
environmental variation. After 180 days all seedlings were
harvested and seedling dry weights were measured. The
relative growth rate was calculated as

$$\ln W_2 - \ln W_1 \cdot \text{time}^{-1}$$

where W_1 is the initial weight and W_2 is the final dry
weight.

3. Growth rates of lowland species
in three rainforest soils.

   In this experiment seedlings of N. cunninghamii, A.
moschatum, E. lucida and P. aspleniifolius were grown in
soils collected from three rainforest study sites.
   "Soil" was collected from forest edges on three study
sites. The material collected from Dempster was peat rather
than soil but will be referred to as a soil. The sites
selected varied in the canopy composition or proportions of
species in the canopy, and soils were markedly different
(Table 9.2). In each case the soil was exposed due to forest
clearing in association with road-making, without either
plant cover or a surface layer of humus. The soil was
collected from the top approximately 20 cm and was sieved
through a 0.3 cm mesh. A sample of each soil was analysed by
the Government Analyst, Hobart, for nitrogen, phosphorus,
potassium, magnesium, calcium and iron (Table 9.2).
   Seedlings at the 2-6 leaf stage (two-three years old)
were collected from Frodsham's Pass and grown in nutriented
vermiculite as described in the above section, for four
weeks. At the end of this period ten seedlings of each
species were harvested and their dry weights measured. The
remaining seedlings were transplanted into the field soils,
fifteen seedlings of each species into each soil (one plant
per pot). Approximately 1 cm of vermiculite was placed over
the soil surface of each pot to prevent any differential

Table 9.2   Site and soil characteristics of the soil used in seedling growth rate
experiments in the glasshouse.

| | Soil collection site | | |
	Parrawe	Frodsham's Pass	Dempster
Canopy composition &	N. cunninghamii 66	N. cunninghamii 53	N. cunninghamii 39
% of total basal area	A. moschatum 34	A. moschatum 43	E. lucida 29
		E. lucida 4	P. aspleniifolius 28
			A. biglandulosum 4
Soil	Strong brown gradational soil	Yellowish brown duplex soil	Dark brown peat
Bedrock	Tertiary basalt	Cambrian mudstone	Precambrian dolomite
Soil pH	4.7	4.4	3.8
Nutrient analysis[1]			
Total N (per cent)	0.41	0.17	0.74
Total Fe (per cent)	5.6	2.5	0.01
Total P (ppm)	1100	440	200
Available P (ppm)	5	<2	31
Exchangeable Mg (ppm)	69	65	740
Exchangeable Ca (ppm)	340	110	1440
Exchangeable K (ppm)	180	50	240

[1] The nutrient analysis was performed by the Goverment Analyst, Hobart.
The exchange medium for Mg, Ca and K was 1 M sodium acetate. Available P was
determined by extraction with acidified 0.02 M ammonium sulphate.

soil temperatures caused by soil colour. Seedlings were watered daily for and were harvested when the fastest growing seedlings were reaching the upper size limit considered appropriate for the pot size (196 days). All seedlings were then harvested and dry weights were measured. Relative growth rates were calculated as in section 2.

4. Growth rates of seedlings
collected in the field.

Pot experiments conducted in the glasshouse may not necessarily reflect the behaviour of plants in response to soil in the field environment. Therefore sapling ages were determined in field-grown plants and related to sizes of the individuals. Seedlings growing on forest edges were used to avoid effects of shading and severe competition that may be expected under a forest canopy or among mature trees.

Five to twelve seedlings of each species were collected from the forest edge, i.e. an exposed site so that light is not limiting, on most of the sites studied in Chapter 2. On all sites except Mt Field and Sawback, the edge was associated with artificial forest clearing practices (road-making, logging). At Sawback the forest edge had been cleared by fire. The seedlings from the Mt Field site were collected within the open forest from open, unshaded sites.

It was difficult to consistently obtain seedlings of all species of a particular size. Therefore seedlings/saplings were collected over a size range (50-150 cm high) and age was regressed against size. All seedlings were sectioned at the base and ages were determined by ring counts. The growth parameter used was the seedling height which is probably the most meaningful parameter of growth in competition since the ability to reach the canopy is important particularly for the more light-demanding species. The line of best fit for this relationship was a straight line in each case. The stem ages for each species at each site were therefore regressed against stem height using a simple linear regression with

untransformed data through the origin (0,0).

Results

1. Pot growth rate trials

    N. cunninghamii and E. lucida grow faster in terms of
both dry weight and height than A. moschatum and A.
selaginoides (Fig. 9.1). The mean dry weight of N.
cunninghamii is significantly higher (p<0.05) than that of
E. lucida in the first six harvests. The mean relative
growth rates of N. cunninghamii and E. lucida seedlings
raised under the three growth conditions are not
significantly different (Table 9.3). There is a general
trend of maximum growth rates in the glasshouse treatment
and minimum growth rates in the shadehouse in all species
except A. moschatum which has a higher growth rate in the
shadehouse than outside in full sunlight. However
statistical differences (at the 95% level) do not occur for
N. cunninghamii and P. aspleniifolius between the seedlings
raised outside in full sunlight and in the shadehouse, and
in E. lucida and A. selaginoides between the seedlings
raised in the glasshouse and outside in full sunlight. There
was no significant difference between the growth rates of A.
selaginoides and P. aspleniifolius at any of the treatments
(Table 9.3).

    The leaf area ratio (LAR) is highest for all species in
the shadehouse treatment (Table 9.3). The gymnosperms, P.
aspleniifolius and A. selaginoides have relatively low LARs
in the glasshouse and shadehouse treatments. This is most
pronounced in glasshouse-raised plants, but it is not clear
whether this is due to the growth conditions or to the
larger size (and greater ontogenetic age) of the seedlings,
and in the case of P. aspleniifolius, to the presence of
phylloclades in the glasshouse-raised plants.

Fig. 9.1   Growth of seedlings raised outdoors in Hobart.
Each point is the mean of five replicates, with standard
errors.
a. Total dry weight.
b. Seedling height.

N. cunninghamii: ●
A. moschatum: ▲
E. lucida: ■
A. selaginoides: □
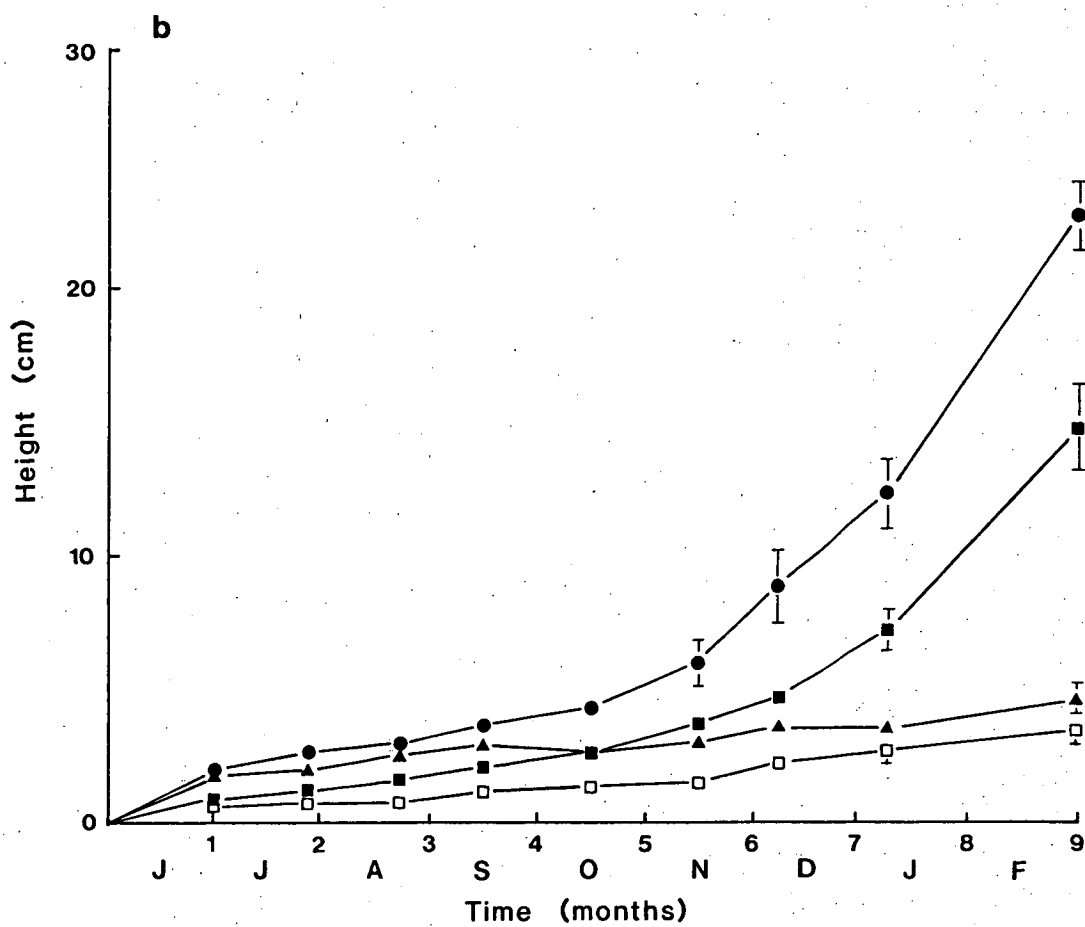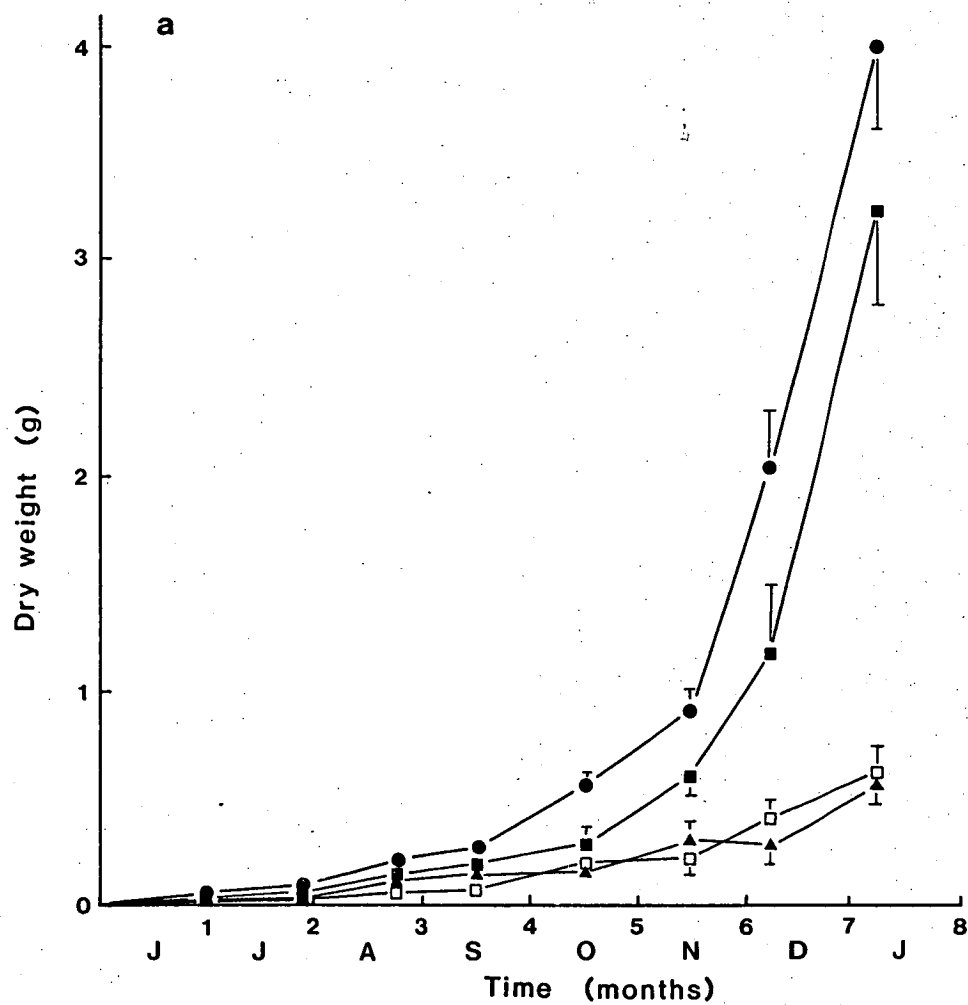
Table 9.3   Mean relative growth rate (RGR, g g^{-1} week^{-1})) and leaf area ratio (LAR, m^2 g^{-1})), with standard errors, of plants raised in three growth treatments in Hobart from September 1984 to February 1985.

	Growth treatment					
	Glasshouse		Outside (full sunlight)		Shadehouse	
Species	RGR	LAR	RGR	LAR	RGR	LAR
N. cunninghamii	0.29 ± 0.02	6.3 ± 0.2	0.21 ± 0.02	4.8 ± 0.2	0.17 ± 0.02	8.8 ± 1.0
E. lucida	0.24 ± 0.02	6.5 ± 0.3	0.22 ± 0.02	4.7 ± 0.5	0.15 ± 0.02	9.3 ± 0.8
A. moschatum	0.18 ± 0.02	7.3 ± 0.3	0.05 ± 0.01	5.0 ± 0.1	0.10 ± 0.02	10.7 ± 1.3
P. aspleniifolius	0.18 ± 0.03	4.3 ± 0.2	0.09 ± 0.02	4.4 ± 0.2	0.05 ± 0.01	7.7 ± 0.2
A. selaginoides	0.14 ± 0.01	5.2 ± 0.1	0.11 ± 0.02	4.0 ± 0.2	0.04 ± 0.01	7.2 ± 0.1

Table 9.4   Mean root/shoot values of species in the nutrient and soil trials.

Species	Nutrient concentration				Soil source		
	(% of full strength Hoaglands Solution)				Parrawe	Frodsham's Pass	Dempster
	0	5	15	25			
N. cunninghamii	0.89	0.47	0.45	0.32	0.74	0.71	0.54
E. lucida	0.43	0.37	0.28	0.28	0.72	1.07	0.81
A. moschatum	1.17	0.54	0.47	0.45	1.00	1.02	0.91
P. aspleniifolius	0.82	0.39	0.37	0.33	0.66	0.90	0.72

Fig. 9.2   The mean relative growth rates (with standard errors) of seedlings grown in vermiculite and nutriented with different concentrations of Hoaglands solution.

N. cunninghamii: ●
E. lucida: ■
A. moschatum: ▲
P. aspleniifolius: ◆

Fig. 9.3   The mean relative growth rates (with standard errors) of seedlings grown in soils from three study sites.

N. cunninghamii: □
E. lucida: ▦
A. moschatum: ▨
P. aspleniifolius: ■
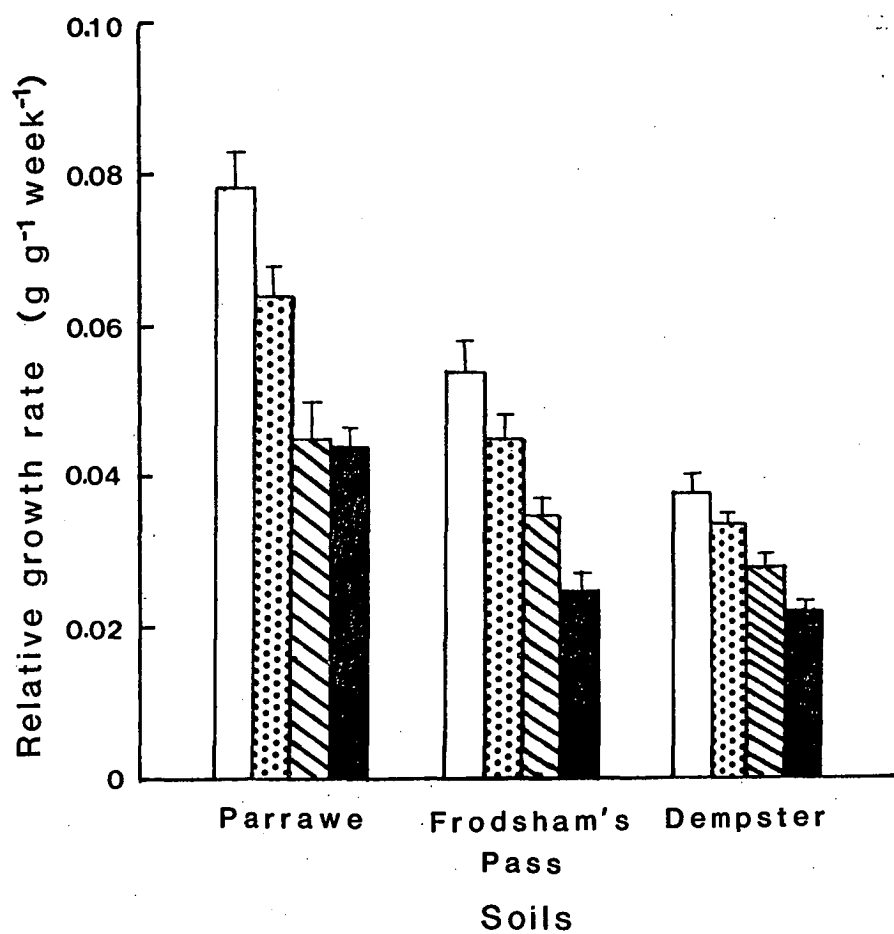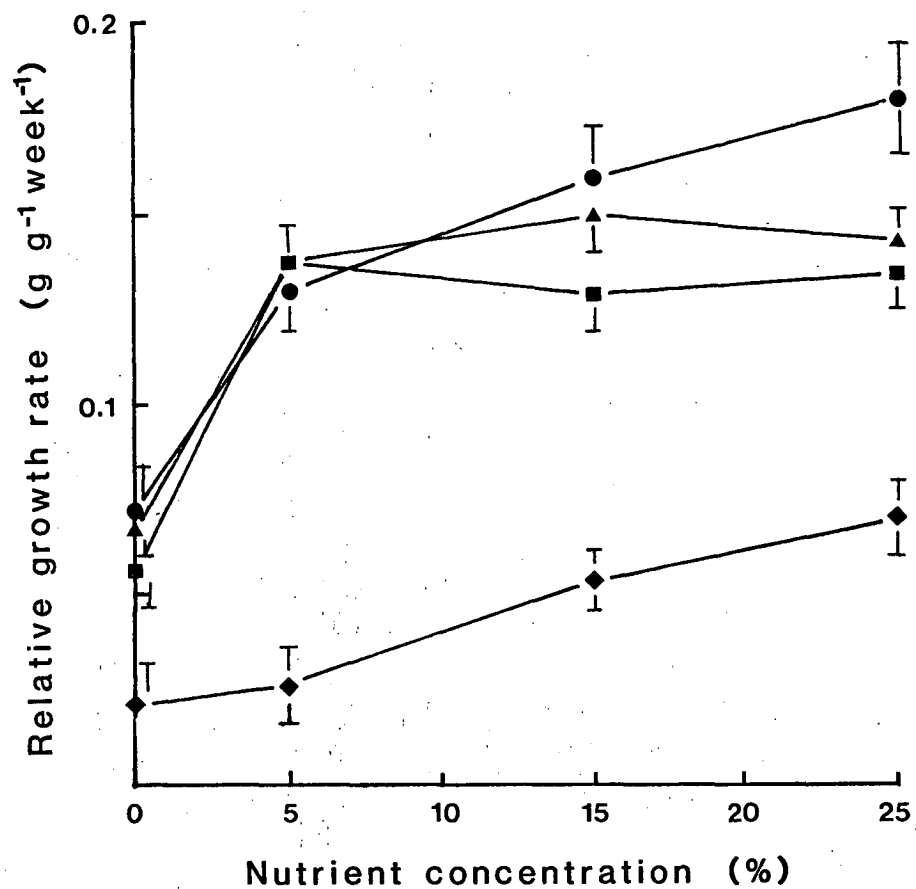
2. Growth rates of lowland species
with respect to nutrient concentration

N. cunninghamii and P. aspleniifolius did not show
evidence of nutrient saturation in this experiment (Fig.
9.2). E. lucida and A. moschatum, however, were nutrient
saturated at 5% Hoaglands solution. Growth occurred at 0%
Hoaglands solution due to nutrient reserves within the
plants from growth in 25% Hoaglands solution during
establishment. However, with the possible exception of E.
lucida, growth under these conditions was primarily in the
root system, resulting in relatively high root/shoot values
(Table 9.4). The root/shoot value increased with decreasing
nutrient concentration, most markedly at 0% nutrient. E.
lucida showed the least change in the root/shoot value. A.
moschatum has the highest root/shoot value of the four
species at all nutrient levels. At 25% nutrients there is no
significant difference between the root/shoot value of N.
cunninghamii, E. lucida and P. aspleniifolius.

3. Growth rates of lowland species
in three rainforest soils

The growth rates on each soil were in the order of N.
cunninghamii > E. lucida > A. moschatum > P. aspleniifolius
(Fig. 9.3). The growth rates of all species were in the
order of Parrawe > Frodsham's Pass > Dempster (Fig. 9.3).
This indicates a trend of soil quality which is consistent
with the trend in pH, total phosphorus and total iron (Table
9.2). The brown soil from Parrawe has consistently higher
values of all nutrients than the yellow clay soil from
Frodsham's Pass, except magnesium which is very similar at
both sites. However the peat from Dempster has very high
levels of exchangeable magnesium, calcium, potassium and
available phosphorus. It is not possible to determine the
importance of individual factors, either of nutrients or of
factors such as water availabilty and aeration, on growth

rates from these results. There is a clear trend however in
overall quality of the soils as indicated by plant growth
rates which corresponds to the pattern of canopy composition
with respect to soil quality as described by Jackson (1965,
1968, 1983) and Kirkpatrick (1977), i.e. the brown soil
supports the highest seedling growth rates, and in the field
supports forest dominated by N. cunninghamii, with A.
moschatum sub-dominant; the yellow clay soil from Frodsham's
Pass supports intermediate seedling growth rates and in the
field supports forest dominated by N. cunninghamii, with A.
moschatum and E. lucida sub-dominant; the peat supports the
lowest seedling growth rates, and in the field supports
rainforest of N. cunninghamii, E. lucida and P.
aspleniifolius.

The root/shoot values did not follow the trend in growth
rates that occurred in the experiment with varying nutrient
concentrations (Table 9.4). This may be due to the more
complex nature of nutrient concentrations in the soils, ie.
not all nutrients follow the same trend, and differences in
soil water availability and aeration. Root/shoot values in
A. moschatum are consistently high, in N. cunninghamii the
root/shoot value was low in the Dempster soil, and in P.
aspleniifolius and E. lucida it was high in the Frodsham's
Pass soil. The root/shoot values of all species are high in
comparison with the values obtained under high nutrient
concentrations in Experiment 3. This suggests that nutrients
or other soil features are limiting even on the relatively
well-drained and fertile brown soil.

4. Growth rates of seedlings
collected in the field

The highest growth rates as indicated by the slope of
the regression of seedling age against height, are recorded
in N. cunninghamii (Table 9.5). The maximum growth rates of
this species (slope = 0.06-0.07) are in general associated
with the maximum growth rates of co-occurring species.

Table 9.5   Growth rates of seedlings obtained from age determinations of seedlings growing in open conditions on each field site. The tabulated values given are the slopes of the regression through (0,0) of seedling age against height for 5-10 seedlings of each species, with the standard error of the slope. In each case the regressions are highly significant ($p < 0.005$).

Site	Species				
	A. moschatum	N. cunninghamii	E. lucida	P. aspleniifolius	A. selaginoides
Sumac		0.06 (0.01)	0.09 (0.01)		
Parrawe	0.09 (0.00)	0.07 (0.01)			
Pipeline	0.09 (0.01)	0.06 (0.00)			
Stephen's Rivulet		0.06 (0.00)	0.11 (0.01)		
Frodsham's Pass	0.16 (0.02)	0.17 (0.02)	0.15 (0.01)		
Mt Michael		0.17 (0.01)		0.21 (0.01)	
Diddleum	0.10 (0.01)	0.07 (0.01)			
Weindorfer's Forest		0.21 (0.04)			0.46 (0.02)
Ballroom Forest		0.25 (0.02)			0.46 (0.04)
Dempster		0.10 (0.01)	0.12 (0.01)	0.13 (0.00)	
Howards Road		0.20 (0.03)	0.18 (0.01)	0.20 (0.03)	0.63 (0.06)
Pieman		0.06 (0.00)		0.12 (0.01)	
Sawback		0.11 (0.00)	0.12 (0.01)	0.12 (0.01)	
Hastings		0.21 (0.01)	0.18 (0.01)	0.16 (0.02)	
Mt Field		0.42 (0.02)		0.31 (0.02)	

However on these sites, the growth rate of N. cunninghamii
is significantly higher than the growth rates of
co-occurring species (p<0.05), and the difference in growth
rate between N. cunninghamii and co-occurring species is
proportionately large (Table 9.5). On Dempster, Sawback, H2
and Frodsham´s Pass, the growth rate of N. cunninghamii is
lower and not significantly different from the growth rates
of co-occurring species, with the exception of
A.selaginoides at H2 (p<0.05) (Table 9.5). At Mt Field,
where the lowest growth rate of N. cunninghamii is recorded,
the growth rate of P. aspleniifolius exceeds that of N.
cunninghamii (Table 9.5). These results reflect to some
degree the current canopy composition of the forest on these
sites (Table 2.1), with the greatest dominance by N.
cunninghamii generally occurring on sites where it's growth
rate is highest (with the exception of Parrawe and Pieman),
and the canopies containing a more even mix of species
occurring on sites where there the growth rates of N.
cunninghamii are low and not significantly different from
the growth rates of co-occurring species.

A. selaginoides is the only species other than N.
cunninghamii which commonly occurs as seedlings at
Weindorfer´s Forest and Ballroom Forest. The growth rate of
N. cunninghamii is low on both of these sites, but is
approximately twice the growth rate (half the slope of the
regression) of A. selaginoides (Table 9.5). Similarly at H2
where the growth rates of all species are low, A.
selaginoides has an extremely low growth rate (Table 9.5).

Discussion

The features limiting the growth rates of the seedlings
in the glasshouse vs the two outside treatments may be
complex and may vary among the different species. The most
important features of the results are the high growth rates
of N. cunninghamii and E. lucida seedlings relative to the
other rainforest species over a range of growth conditions

(Fig. 9.1, Table 9.3), although under heavy shading the growth rates of these species are low relative to that of A. moschatum (Chapter 6).

It is not clear to what extent the field growth rates reflect features of the site climate as well as soil quality. The differences in growth rates among the low altitude sites (below 650 m) do appear to follow trends in soil quality. In the field, under less optimal growth conditions than those experienced by potted seedlings in Hobart (judged by the lower seasonal growth increments), the highest growth rates were also recorded in N. cunninghamii (Table 9.5). However, as soil quality decreases on lowland sites, the growth rate advantage of N. cunninghamii declines (Table 9.5). At the high nutrient concentrations in the nutrient pot trial, the growth rate of N. cunninghamii is not significantly different from those of E. lucida and A. moschatum, but does not show evidence of nutrient saturation; at 5% Hoaglands solution the growth rates of N. cunninghamii, E. lucida and A. moschatum do not differ significantly from each other and are separate from that of P. aspleniifolius, but there is a large decline in the growth rate of the former three species between 0% and 5%, which if extrapolated to lower nutrient levels, i.e. where there are no stored nutrients in the plant, suggests a point at which the growth rate of P. aspleniifolius may equal that of the other species. This is observed in field determinations of growth rates on different soils. There is no evidence of actual preference of P. aspleniifolius or E. lucida for the soils in which they are most frequent as canopy species. The differences lie predominantly in the growth rates of the species relative to each other. Although the soil pot trials and the growth rates obtained from young plants in the field cannot be assumed to be determined by soil nutrients alone (also drainage, organic substances, fauna, pathogens), the nutrient experiment does indicate similar trends in species responses to decreasing substrate quality.

These trends have important implications for the understanding of the broad gradient of canopy composition which follows the gradient of soil quality (described by Jackson 1965, 1968, 1983; Kirkpatrick 1977). All species except A. moschatum show an increase in the number of small stems which have originated from seed with increasing canopy opening of the forest (Chapter 2). The size of the gap required for successful establishment from seed follows a general trend of N. cunninghamii < E. lucida < A. selaginoides < P. aspleniifolius (Chapter 2). N. cunninghamii, E. lucida and P. aspleniifolius are shade-intolerant relative to A. moschatum, but do not separate clearly from each other in their instantaneous light compensation points, and the shade-tolerance of A. selaginoides is uncertain. The alternative strategy to shade-tolerance is to avoid shading (Grime 1979). Therefore any trend in gap requirement (due to shade-intolerance or any other feature) is likely to correspond with the importance of reaching the canopy before canopy closure by other species (if regeneration is occurring in a canopy gap) or remaining in the upper levels of the developing canopy (if regeneration is occurring on a widely disturbed site). If only the lowland, gap-regenerating species are considered, it is clear that the trend in gap size requirement is opposite to the trend in growth rates on soils of decreasing quality. N. cunninghamii with its lower gap requirement and a high potential growth rate, establishes in small canopy gaps and quickly dominates them on good soils. At the other extreme, P. aspleniifolius appears to require more light for regeneration and therefore must reach the canopy before canopy closure to obtain sufficient light for continued growth. However it has the lowest potential growth rate and becomes competitive in terms of growth rate relative to the other species only on the poorest soils. Therefore the general trends in species composition with respect to soil type can be explained in terms of the comparative growth rates of the available

gap-regenerating species, determined by their light
requirements and growth responses to the soil
characteristics.

On the most severe site with respect to soil quality (Mt
Field), the growth rate of P. aspleniifolius exceeds that of
N. cunninghamii (Table 9.5), indicating that a crossover of
growth rates among species does occur in the field. However
even on sites where P. aspleniifolius has a growth rate
which does not differ significantly from the other species
in open conditions, the intolerance of shade prevents
regeneration of P. aspleniifolius within the rainforest,
especially where species such as Anodopetalum biglandulosum
and Anopterus glandulosus are present and reproducing
vegetatively (Chapter 2). The higher fire frequency on poor
soils suggested by Jackson (1968) appears to be fundamental
to the regeneration of this species, not only in its
detrimental effect on the nutrient status of the soil in
areas of high rainfall (Jackson 1968), but also by creating
an open canopy suited to the relatively high gap
requirements of P. aspleniifolius.

The characteristics of P. aspleniifolius which enable it
to grow faster on poor soils than the species with higher
potential growth rates are uncertain. Bowen (1980) notes
that there is no single dominant strategy for coping with
low nutrients in the soil. The tendency for plants with low
potential growth rates to colonise severe environments,
including those related to nutrient deficiencies has often
been noted (Beadle 1966; Grime & Hunt 1975). The
physiological reasons for this are not clear but low
potential growth rates have been suggested to be of
selective advantage per se (Parsons 1968; Grime & Hunt 1975;
Grime 1979). It should also be noted that the general slow
growth rates among species on poor soils reduces the rate at
which the community develops and therefore decreases the
rate of development of competitive interactions. This may
allow a longer period of coexistence and consequently a
greater species diversity than occurs on better soils

(Huston 1979, 1980). The vegetative reproduction of many species, which is predominant on the poor soils, produces self-replacement and consequently permits species coexistence for a longer period (chronological time and the number of generations) than might occur under seedling reproduction where there is no subsidy from the parent stem.

By the hypothesis expressed above, of the importance of a competitive growth rate for the more shade-intolerant species, any decline in the growth rate of A. moschatum is likely to have less of an impact on its competitiveness due to its greater shade-tolerance. However its distribution with respect to soil quality has not been well-described, and since its establishment from seed is often poor, it may be disadvantaged on poor soils due to the greater incidence of fire.

The effects of mycorrhizal associations on growth rates have not been examined in this study. All P. aspleniifolius seedlings had nodulated roots, including those that were germinated in Hobart in sterilised commercial potting soil. There was no apparent difference in nodule frequency in any of the nutrient or soil growth rate experiments. Howard (1973b) noted that infection of N. cunninghamii seedlings by ectotrophic mycorrhizae in Victoria had occurred by the time they were one-year-old, and that mycorrhizae were well-developed on N. cunninghamii trees of all ages in the field. No data is available regarding the frequency of mycorrhizal associations in the rainforest trees in Tasmania, and consequently nothing is known of their ecological significance.

As mentioned earlier in this discussion, the site climate must also have an impact on the growth rates, with differential responses among the species, so that observed growth rates may be the result of many limiting features of the environment. These features may potentially be either interacting or independent in their effects, and may be either short- or long-term in their duration. The only

feature of the environment that has been examined in this study that may potentially advantage A. selaginoides is growth at low temperatures. A. selaginoides has a relatively high gap requirement for regeneration (Chapter 2) and therefore commonly establishes in association with species with high potential growth rates such as N. cunninghamii and E. lucida. Under the climatic regimes of the pot trials, A. selaginoides has a low growth rate relative to these species. A. selaginoides regenerates in relatively high light-low temperature environments (Chapter 2). This correlates with the physiological responses to temperature (Chapter 7), but its response to light under its optimal temperature regime has not been measured. The growth response of A. selaginoides to different soils has not been studied and growth rates in the field are recorded only from three sites. However it is clear that on all of these sites its growth rate is considerably lower than the growth rates of all the co-occurring species. If the large gap requirement for regeneration shown by A. selaginoides (Chapter 2) is due to its light requirements, its low growth rate will prevent it from reaching the canopy where it establishes with faster-growing species, and its establishment to form forests on these sites must be explained in historical terms such as a previously colder climate or chance early colonisation of disturbed sites. It can dominate such sites for a long time by virtue of its life span of up to approximately 1000 years (Ogden 1978), so that current climatic conditions may not be indicative of the climate under which forests formed by this species developed.

Chapter 10   Summary to Parts A & B

The sum of the plant responses to environmental
conditions is expressed in the potential habitat and
regeneration niches of the species, and the success of
competition with other species. The original problem set in
this thesis was to define the mechanisms determining the
canopy composition of Tasmanian rainforest. The results
obtained from studies of regeneration patterns in the field
(Part A) and of the comparative physiology of the species
(Part B) indicate the following major mechanisms:

1.   Characteristics of dispersal and reproduction

A. moschatum seed is wind-dispersed, but the other
species, with the possible exception of P. aspleniifolius,
have poorly dispersed seed with most seed falling well
within one tree height of the parent tree (personal
observations; Hickey et al. 1982). Kirkpatrick (1977) has
suggested that P. aspleniifolius seed may be bird-dispersed
since it appears early on disturbed sites, but I am not
aware of any direct evidence that it is bird-dispersed. Its
seed is heavy and tends to be concentrated around the parent
tree. Even A. moschatum seed is commonly concentrated around
the parent tree (Hickey et al. 1982), within the
rainforest.

Although A. moschatum is relatively shade-tolerant
(Chapter 6), its reproduction primarily by basal stem
sprouts limits its ability to expand within the rainforest
and consequently to compete with the regeneration of the
co-occurring species (Chapter 2). A. moschatum may
potentially replace the more light-demanding species as
suggested by Noble & Slatyer (1978) given sufficient time to
spread through the forest by slow vegetative expansion and
infrequent seedling establishment. However the time scale
must be long and free of catastrophic events such as fire.

Apparent autogenic replacement of N. cunninghamii by A. moschatum has been reported only once in the literature (Gilbert 1959), on a site where it was establishing from seed, and has not been recorded in extant vegetation. Therefore either the frequency (and intensity) of exogenous disturbance (needed at only an extremely low frequency) is maintaining the frequency of N. cunninghamii, or the regeneration strategies of A. moschatum are insufficient to prevent the regeneration of N. cunninghamii in canopy gaps, irrespective of the age of the forest. Although the predominance of vegetative reproduction limits its rate of spread in the rainforest, it leads to self-replacement of the species. E. lucida, and to a lesser extent N. cunninghamii, also reproduce vegetatively and therefore are commonly self-replacing, often under canopy conditions where seedlings cannot establish due to the heavy shading. Vegetative reproduction has not been observed in P. aspleniifolius, and is infrequent in A. selaginoides (a few examples of root suckering and layering have been observed).

There is little variability in the gross germination requirements among the species, with the exception of P. aspleniifolius seed which has a poorly understood dormancy mechanism (Chapter 5). However the more rapid germination of A. selaginoides at low temperatures, and the failure of A. moschatum to germinate if conditions suited to germination do not occur soon after release (Chapter 5), may be indicative of the environments to which they are best adapted. The irregular seed production of N. cunninghamii and A. selaginoides (Chapter 4) may affect the colonisation of newly disturbed sites, including canopy gaps, particularly since germination must coincide with conditions suited to establishment for succesful reproduction.

2. Shade-tolerance

A. moschatum is the most shade-tolerant of these species

(Chapter 6), but rarely establishes from seed within the rainforest (Chapter 2). The infrequency of establishment from seed within the rainforest and the nature of the vegetative reproduction of A. moschatum causes establishment under its own canopy, rather than in canopy gaps created by the death of old trees of other species.

Studies of the spatial patterns of seedling regeneration indicate a gap size preference for regeneration from seed in the order N. cunninghamii < E. lucida < A. selaginoides < P. aspleniifolius (Chapter 2). Differences in the light compensation points of N. cunninghamii, E. lucida and P. aspleniifolius were not detected but N. cunninghamii and E. lucida have higher growth rates than P. aspleniifolius (and A. selaginoides) in moderate shade and under a natural woodland canopy (Chapters 6 & 9). N. cunninghamii and E. lucida commonly regenerate from seed in the canopy gaps created by the death of large, old trees (Chapter 2). They are less likely to regenerate in gaps caused by the death of an old A. moschatum stem, due to the advanced vegetative shoots which are usually present, often in the lower canopy already, and due to the smaller size of the gap caused by the conical, multi-layered canopy of this lower canopy species.

The tendency for species self-replacement in A. moschatum, N. cunninghamii and E. lucida due to characteristics of reproduction and light requirements indicates the importance of the initial floristic composition (Egler 1954) after disturbance. This is partly determined by selective survival e.g. vegetative reproduction, but also by chance, and it may affect the canopy composition and dominance for a long time - several generations - during which further disturbance may occur.

While P. aspleniifolius and A. selaginoides have long life-spans relative to the other canopy species and may therefore persist for a long period on a site due to this feature, they do not in general have the benefit of vegetative reproduction to allow indefinite

self-replacement. In addition, they require larger gaps for establishment from seed than N. cunninghamii and E. lucida, and on many sites are unable to replace individuals of their own species (Chapter 2). The regeneration patterns suggest that these patterns are caused by low shade-tolerance but a lower shade-tolerance of the gymnosperms than N. cunninghamii and E. lucida has not been demonstrated experimentally.

3. Growth rates

The predominantly vegetative reproduction of A. moschatum limits its ability to regenerate in canopy gaps and therefore competition between A. moschatum and the more shade-intolerant species is probably less direct during establishment than competition among the shade-intolerant species, within the rainforest. These species characteristically regenerate in canopy gaps or after larger disturbances (Chapter 2). The processes involved in the successful invasion of a gap by a particular species and the characteristics of the gap that may be important are summarised by Grubb (1977) (Table 10.1), and some features affecting establishment have been discussed already. The trends in species composition can be explained best if for the purpose of argument it is assumed that seeds of all the gap-regenerating species are available on site and that seedlings have established. A light-demanding species must reach the canopy ahead of competing species - the more light-demanding the species, the greater the need to reach the canopy first. The species reaching the canopy first is determined by relative growth rates, which are in turn determined by photosynthetic response to the light, temperature and moisture regime, losses due to tissue death (drought, frost, consumption by animals), and growth responses to soil characteristics.

Table 10.1   Processes involved in the successful invasion of a gap by a given plant species and characters of the gap that may be important (from Grubb 1977).

Processes	Characters
Production of viable seed	Time of formation
Flowering	Size and shape
Pollination	Orientation
Setting of seed	Nature of soil surface
Dispersal of seed	Litter present
Through space	Other plants present
Through time	Animals present
Germination	Fungi, bacteria and viruses
Establishment	present
Onward growth	

a. Growth with respect to soil

N. cunninghamii has a relatively high growth rate under ideal growth conditions (moist, mild temperatures and fertile soils) (Chapter 9). It has a photosynthetic tolerance of a wide range of temperatures (Chapter 7), and its water-spending characteristics probably allow it to continue photosynthesis and growth under mild water deficit stress (Chapter 8). It is also relatively frost resistant (Chapter 7) and is relatively unpalatable to browsers (Hickey 1982). These characteristics would be expected to lead to a high relative growth rate and yield over a wide range of conditions and therefore facilitate continuous regeneration of N. cunninghamii over a wide range of conditions. However, it shows a greater decline in growth rate than E. lucida and P. aspleniifolius (and A. moschatum) with declining soil quality, so that on relatively poor soils its growth rate advantage with respect to other species decreases (Chapter 9). There is also an interaction of tree height with soil quality, with N. cunninghamii reaching heights of 35-40 m on good soils with the other lowland canopy species (E. lucida, A. moschatum and P. aspleniifolius). Therefore if these species establish together on a fertile, well-drained soil, N. cunninghamii can potentially monopolise resources such as light and nutrients due to its growth rate and potential size advantage. This would occur whether the gap was created by the death of an old stem, or whether it was an exposed site after a fire, and the forest may potentially take several generations to reach a canopy composition in equilibrium with the environmental characteristics due to the potentially long-lasting effects of the initial floristic composition. On the poorer soils however, N. cunninghamii may not exceed the height of E. lucida and P. aspleniifolius (e.g. Sawback, Dempster, Pieman and Murchison) (Chapter 2) and there is greater similarity in the growth rates of different species (Chapter 9). This includes the species of small trees such as Anodopetalum biglandulosum, Anopterus

glandulosus and Cenarrhenes nitida. Due to the slow growth
rates on these sites (Chapter 9), the long lifespan of P.
aspleniifolius and the predominance of vegetative
reproduction (Table 2.3), these forests may persist for a
long time. However the studies of population size structures
of P. aspleniifolius indicate that it does not regenerate in
these forests (other than in the open forest on the poorest
soil), due probably to a higher light requirement for
succesful seedling establishment and failure of this species
to reproduce vegetatively. However there is evidence that
exogenous disturbance (fire) may be sufficiently frequent to
allow regeneration of this species. By this scheme, any
improvement in the soil quality, such as may occur with time
without disturbance, must therefore reduce the probability
of successful regeneration by P. aspleniifolius with a drift
towards dominance by N. cunninghamii as suggested by Jackson
(1968).

The importance of slow growth rates on poor soils in
allowing species coexistence and high diversity has been
observed elsewhere (Grime 1979; Huston 1979, 1980), and
together with the higher incidence of fire on poor soils
(Jackson 1968) must be significant in maintaining the
species diversity. These observations are in agreement with
Jackson's hypothesis that N. cunninghamii is the climax
species in lowland Tasmanian rainforest, given sufficient
time for nutrient accumulation and autogenic processes.
However any feature of the disturbance which favours the
small tree species, e.g. Anodopetalum biglandulosum, such as
by a relatively high frequency of low intensity fires which
permits vegetative regeneration, or by disturbance
associated with logging, is likely to lead to forest
degradation.

b. Growth with respect to climatic features

On sites which experience low temperatures, A.
selaginoides would be expected to increase its advantage due
to its photosynthetic tolerance of low temperatures and its

frost resistance (Chapter 7). N. cunninghamii is also tolerant of cold temperatures relative to the other canopy species, and both these species are common components of high altitude vegetation (e.g. Jackson 1965, 1972; Kirkpatrick 1977). It was hypothesised in Chapter 8 that N. cunninghamii would have a growth advantage over the other species under conditions where mild water deficits occurred due to its water-spender characteristics. However it is likely that this species may be intolerant of a more severe water deficit, so that on a gradient towards site dryness, it may decrease in abundance due to death caused by infrequent severe droughts. The only evidence to support the latter hypothesis at present lies in its absence from many gully forests of A. moschatum, but this distribution may also be explained in terms of fire history and dispersal characteristics. There is insufficient data to verify these hypotheses at present.

On the most extreme sites (temperature, soil quality, dryness) the canopy composition may be determined by tolerance rather than the outcome of competition processes, with the same trend in species composition shown in Fig. 10.1. Parsons (1966) and Grime (1979) suggest that an inherent slow growth rate is often a factor allowing tolerance of extreme conditions but it is not really clear whether this is a "strategy" or a cost, and Huston (1979, 1980) noted that on sub-optimal sites competition processes will be slowed by slow growth rates so that species may co-occur together for longer.

In summary then, the canopy composition of Tasmanian rainforest is determined by the interactions of the availabilty of propagules together with growth rate responses to site conditions (physical and biotic) and life history and size characteristics, and the disturbance regime. Where one feature of the environment is clearly dominating, e.g. temperature, the outcome is predictable, but interacting features of the environment will complicate

Fig. 10.1 Predicted patterns of species distribution
along three environmental gradients away from the moist,
mild, fertile optimum. Species are listed where they
would be expected to increase in proportion in the canopy.

A. selaginoides   A. moschatum

            ↖   ↗
                Decreasing   Increasing
                temperature   dryness

                ↖ Moist, mild, fertile ↗
                        optimum
                    N. cunninghamii

                    ↘
                Decreasing
                soil quality

                        ↙
E. lucida
P. aspleniifolius

the canopy composition of many sites, particularly in
association with unknown historical events which affect the
canopy composition by determining the initial floristic
composition.

Part C

Comparisons with _Nothofagus_ closed forest associations
on mainland Australia and in Chile.

Chapter 11   The population dynamics of some <u>Nothofagus</u>
              <u>moorei</u>-dominated rainforests.

Introduction

<u>N. moorei</u> occurs in disjunct stands of rainforest in the
highlands of north-eastern New South Wales and south-eastern
Queensland (Fig. 1.2). Unlike <u>N. cunninghamii</u> associations,
forests dominated by <u>N. moorei</u> are commonly bordered by
rainforests consisting of warm temperate and sub-tropical
species. Seedlings and saplings of these species are often
observed in forests dominated by <u>N. moorei</u> (Howard 1981) and
trees may occur in the canopy with <u>N. moorei</u>, and on these
sites <u>N. moorei</u> commonly fails to regenerate (Turner 1976).

In this chapter the population dynamics of <u>N. moorei</u> and
co-occurring woody species is examined on three sites in
N.S.W. and comparisons are made with the population dynamics
of <u>N. cunninghamii</u> as described in Chapter 2.

Methods

Site locations and details are summarised in Table 11.1.
The forests studied are dominated by <u>N. moorei</u> and did not
show any evidence of disturbance within the lifetime of the
living trees. A study site of 50 x 20 m, considered to be
representative of a large area of forest, was selected in
each forest. Tree diameters at breast height were recorded
in each site and canopy cover was measured by hemispherical
photographs as described in the methods section of Chapter
2. Ground cover by ferns and herbs was estimated in each
contiguous 5 x 5 m quadrat.

Results

New England
The study area is located in tall closed forest on a
35° north-easterly facing slope. <u>N. moorei</u> trees reach

Table 11.1 Summary of New South Wales study sites
with coordinates, altitude and % total basal area
of woody species.

New England National Park 30°30´S 152°25´E, 1560 m

Nothofagus moorei	82
Vesselowskya rubifolia	3
Ceratopetalum apetalum	3
Doryphora sassafras	1
Eucalyptus obliqua	10

Banda Banda Forest Preserve 31°10´S 152°24´E, 1050 m

N. moorei	65
C. apetalum	32
D. sassafras	1
Cryptocarya meisnerana	1
Orites excelsa	1

Barrington Tops State Forest 31°50´S 151°27´E, 1500 m

N. moorei	81
D. sassafras	15
Trochocarpa laurina	4

Table 11.2 Percentage of saplings (>10 cm high and <5 cm dbh) that have
originated vegetatively from the base of an older stem. Data is for each
canopy species containing $\geq$ 20 stems in this size class.

Species	Site		
	New England	Banda Banda	Barrington Tops
Nothofagus moorei	100	100	99
Doryphora sassafras	95	21	83
Ceratopetalum apetalum	82	85	
Vesselowskya rubifolia	100		
Cryptocarya meisnerana		38	
Tasmannia sp.		0	

38-40 m in height, with <u>Ceratopetalum apetalum</u> and <u>Doryphora</u> <u>sassafras</u> up to 20 m high. A single emergent <u>Eucalyptus</u> <u>obliqua</u> forms 10% of the total basal area. Ground ferns (including tree ferns) form 35% cover of the forest floor.

N. <u>moorei</u> is exhibiting continuous regeneration (Fig. 11.1) by vegetative reproduction (basal stem sprouts) (Table 11.2). Seedlings are infrequent in the rainforest and do not in general reach sapling size. However seedlings and saplings are common in nearby tall open forest dominated by eucalypts and on road edges. <u>C. apetalum</u> and <u>D. sassafras</u> are only represented in the small size classes (Fig. 11.1) and are regenerating primarily by vegetative reproduction (Table 11.2). <u>Vesselowskia rubifolia</u> is most frequent in the 5-14 cm size class (Fig. 11.1) and is regenerating only by vegetative sprouts (Table 11.2).

Barrington Tops

The study area is located in closed forest on a level site on the Barrington Tops plateau. N. <u>moorei</u> trees reach up to 28 m in height, with <u>D. sassafras</u> up to 15 m high and <u>Trochocarpa laurina</u> 5-8 m high. Ground ferns form less than 10% cover of the forest floor.

N. <u>moorei</u> is regenerating continuously on this site (Fig. 11.1), mainly by vegetative reproduction (Table 11.2). Small seedlings (<10 cm high) are common in canopy gaps created by the death of old trees but larger seedlings are common only on forest edges. <u>D. sassafras</u> is also regenerating continuously, mainly by vegetative stem sprouts (Table 11.2).

Banda Banda

The study area is located on a level site in a tall closed forest containing <u>N. moorei</u> trees up to 40 m high with <u>Ceratopetalum apetalum</u> up to 32 m high. Smaller trees of up to 10 m in height are also common, including <u>Cryptocarya meisnerana</u>, <u>D. sassafras</u> and <u>Tasmannia sp.</u> Ground ferns form less than 5% ground cover.

Fig. 11.1   Population size structures of the major
woody species on study sites (0.1 ha) in three
rainforests dominated by <u>Nothofagus moorei</u> in N.S.W.

a. New England National Park
b. Banda Banda Forest Preserve
c. Barrington Tops State Forest

a

N. moorei

C. apetalum

V. rubifolia

D. sassafras

No. of stems (log$_e$y+1)

Stem diameter (cm)

b

N. moorei

C. apetalum

D. sassafras

C. meisnerana

No. of stems (log$_e$y+1)

Stem diameter (cm)

c

N. moorei

D. sassafras

T. laurina

No. of stems (log$_e$y+1)

Stem diameter (cm)
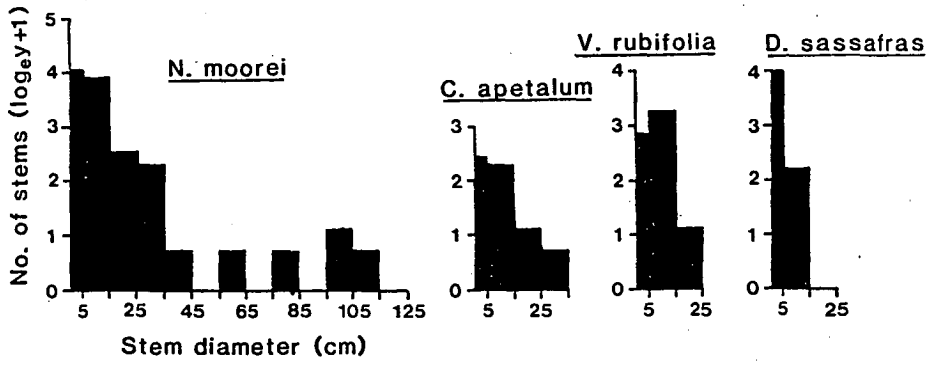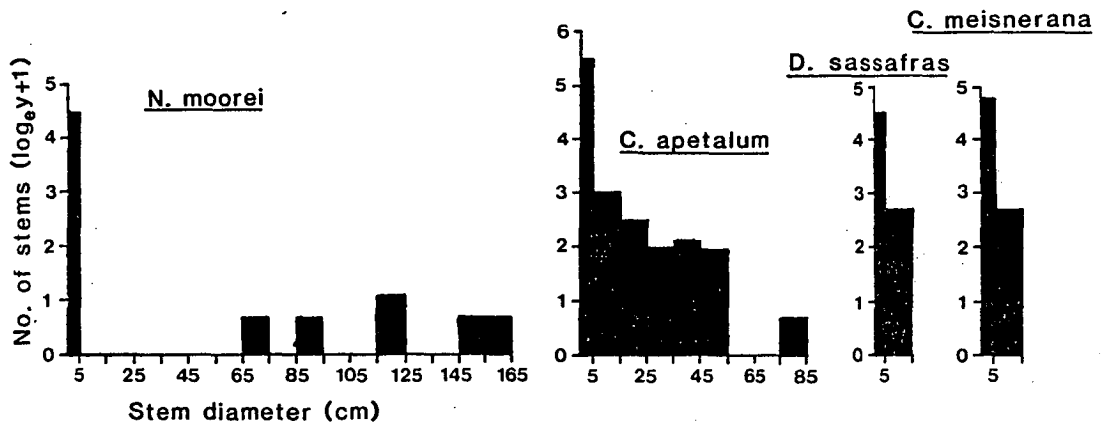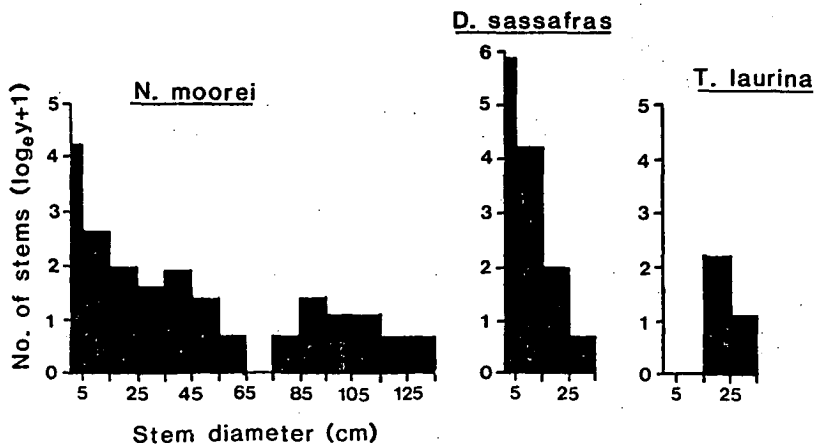
N. moorei is not regenerating continuously on this site
(Fig. 11.1). Although small seedlings (<10 cm high) occur
under the canopy and in canopy gaps caused by the death of a
large tree, larger seedlings are rare. The small stems
recorded on this site (Fig. 11.1) are stem sprouts which
originated from the base of three large trees. There was no
indication of any stem sprouts successfully reaching the
canopy on this site. Seedlings, saplings and stem sprouts of
N. moorei are common on nearby road edges. The other major
canopy species, C. apetalum, is regenerating continuously
(Fig. 11.1), mostly by vegetative means but also from seed
(Table 11.2). Saplings of this species persist under the
canopy and appear to replace N. moorei individuals on their
death. D. sassafras, C. meisnerana and Tasmannia sp. are
common in the small size classes and are regenerating under
the canopy vegetatively (except Tasmannia sp.) and from
seed.

The Banda Banda study site has the lowest percentage of
canopy opening of the sites measured (Table 12.3) and is
also the site of least N. moorei dominance and regeneration
and greatest percentage regeneration from seed of species
other than N. moorei (Table 11.2).

Discussion

Howard (1981) described the predominance of vegetative
reproduction in N. moorei, particularly at the northern
extreme of its range, although she noted that seedlings
readily establish on road edges. The predominance of
vegetative regeneration in N. moorei suggests that
rainforest dominated by this species may by
self-perpetuating, with self-replacement and overall
dynamics similar to those described in N.
cunninghamii-dominated rainforests. This appears true of N.
moorei in the Barrington Tops and New England study sites
where N. moorei is well-represented in the small size
classes. However, at Banda Banda, where warm temperate

species are common and the canopy is more closed, N. moorei
is failing to regenerate in the forest. Failure of N. moorei

regeneration and invasion by sub-tropical species is
reported in the lower altitudinal range of N. moorei at
Barrington Tops (Turner 1976). There is an apparent
correlation between succesful regeneration of N. moorei and
the infrequency of warm temperate and sub-tropical trees.
This appears to be related to the light environment for
regeneration of N. moorei since regeneration occurs on
adjacent disturbed sites and regeneration from seed is
observed in open forest dominated by eucalypts over a range
of altitudes and latitudes (Turner 1976). The lower light
levels associated with the presence of warm temperate and
sub-tropical species may be caused by a greater density of
foliage in the canopy or to a greater number of supressed
shade-tolerant species under the canopy in the more
species-diverse forests so that canopy gaps created by the
death of old N. moorei trees are effectively smaller and
quickly occupied by the shade-tolerant species. Some
evidence for the latter effect is shown in the frequency of
stems <5 cm dbh and >10 cm high of species other than N.
moorei in the Banda Banda study site which was twice the
number at Barrington Tops and nine times the number at New
England. The predominance of N. moorei seedlings and
saplings on disturbed sites suggests that the invading warm
temperate and sub-tropical species are most competitive in
shaded environments (within the current geographical range
of N. moorei).

The dynamics of the forests with a low frequency of warm
temperate and sub-tropical species are similar to the N.
cunninghamii forests in that Nothofagus is dominating the
forest and is self-replacing. The major difference lies in
the absence of seedling regeneration of N. moorei within any
forests except the eucalypt-dominated open forests. The N.
moorei-dominated rainforests examined in this study have
similar levels of canopy cover to those rainforests in which
N. cunninghamii is regenerating vegetatively and from seed

(Table 12.3). Therefore the light requirements of _N. moorei_ compared with _N. cunninghamii_ may explain the differences in dynamics of these two species, i.e. the widespread and successful regeneration of _N. cunninghamii_ in closed forest could be explained by greater shade-tolerance than _N. moorei_. This is further examined in the following chapter.

Chapter 12   Photosynthetic responses to light of some
            Australian and Chilean temperate rainforest
            species and their relevance to the rainforest
            dynamics.

Introduction

      There are some marked differences in the population
dynamics of the three Australian Nothofagus species. N.
gunnii fails to regenerate in closed forest although
seedlings may be common on the forest edge (Read & Hill
unpublished data). N. cunninghamii regenerates continuously
throughout the range of rainforest associations so far
studied (Chapter 2). The closely related N. moorei
regenerates in rainforest primarily by vegetative
reproduction but in its milder climatic range it often fails
to regenerate continuously and is being replaced by warm
temperate and sub-tropical rainforest species (Chapter 11).
The differences in dynamics of these forests suggests that
there may be differences in light requirements among the
Australian Nothofagus species, or in the characteristics of
co-occurring species.
      In Chile and New Zealand, Nothofagus species tend to be
restricted to sites which are climatically or edaphically
sub-optimal, or to sites which are exposed to recurrent
catastrophic disturbance (Wardle 1983,1984; Veblen et al.
1981). Wardle (1984) suggests that Nothofagus is better able
to tolerate harsh conditions than most other rainforest
species but that its seedlings are poor competitors. This
poor competitive ability on the more equable sites (moist
and mild on fertile soils) has been related at least in part
to higher light requirements of the Nothofagus species
relative to co-occurring canopy species (Veblen et al. 1981;
Wardle 1970). In south-eastern Australia, where N.
cunninghamii dominates rainforest on equable sites and
regenerates continuously, only Atherosperma moschatum has
been shown to be more shade-tolerant (Chapter 6), and it is

limited in its ability to expand its distribution in the
rainforest due to regeneration almost entirely by basal
sprouts from older stems (Chapter 2).

This chapter examines:

1) The comparative light requirements of the three
Australian Nothofagus species in order to relate these to
differences in the dynamics of the rainforests.

2) The light requirements of N. moorei relative to
co-occurring species (Ceratopetalum apetalum and Doryphora
sassafras, in order to relate any differences to the
dynamics of the N. moorei rainforests.

3) The light requirements of Eucryphia moorei relative to
co-occurring species (D. sassafras and C. apetalum) in order
to determine whether the relationship between dominant and
sub-dominant canopy species in terms of light requirements
is similar to the N. moorei rainforests. E. moorei dominates
cool temperate rainforest in north-east Victoria and
south-east New South Wales, between the distributions of N.
cunninghamii and N. moorei.

4) The light requirements of N. cunninghamii relative to the
Chilean lowland and mid-altitude species, N. dombeyi, N.
alpina and N. obliqua, in order to determine whether
differences in dynamics between the N. cunninghamii
rainforests of Tasmania and Victoria, and the lowland and
mid-altitude Nothofagus rainforests of south-central Chile
(39-42°S) can be related to differences in light
requirements of the Nothofagus species.

Methods

The Tasmanian species were grown from seed collected at
Mt Field National Park (42°41′S 146°40′E). Seedlings of the
New South Wales species were collected from Banda Banda
(31°10′S 152°24′E) (N. moorei, C. apetalum and D. sassafras)
and from Clyde Mountain (35°36′S 149°57′E) (E. moorei). The
Chilean species were grown from seed collected from the
botanical gardens of the Universidad Austral de Chile,

Valdivia. Seedlings of each species (six months-two years old at the start of the conditioning period) were grown in contrasting light regimes in a glasshouse from August to December 1984. All plants were grown in sandy loam, watered daily and nutriented weekly. This experiment was performed in conjunction with a comparative study of the light requirements of Tasmanian rainforest canopy species, and methods and results have been described for N. cunninghamii and A. moschatum already (Chapter 6). Eight plants of each species were grown unshaded in the glasshouse (approx. 80% of the P.A.R. of natural sunlight), and the same number shaded from direct sunlight so that maximum photon flux density (PFD) of unfiltered diffuse light was 30-80 μmol quanta m^{-2} s^{-1}. The daily maximum temperatures in the glasshouse for the seven weeks prior to and during measurement ranged from 23-31 ^{O}C with a mean maximum daily temperature of 26°C. Leaf temperature varied by less than 1^{O}C between the two light regimes.

N. gunnii has a poor survival rate when grown outdoors or in glasshouse conditions in Hobart. This is probably due to climatic differences between Hobart and the areas of natural occurrence of N. gunnii. Therefore, comparison of this species with N. cunninghamii was made by growing seedlings of both species in a controlled environment growth cabinet at 23°C day temperature and 20°C night temperature. The light source was composed of a 400W metal arc lamp, eight 40W fluorescent lamps and four 60W incandescent lamps during a 12 hour photoperiod. One group of plants was positioned to receive a PFD of 700-800 μmol quanta m^{-2} s^{-1} (daily photon flux = 30-35 mol quanta m^{-2} day^{-1}). This was the highest PFD possible in the growth cabinet. The second group of plants was shaded from the 400W metalarc lamp and received 50 μmol quanta m^{-2} s^{-1} (daily photon flux = 2 mol quanta m^{-2} day^{-1}) from the fluorescent and incandescant lights. Leaf temperature was 1-2^{O}C higher in the plants grown under the higher light intensity during the photoperiod. N. gunnii leaves produced in the shade regime

are similar in form to juvenile leaves (described by Hill 1984) and are not suitable for measurement of photosynthesis because of the small leaf size and leaf arrangement which prevents enclosure in the leaf chamber. This response of developing leaves is occasionally observed in seedlings of N. gunnii in the field where they are growing in relatively shaded sites but has not been observed in older plants.

An open gas exchange system incorporating a Series 225 infra-red gas analyser (Analytical Development Co. Ltd.) was used to measure the net rate of CO_2 assimilation at selected incident photon flux densities. The light source was a Sylvania 400W metalarc lamp. Photosynthetically active radiation was measured by a LiCor LI-185 meter with quantum sensor. The light intensities were obtained by varying the distance of the leaf chamber from the light source, and using shade cloth screens. Humidified air (317-340 μl l^{-1} CO_2) was pumped through a leaf chamber of cross-sectional area 10 cm^2 at a flow rate of 0.4 l min^{-1}. Moisture was condensed from the gas lines prior to analysis. CO_2 differentials were recorded on chart following equilibration of the leaf to the incident light conditions. Responses were first measured at 750 μmol quanta m^{-2} s^{-1} and subsequently at decreasing light intensities. Responses at PFDs higher than 750 μmol quanta m^{-2} s^{-1} were measured last to avoid potential lasting effects of photoinhibition at high PFDs. Leaf temperature was monitored by a thermocouple on the lower leaf surface and was maintained at 21$\pm$1°C. Temperatures of 20-23°C were optimal for all species. Leaf photosynthesis was measured only on young fully expanded leaves which developed in the experimental light conditions. Total replicates were five to eight, one leaf per plant. Leaf area was measured photometrically, varying in the range 3-10 cm^2, and leaf dry weight was measured. Leaf chlorophylls were extracted from one leaf per plant of each species, in 80% (v/v) acetone and estimated spectrophotometrically.

Results

All species show some photosynthetic acclimation to their growth light regime. N. moorei, N. cunninghamii and N. dombeyi grown in full sunlight have higher dark respiration rates (DRR), instantaneous light compensation points (LCP) and maximum rates of net photosynthesis (P_{max}) on a leaf area basis than shade-raised seedlings (Fig. 12.1, Tables 12.1 & 12.2). Sun-raised seedlings of N. obliqua and E. moorei have a higher DRR (Table 12.1) and P_{max} (Fig. 12.1) than shade-raised seedlings. Shade-raised seedlings of N. alpina have a lower LCP but there is no significant difference ($p < 0.05$) in DRR (Table 12.1) or P_{max} on a leaf area basis (Fig. 12.1e). Shade-raised seedlings of D. sassafras have a lower DRR and LCP (Table 12.1), and a slightly lower P_{max} on a leaf area basis than sun-raised seedlings (Fig. 12.1f). C. apetalum shows no significant difference in DRR, LCP (Table 12.1) and P_{max} on a leaf area basis (Fig. 12.1g) between treatments. Leaf chlorophyll was significantly higher in shade-raised seedlings of N. obliqua, N. dombeyi, C. apetalum, D. sassafras and E. moorei (Table 12.1). All species have lower light saturation points in shade-raised seedlings (Fig. 12.1) and there is no significant difference in apparent quantum yield between treatments or species (mean quantum yield is 0.066 μmol CO_2 μmol quanta^{-1}). There was no evidence of photoinhibition at PFD of up to 2500 μmol quanta m^{-2}s^{-1}.

There is no significant difference ($p < 0.05$) between N. moorei and N. cunninghamii in DRR, LCP or P_{max} on a leaf area basis or leaf dry weight basis, in either sun- or shade-raised seedlings (Fig. 12.1, Table 12.1). Similarly, N. cunninghamii and N. moorei do not differ from N. dombeyi in any of these features with the exception of P_{max} on a leaf dry weight basis which is higher in shade-raised N. dombeyi than in shade-raised seedlings of the other species, due to the high specific leaf area (SLA) of shade-raised N. dombeyi (Table 12.1).

Fig. 12.1.   Light-dependence curves of photosynthesis of
rainforest species grown in sun (▲) and shade (△)
conditions in a glasshouse. Each point is the mean of 5-8
replicates. The largest standard error is shown on each
curve, where it is greater than 0.25.

a. N. cunninghamii
b. N. moorei
c. N. dombeyi
d. N. obliqua
e. N. alpina
f. D. sassafras
g. C. apetalum
h. E. moorei.

f

Net photosynthesis (μmol m^{-2} s^{-1})

Photon flux density (μmol quanta m^{-2} s^{-1})

g

Net photosynthesis (μmol m^{-2} s^{-1})

Photon flux density (μmol quanta m^{-2} s^{-1})

h

Net photosynthesis (μmol m^{-2} s^{-1})

Photon flux density (μmol quanta m^{-2} s^{-1})
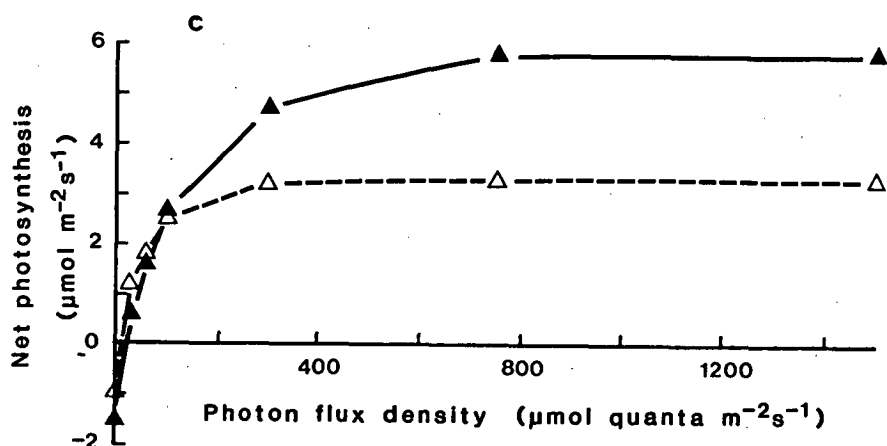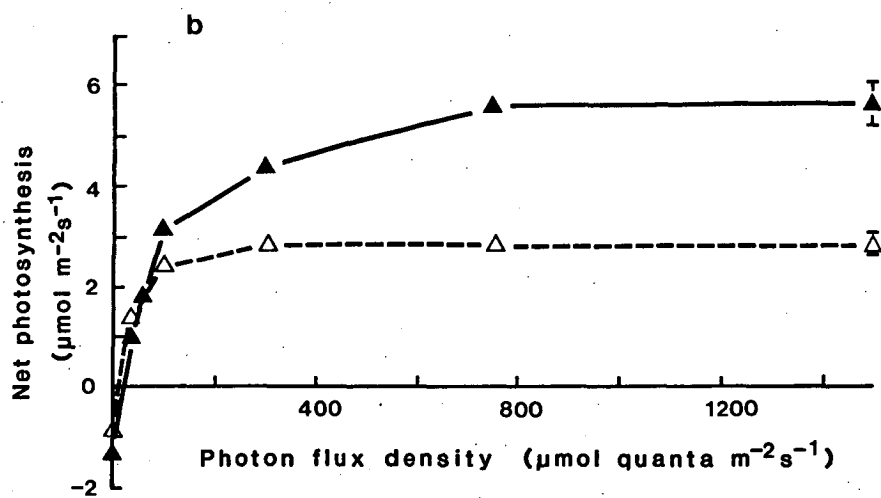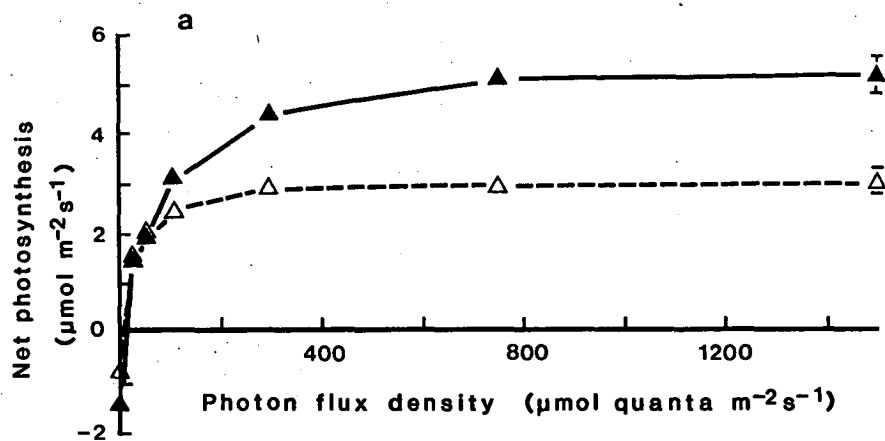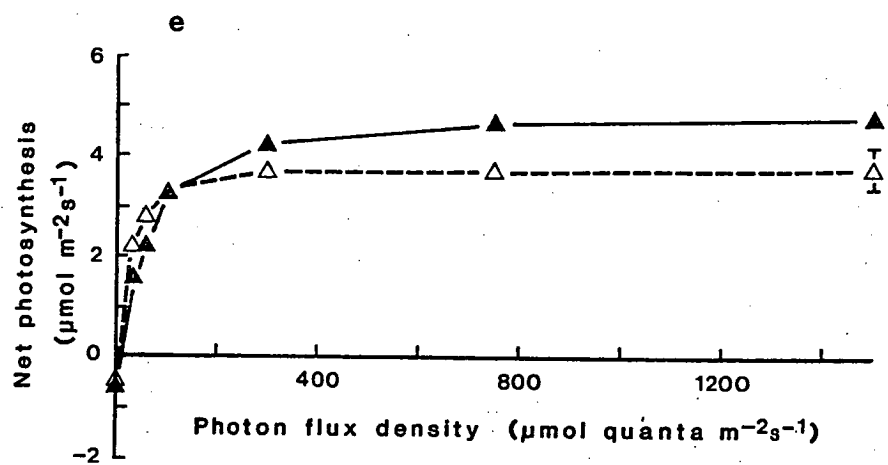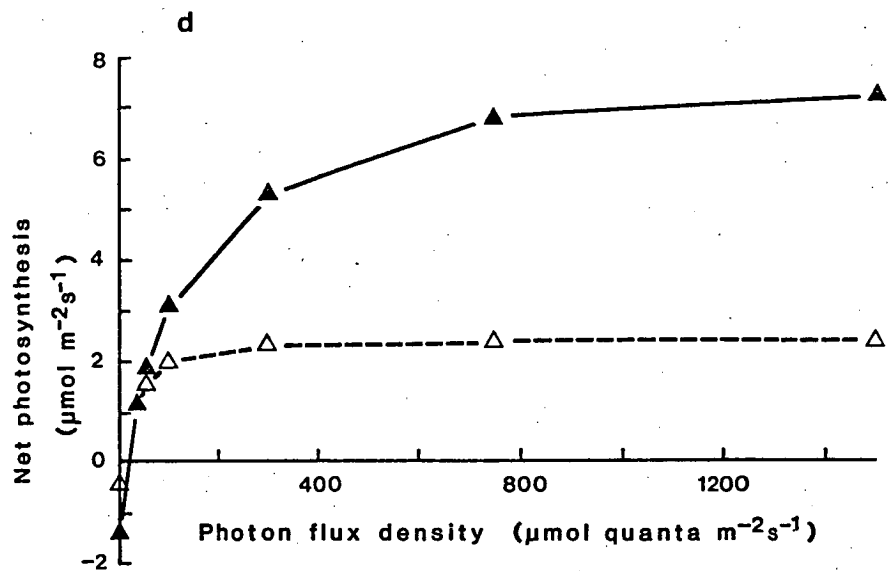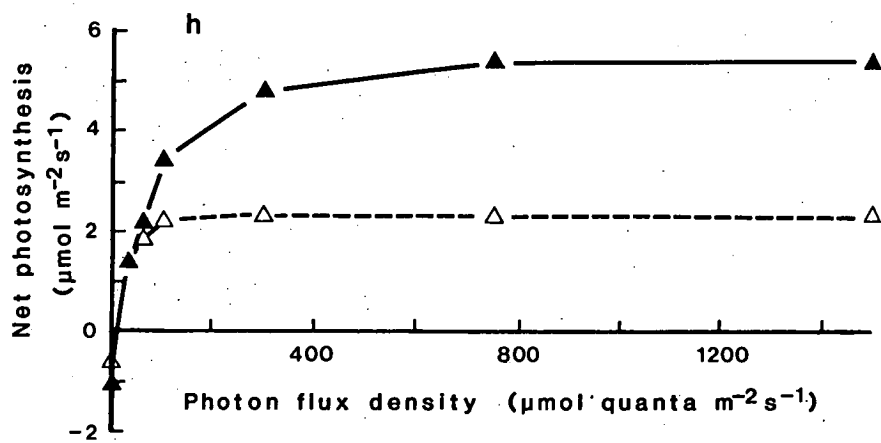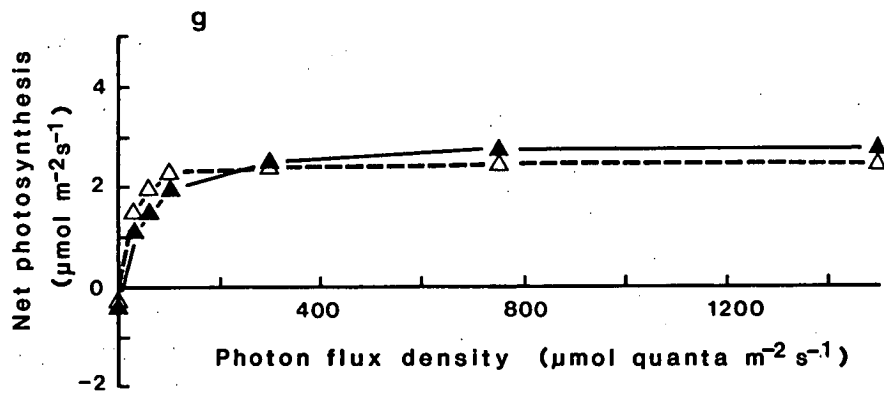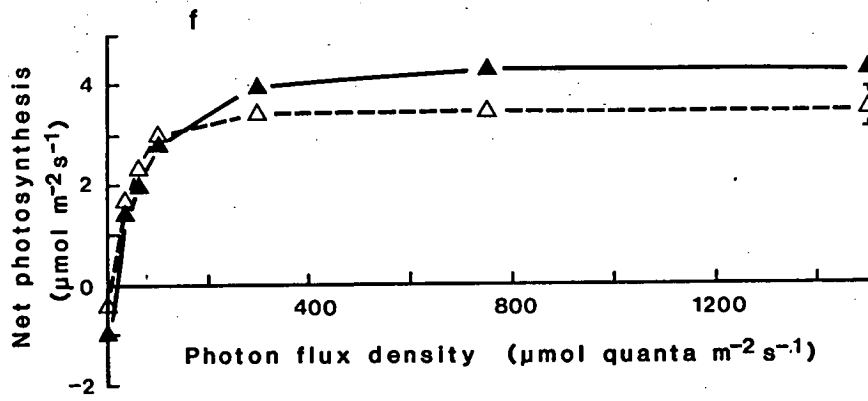
Fig. 12.2.   Light-dependence curves of photosynthesis of
seedlings of the Tasmanian <u>Nothofagus</u> species grown at high
(700-800 umol quanta $m^{-2}s^{-1}$) and low (50 umol quanta m^{-2} s^{-1})
photon flux densities in a controlled environment growth
cabinet. Each point is the mean of 5 replicates. The
largest standard error is shown on each curve, where it
is greater than 0.25.

<u>N. cunninghamii</u> raised in high PFD (▲) and low PFD (△).
<u>N. gunnii raised</u> in high PFD (●).
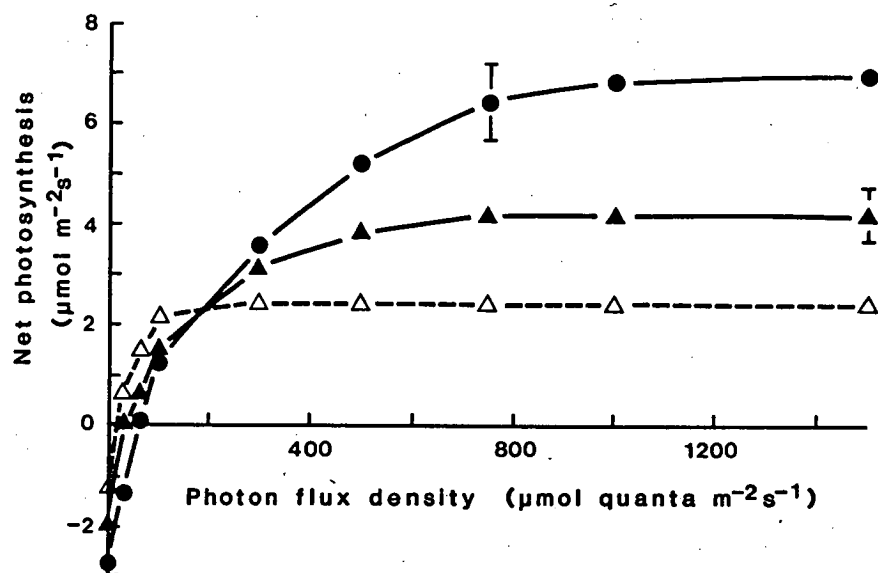
Table 12.1 Leaf characteristics and details from the light-dependence curves of plants raised in sun and shade conditions in the glasshouse. Each value is the mean of 5-8 replicates, with standard errors.

Species	Growth Light Regime	Specific Leaf Area ($m^2 g^{-1} \times 10^{-3}$)	Chlorophyll (mg m^{-2})	Dark Respiration Rate ($\mu mol\ m^{-2} s^{-1}$)	Light Compensation Point ($\mu mol\ quanta\ m^{-2} s^{-1}$)	P_{max} ($\mu mol\ g^{-1}$ leaf dry weight s$^{-1} \times 10^{-4}$)
Nothofagus cunninghamii[1]	sun	131 ± 7	383 ± 24	1.73 ± 0.12*	27 ± 3*	8.10 ± 0.61*
	shade	149 ± 8	406 ± 15	1.05 ± 0.12	17 ± 1	4.96 ± 0.31
Nothofagus moorei	sun	117 ± 3	403 ± 49	1.31 ± 0.15*	22 ± 3*	6.75 ± 0.48*
	shade	138 ± 12	416 ± 13	0.90 ± 0.14	13 ± 1	4.04 ± 0.58
Nothofagus obliqua	sun	228 ± 7*	263 ± 25*	1.44 ± 0.26*	19 ± 3	16.70 ± 1.12*
	shade	442 ± 4	460 ± 11	0.44 ± 0.10	12 ± 2	10.79 ± 1.46
Nothofagus alpina	sun	238 ± 20*	246 ± 26	0.65 ± 0.11	10 ± 1*	11.18 ± 0.95*
	shade	417 ± 18	293 ± 10	0.46 ± 0.10	7 ± 0	15.17 ± 1.10
Nothofagus dombeyi	sun	137 ± 16*	440 ± 41*	1.38 ± 0.15*	20 ± 2*	7.04 ± 1.14
	shade	316 ± 16	541 ± 8	0.85 ± 0.13	13 ± 1	8.85 ± 1.35
Ceratopetalum apetalum	sun	113 ± 5*	337 ± 32*	0.40 ± 0.07	9 ± 1	3.15 ± 0.31*
	shade	220 ± 26	434 ± 22	0.31 ± 0.04	6 ± 1	5.29 ± 0.50
Doryphora sassafras	sun	109 ± 4*	433 ± 10*	0.99 ± 0.18*	12 ± 3*	4.71 ± 0.36*
	shade	196 ± 19	611 ± 31	0.37 ± 0.06	6 ± 2	7.11 ± 0.59
Eucryphia moorei	sun	137 ± 6*	377 ± 20*	1.02 ± 0.07*	14 ± 2	7.26 ± 0.40*
	shade	186 ± 15	487 ± 1	0.60 ± 0.14	11 ± 2	4.26 ± 0.27

* Sun and shade treatments of the same species differ at the 95% significance level.
[1] Data from Chapter 6.

Table 12.2 Leaf characteristics and details from the light-dependence curves of plants raised in a controlled environment growth cabinet. Each value is the mean of five replicates, with standard errors.

Species	Growth Light Regime ($\mu mol\ quanta\ m^{-2} s^{-1}$)	Specific Leaf Area ($m^2 g^{-1} \times 10^{-3}$)	Chlorophyll (mg m^{-2})	Dark Respiration Rate ($\mu mol\ m^{-2} s^{-1}$)	Light Compensation Point ($\mu mol\ quanta\ m^{-2} s^{-1}$)	P_{max} ($\mu mol\ g^{-1}$ leaf dry weight s$^{-1} \times 10^{-4}$)
Nothofagus cunninghamii	700-800	119 ± 9*	402 ± 9*	1.90 ± 0.08*	31 ± 4*	5.06 ± 0.39*
	50	152 ± 11	451 ± 12	1.27 ± 0.18	18 ± 2	3.65 ± 0.21
Nothofagus gunnii	700-800	151 ± 7	380 ± 14	2.78 ± 0.10	62 ± 7	11.97 ± 1.01

* Values differ between light treatments at the 95% significance level.

N. alpina, C. apetalum and D. sassafras have lower DRRs and LCPs than the other species (Table 12.1), and have a relatively poor ability to acclimate photosynthetically to high light intensities during growth (Fig. 12.1). Shade-raised seedlings of these species have a higher P_{max} on a leaf dry weight basis than sun-raised seedlings due to high SLAs (Table 12.1).

The three deciduous Nothofagus species, N. gunnii, N. alpina and N. obliqua, have a high SLA and P_{max} on a dry weight basis compared with seedlings of the other species (Tables 12.1 & 12.2). The P_{max} of N. obliqua is highest in sun-raised seedlings and of N. alpina is highest in shade-raised seedlings (Table 12.1). N. gunnii has a higher DRR, LCP and light saturation point than N. cunninghamii (Fig. 12.2, Table 12.2). It also has a high P_{max} on both leaf area and leaf dry weight bases (Fig. 12.2, Table 12.2).

Discussion

Australian Nothofagus species

N. gunnii has a higher light requirement for net photosynthesis than N. cunninghamii, based on its higher P_{max}, LCP, DRR and light saturation point and its production of juvenile leaves in shaded conditions. This is consistent with the observed failure of N. gunnii to regenerate in closed vegetation (Read & Hill unpublished data) in contrast with the continuous regeneration of N. cunninghamii in closed forest in which it commonly occurs with the more shade-tolerant Atherosperma moschatum.

N. cunninghamii and N. moorei do not differ significantly in any of the responses to light examined. However N. moorei regenerates in rainforest only in the species-poor forests occurring in the cooler climates at high altitudes and latitudes, although it commonly regenerates from seed throughout its range on disturbed

sites and in the more open-canopied Eucalyptus forests
(Herbert 1936; Fraser & Vickery 1938; Turner 1976; Read &
Hill 1985). Sub-tropical and warm temperate species
including Doryphora sassafras and Ceratopetalum apetalum,
commonly occur with N. moorei in its warmer climatic range
and regenerate continuously (Turner 1976; Read & Hill 1985).
Similarly, in southern New South Wales Eucryphia moorei
commonly dominates temperate rainforest at high altitudes
and in its lower altitudinal range occurs with D. sassafras
and C. apetalum (Helman 1983). The low DRR, LCP and poor
photosynthetic acclimation to high light conditions
exhibited by D. sassafras and C. apetalum are typical of
shade-tolerant plants (Bjorkman 1981) and indicate that they
are more shade-tolerant than both N. moorei and E. moorei.
It appears that the low altitude and latitude limit of N.
moorei regeneration within undisturbed rainforest is caused
primarily by its shade-intolerance relative to co-occurring
warm temperate and sub-tropical tree species. This may also
be true of E. moorei but there is little information
regarding its regeneration.

Chilean Nothofagus species

The photosynthetic light-dependence curves indicate
that the deciduous N. alpina is the most shade-tolerant of
the Nothofagus species examined, based on its low DRR and
instantaneous LCP. Veblen et al. (1980) note the apparent
shade-tolerance of N. alpina compared with N. dombeyi, based
on its more frequent regeneration in canopy gaps in mixed
rainforest though the regeneration is commonly insufficient
to maintain its abundance. N. obliqua does not show any
significant difference in photosynthetic characteristics
from N. dombeyi other than in a higher P_{max} in sun-grown
plants. Both species fail to regenerate in mixed rainforests
at low to mid-altitudes in Chile (Veblen et al. 1979).

Comparisons of the Nothofagus forests of
south-central Chile and Australia

The structure of the mixed rainforests (rainforests
composed of Nothofagus and other canopy species) occurring
on relatively fertile soils in Chile and Australia is
similar in the relatively open understorey and closed
canopy, usually with the crowns of the large, old Nothofagus
trees extending above the other canopy species (described by
Howard (1981) and Veblen et al. (1980)). Two hypotheses,
that there are physiological differences among these
Nothofagus species, and that competition with co-occurring
species accounts for these differences in dynamics, are
proposed by Read & Hill (1985) to account for the
differences in dynamics between the Nothofagus rainforests
of south-central Chile and south-east Australia (dominated
by N. cunninghamii). These hypotheses can be extended to
include N. moorei rainforests since N. moorei regenerates
continuously only at the cooler extremes of its range (high
altitudes and/or latitudes) (Turner 1976; Howard 1981;
Chapter 11) and therefore more closely resembles the
dynamics of Chilean Nothofagus rainforests than the N.
cunninghamii rainforests.

Shade-tolerance is the most likely physiological
characteristic of the Nothofagus species to correlate with
the observed differences in dynamics. However results
presented here show no significant difference in the
photosynthetic light-dependence curves of N. cunninghamii,
N. moorei and N. dombeyi that could account for the ability
of N. cunninghamii to regenerate continuously in mixed
rainforest. The levels of canopy cover in Tasmanian
rainforests are within the range of those of Chilean and
N.S.W. forests (Table 12.3). The Banda Banda forest of has
the lowest percentage of canopy opening of the N.S.W.
rainforests that were measured (Table 3), and is the site
where shade-tolerant trees form a significant proportion of
the canopy and where N. moorei is not regenerating

continuously (Chapter 11). However, several Tasmanian sites where N. cunninghamii is regenerating continuously have similarly low levels of canopy opening (Table 12.3). Differences in the light climate of these regions may explain the failure of N. moorei to regenerate from seed in the forests where shade-tolerant species do not form a large component of the basal area of the forest e.g. Barrington Tops and New England. Sunlight hours in Coffs Harbour (30°19′S 153°07′E, 5 m a.s.l.), the nearest station for which this data is recorded, are similar in summer to the sunlight hours recorded at Tasmanian stations, and are higher in winter (Bureau of Meteorology records). However there is no reliable means of estimating photosynthetically active radiation from this data.

The major differences between cool temperate rainforests of Chile and Tasmania are the consistently low number of shade-tolerant canopy species in Tasmania (Table 12.3) and the regeneration strategies and light requirements of species which occupy canopy gaps. Gaps in Chilean mixed rainforest are quickly occupied by bamboo (Chusquea species) and root suckers and seedlings of shade-tolerant canopy species which may already be present in supressed form and which prevent regeneration of Nothofagus species (Veblen et al. 1980, 1981). In contrast, canopy gaps in mixed rainforest in Tasmania are usually occupied by saplings of the relatively shade-intolerant species (e.g. N. cunninghamii and Eucryphia lucida) except where gaps are created by the death of stems of A. moschatum which is usually multi-stemmed and self-replacing (Chapter 2). A. moschatum is the only common canopy species occurring with N. cunninghamii that is more shade-tolerant and its distribution through the forest is limited by its localised vegetative reproduction and infrequent establishment from seed. There is no evidence of any widespread cool temperate shade-tolerant canopy species occurring with N. moorei but in its warmer climatic range it is being replaced by warm temperate and sub-tropical species (Turner 1976, Howard

Table 12.3 Site data from <u>Nothofagus</u> associations in Chile and Australia.

Site		Altitude (m a.s.l.)	Potential diffuse and direct sunlight (%)	No. of canopy species[1]			Reference
				Total	Nothofagus[2]	Shade-tolerant[3]	
Chile [4]							
Conguillo N.P.	C3	1460	55.8 ± 7.5	2	1 (1)	1	Veblen (1982)
38°40′S 71°39′W	4	1440	29.4 ± 5.6	2	1 (1)	1	"
	5	1410	41.0 ± 8.3	2	1 (1)	1	"
	6	1330	37.0 ± 1.7	2	1 (0)	1	"
Nahuelbuta N.P.	N1	1330	28.2 ± 2.5	2	1 (1)	1	"
37°38′S 73°03′W							
Antillanca		1020		2	2 (1)	0	Veblen et al.
40°47′S 72°12′W		1040		2	2 (1)	0	(1977ab)
		1020		2	2 (1)	0	"
		1040		2	2 (1)	0	"
San Pablo	S1&2	810	17.3 ± 1.5	4	1 (0)	3	Veblen, Schlegel
39°33′S 72°03′W	3	850	14.0 ± 1.6	4	1 (0)	3	& Escobar (1980)
Valle Hermoso	V1	830		4	2 (0)	2	"
40°01′S 71°55′W	2	800	26.5 ± 2.1	4	2 (0)	2	"
	3	880	22.2 ± 1.3	5	2 (0)	3	"
Pirihueico	P1,2&3	1060	31.3 ± 2.2	4	2 (0)	2	"
39°54′S 71°52′W							
Lake Villarrica		250		6	2 (0)	4	Veblen, Ashton
39°12′S 72°10′W							& Schlegel (1979)
Valle Hermoso	H1	940	46.9 ± 3.0	2	2 (1)	0	Veblen et al.
40°01′S 71°55′W	2	940	27.9 ± 1.3	2	2 (1)	0	(1981)
	3	950	30.4 ± 1.7	3	2 (0)	1	"
	4	880	24.3 ± 1.6	5	2 (0)	3	"
Pilmaiquen	Q1	740	34.2 ± 1.3	1	1 (0)	0	"
39°57′S 71°55′W	2	810	28.0 ± 2.1	4	2 (0)	2	"
Remeco	R1	1250	48.2 ± 5.8	2	2 (0)	0	"
39°46′S 71°56′W	2	1200	46.6 ± 4.5	2	2 (2)	0	"
	3	1250	35.5 ± 2.2	2	2 (?)	0	"
Choshuenco	C1	1200	40.4 ± 2.5	1	1 (0)	0	"
39°56′S 72°03′W	2	1120	44.2 ± 3.1	1	1 (?)	0	"
New South Wales [5]							
Barrington Tops		1500	21.1 ± 3.6	2	1 (1)	1	Chapter 11
31°50′S 151°27′E							
Banda Banda		1050	8.7 ± 1.4	4	1 (0)	2	"
31°10′S 152°24′E							
New England N.P.		1560	17.5 ± 3.3	3	1 (1)	1	"
30°30′S 152°25′E							

Continued overleaf

Table 12.3   Continued

Site		Altitude (m a.s.l.)	Potential diffuse and direct sunlight (%)	No. of canopy species			Reference
				Total	Nothofagus	Shade-tolerant	
Tasmania [6]							
Sumac Road 41°09′S 145°01′E		180	24.8 ± 3.5	3	1 (1)	1	Chapter 2
Parrawe 41°21′S 145°34′E		580	19.2 ± 4.0	2	1 (1)	1	"
Stephens Rivulet 41°10′S 144°57′E		140	31.3 ± 3.6	2	1 (1)	1	"
Frodsham's Pass 42°50′S 146°23′E		580	12.8 ± 2.8	3	1 (1)	1	"
Arve Loop 43°08′S 146°45′E		360	22.5 ± 4.3	3	1 (1)	1	"
Mt Michael 41°10′S 148°00′E		740	14.0 ± 2.4	3	1 (1)	1	"
Diddleum 41°22′S 147°31′E		820	14.1 ± 2.6	2	1 (?)	1	"
Weindorfer's Forest 41°38′S 145°57′E	W1	920	17.0 ± 2.2	2	1 (1)	0	"
	W2	920	30.7 ± 3.4	3	1 (1)	1	"
Ballroom Forest 41°40′S 145°57′E	B1	940	5.0 ± 1.6	3	1 (1)	1	"
Mt Anne 42°56′S 146°26′E		850	22.4 ± 3.6	3	1 (1)	1	"
Dempster 41°12′S 145°03′E		220	15.7 ± 2.7	5	1 (1)	1-2	"
Pieman Dam Road 41°44′S 145°26′E		200	7.3 ± 2.6	5	1 (1)	1-2	"
Murchison 41°47′S 145°38′E		300	10.5 ± 4.2	6	1 (1)	1-2	"
Hastings 43°24′S 146°51′E		120	9.1 ± 3.7	6	1 (1)	1-2	"
Sawback 42°49′S 146°21′E		480	6.9 ± 1.1	6	1 (?)	1?	"

[1] Species are only included where they form part of the canopy or are emergent.

[2] The number in brackets indicates the number of Nothofagus species on the study site that are regenerating continuously.

[3] Species listed are considered to be more shade-tolerant than co-occurring Nothofagus species.

[4] Chilean canopy trees suggested as more shade-tolerant than Nothofagus species: Aextoxicon punctatum, Laurelia philippiana, L. sempervirens, Dasyphyllum diacanthoides, Saxegothea conspicua and Persea linque (Veblen & Ashton 1978); Araucauria araucana (Veblen 1982); Eucryphia cordifolia and Weinmannia trichosperma are uncertain (Veblen et al. 1981) and are not included.

[5] C. apetalum and D. sassafras are the only canopy species on these sites that are more shade-tolerant than N. moorei.

[6] A. moschatum is known to be more shade-tolerant than N. cunninghamii (Chapter 6). Anodopetalum biglandulosum occurs in the canopy with N. cunninghamii on some sites and regenerates continuously by vegetative reprodution, but its shade-tolerance relative to N. cunninghamii is not known.

1981) including the relatively shade-tolerant <u>D. sassafras</u>
and <u>C. apetalum</u> (Chapter 11). The success of these species
in autogenically replacing <u>N. moorei</u>, compared with the
failure of <u>A. moschatum</u> to replace <u>N. cunninghamii</u>, may
result from more succesful establishment strategies than <u>A.
moschatum</u>. For example, at Banda Banda, where shade-tolerant
species are replacing <u>N. moorei</u>, regeneration from seed is
more common in <u>C. apetalum</u> and <u>D. sassafras</u> than usually
occurs in <u>A. moschatum</u> (0-18%, Chapter 2). The average
percentage of establishments from seed are also higher at
Banda Banda in species other than <u>N. moorei</u> than at the
other N.S.W. sites. The only site recorded in Tasmania
(Gilbert 1959) where <u>A. moschatum</u> appeared to be replacing
<u>N. cunninghamii</u> was one on which <u>A. moschatum</u> was frequently
establishing from seed. The photosynthetic light-dependence
curves presented here and in Chapter 2 do not indicate any
superiority in the shade-tolerance of <u>D. sassafras</u> and <u>C.
apetalum</u> compared with <u>A. moschatum</u>, but ecologically
significant differences may not be distinguishable
experimentally with such low light compensation points (5-6
μmol quanta m^{-2} s^{-1}).

 <u>Nothofagus</u> in New Zealand increases in importance in
forests away from the moist, mild, fertile optimum (P.
Wardle 1964, 1983). On these less optimal sites <u>Nothofagus</u>
may regenerate continuously, primarily by seedling
establishment in canopy gaps created by the death of old
trees (e.g. June & Ogden 1978). J. Wardle (1970) suggested
that the decline in importance of <u>Nothofagus</u> species towards
the moist, mild fertile optimum was due to a lower
shade-tolerance relative to co-occurring species on optimal
sites (no data on comparative shade-tolerance is available).
He also noted that the density and species richness of the
forest understorey increases towards the ecotone with the
softwood/broad-leaved hardwood forest. On these sites,
species which sucker or develop epicormic branches such as
<u>Weinmannia</u> and <u>Quintinia</u> have an advantage after partial
forest disturbance. However, as in Chile, catastrophic

disturbance (fire, mass movements and climatic disturbances)
commonly leads to regeneration of <u>Nothofagus</u> species
(summarised by J. Wardle 1984) and some forests consist of a
mosaic of single, two-aged or three-aged stands (J. Wardle
1970).

The impact of catastrophic disturbance
on <u>Nothofagus</u> in Australia

The impact of catastrophic disturbance on the
regeneration of <u>Nothofagus</u> in Australia is less predictable
than in Chile (and probably New Zealand) and may differ
among the three species. Fire is the most commonly reported
type of disturbance in temperate Australia. <u>N. gunnii</u> is
very fire-sensitive and regenerates after fire only in a
restricted range of conditions (Kirkpatrick 1977). <u>N.
cunninghamii</u> may regenerate after fire if the fire-free
intervals are·long and a seed source is available (Gilbert
1959). However, unlike the situation in Chile (Veblen <u>et. al</u>
1981), catastrophic disturbance (usually fire) has in
general restricted the distribution of <u>N. cunninghamii</u>
within its climatic range. Communities of plants with
relatively xeromorphic characters are promoted by
interactions of fire-frequency with vegetation and soil
nutrients (Jackson 1968; Howard 1981). <u>N. moorei</u> forests are
often similarly constrained in their distribution (Howard
1981). The frequency and effect of catastrophic disturbance
on the regeneration of <u>N. moorei</u> where it occurs with warm
temperate and sub-tropical rainforest species would be of
particular interest in understanding whether the commonly
observed failure of <u>N. moorei</u> to regenerate at lower
altitudes and latitudes is due to long-term climatic trends
(Turner 1976) or to cycles of infrequent stand regeneration
following catastrophic events such as fire or storm. Veblen
<u>et al</u>. (1981) noted that <u>Nothofagus</u> is infrequent or absent
in the rainforest of the coastal cordillera in Chile. They
suggested that this was due to the infrequency of

catastrophic disturbance in this region, but noted that the milder climate may be of significance in the low frequency of Nothofagus. These forests have a higher species richness than the forests dominated by Nothofagus (Veblen et al. 1981) and may be analogous to the warm temperate rainforest of eastern Australia in their structure and dynamics.

REFERENCES

Amen, R.D. (1966). The extent and role of seed dormancy in alpine plants. Quart. Rev. Biol., 41, 271-281.

Anderson, M.C. (1970). Radiation and crop structure. In: Plant Photosynthetic Production. Manual of Methods (Ed. by Z. Sestak, J. Catsky & P.G. Jarvis), pp. 412-466. Dr W. Junk N.V. Publishers, The Hague.

Aronsson, A. & Eliasson, L. (1970). Frost hardiness in Scots pine (Pinus sylvestris L.). I. Conditions for test on hardy plant tissues and for evaluation of injuries by conductivity measurements. Stud. For. Suec., 77, 1-30.

Ash, J. (1982). The Nothofagus Blume (Fagaceae) of New Guinea. In: Biogeography and Ecology of New Guinea (Ed. by J.L. Gressitt), Vol. 1, pp. 355-380. Dr W. Junk Publishers, The Hague.

Ashton, D.H., Bond, H. & Morris, G.C. (1975) Drought damage on Mount Towrong, Victoria. Proc. Linn. Soc. N.S.W., 100, 44-69.

Bazzaz, F.A. (1979). The physiological ecology of plant succession. Ann. Rev. Ecol. Syst. 10, 351-371.

Beadle, N.C.W. (1968). Some aspects of the ecology and physiology of Australian xeromorphic plants. Aust. J. Sci., 30, 348-355.

Berry, J.A. & Bjorkman, O. (1980). Photosynthetic response and adaptation to temperature in higher plants. Ann. Rev. Plant Physiol., 31, 491-543.

Billings, W.D. (1938). The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. Ecol. Mono., 8, 437-499.

Björkman, O. (1981). Responses to different quantum flux densities. In: Physiological Plant Ecology I. Physical Environment (Ed. by O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegeler), pp. 58-107. Springer-Verlag,

Berlin.

Boardman, N.K. (1977). Comparative photosynthesis of
sun and shade plants. A. Rev. Pl. Physiol. 28,
355-77.

Bormann, F.H. (1953). Factors determining the role of
loblolly pine and sweetgum in early old-field
succession in the Piedmont of North Carolina.
Ecol. Mono., 23, 339-358.

Bowen, G.D. (1981). Coping with low nutrients. In: The
Biology of Australian Plants (Ed. by J.S. Pate &
A.J. McComb), pp. 33-64. University of Western
Australia Press, Nedlands.

Bray, J.R. (1956). Gap-phase replacement in a maple-
basswood forest. Ecology, 37, 598-600.

Brown, M.J. & Podger, F.D. (1982). Floristics and fire
regimes of a vegetation sequence from sedgeland-heath
to rainforest at Bathurst Harbour, Tasmania. Aust.
J. Bot., 30, 659-676.

Burke, M.J., Gusta, L.V., Quamme, H.A., Weiser, C.J.
& Li, P.H. (1976). Freezing and injury in plants.
Ann. Rev. Plant Physiol., 27, 507-528.

Busby, J.R. (1984). Nothofagus cunninghamii (Southern
Beech) Vegetation in Australia. Australian Flora and
Fauna series, no. 1. Aust. Govt. Publ. Serv.,
Canberra.

Busby, J.R. & Bridgewater, P.B. (1977). Vegetation
associated with Nothofagus cunninghamii. Proc.
Roy. Soc. Vic., 89, 173-182.

Calais, S.S. & Kirkpatrick, J.B. (1983). Tree species
regeneration after logging in temperate rainforest,
Tasmania. Pap. Proc. Roy. Soc. Tasm., 117, 77-83.

Clayton-Greene, K.A. (1977). Structure and origin of
Libocedrus bidwillii stands in the Waikato District,
New Zealand. N.Z. J. Bot., 15, 19-28.

Cockayne, L. (1958). The Vegetation of New Zealand. 3rd
Edn. H.R. Engelmann (J. Cramer), London.

Connell, J.H. & Slatyer, R.O. (1977). Mechanisms of

succession in natural communities and their role in community stability and organisation. Amer. Natur., 111, 1119-1144.

Connor, D.J. & Tunstall, B.R. (1968). Tissue water relations for Brigalow and Mulga. Aust. J. Bot., 16, 487-490.

Curtis, W.M. (1963). The Student's Flora of Tasmania Part 2. pp. 225-475. Govt. Printer, Tasmania.

Curtis, W.M. (1967). The Student's Flora of Tasmania Part 3. pp. 465-661. Govt. Printer, Tasmania.

Curtis, W.M. & Morris D.I. (1975). The Student's Flora of Tasmania Part 1. pp. 1-240. Govt. Printer, Tasmania.

Davies, J.B. (1983). Huon pine survey, 1983. Wildl. Divn. Tech. Rept. 83/2. National Parks & Wildlife Service, Hobart.

Dawson, J.W. (1966). Observations on Nothofagus in New Caledonia. Tuatara, 14, 1-7.

Dexter, S.T., Tottingham, W.E. & Graber, L.F. (1930). Preliminary results in measuring the hardiness of plants. Plant Physiol., 5, 215-223.

Dexter, S.T., Tottingham, W.E. & Graber, L.F. (1932). Investigations of the hardiness of plants by measurement of electrical conductivity. Plant Physiol., 7, 63-78.

Egler, F.E. (1954). Vegetation science concepts. I. Initial floristic composition - a factor in old-field vegetation development. Vegetatio 4, 412-417.

Flint, H.L., Boyce, B.R. & Beattie, D.J. (1967). Index of injury - a useful expression of freezing injury to plant tissues as determined by the electrolytic method. Can. J. Plant Sci., 47, 229-230.

Florence, R.G. (1981). The biology of the eucalypt forest. In: The Biology of Australian Plants (Ed. by J.S. Pate & A.J. McComb), pp. 147-180. University of Western Australia Press.

Floyd, A.G. (1978). N.S.W. Rainforest Trees. Part VII.

Forestry Commission of N.S.W., Sydney.

Forcier, L.K. (1975). Reproductive strategies and the co-occurrence of climax tree species. Science, 189, 808-810.

Fraser, L. & Vickery, J.W. (1938). The ecology of the upper Williams River and Barrington Tops districts. II. The rainforest formations. Proceedings of the Linnean Society of New South Wales, 63, 139-184.

Gilbert, J.M. (1959). Forest succession in the Florentine Valley, Tasmania. Pap. Proc. Roy. Soc.Tasm., 93, 129-151.

Grime, J.P. (1965). Comparative experiments as a key to the ecology of flowering plants. Ecology, 46, 513-515.

Grime, J.P. (1979). Plant Strategies and Vegetation Processes. John Wiley & Sons, New York.

Grime, J.P. & Hunt, R. (1975). Relative growth rate, its range and adaptive significance in a local flora. J. Ecol., 63, 393-422.

Grubb, P.J. (1977). The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52, 107-145.

Harper, J.L. (1977). Population Biology of Plants. Academic Press, New York. 892 pp.

Helman, C.E. (1983). An altitudinal gradient in southern New South Wales rainforests. Proceedings of the Ecological Society of Australia, 12, 166-167.

Herbert, D.A. (1936). An advancing antarctic beech forest. Queensland Naturalist, 10, 8-10.

Hett, J.M. & Loucks, O.L. (1976). Age structure models of balsam fir and eastern hemlock. J. Ecol., 64, 1029-1044.

Hickey, J.E. (1982). Natural and artificial regeneration of some Tasmanian rainforest trees. In: Tasmanian Rainforests - Recent Research Results (Ed. K. Felton), pp. 47-53. Forest Ecology Research Fund, Hobart.

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 Forestry Research_, 13, 21-28.

Hill, R.S. (1982). Rainforest fire in western Tasmania. _Aust. J. Bot._, 30, 583-589.

Hill, R.S. (1983a). _Nothofagus_ macrofossils from the Tertiary of Tasmania. _Alcheringa_, 7, 169-183.

Hill, R.S. (1983b). Evolution of _Nothofagus cunninghamii_ and its relationship to _N. moorei_ as inferred from Tasmanian macrofossils. _Australian Journal of Botany_, 31, 453-465.

Hill, R.S. (1984). Tertiary _Nothofagus_ macrofossils from Cethana, Tasmania. _Alcheringa_, 8, 81-86.

Hill, R.S. & Read, J. (1984). Post-fire regeneration of rainforest and mixed forest in western Tasmania. _Aust. J. Bot._, 32, 481-493.

Hoffmann J., A. (1982). _Flora Silvestre de Chile: Zona Austral_. Fundacion Claudio Gay, Santiago.

Holloway, J.T. (1964) The forests of the South Island: the the status of the climate change hypothesis. _N.Z. Geogr._, 20, 1-9.

Howard, T.M. (1970). The ecology of _Nothofagus cunninghamii_ Oerst. Ph.D. Thesis, University of Melbourne.

Howard, T.M. (1973a). Studies in the ecology of _Nothofagus cunninghamii_ Oerst. I. Natural regeneration on the Mt Donna Buang Massif, Victoria. _Australian Journal of Botany_, 21, 67-78

Howard, T.M. (1973b). Studies in the ecology of _Nothofagus cunninghamii_ Oerst. II. Phenology. _Aust. J. Bot_. 21, 79-92.

Howard, T.M. (1973c). Studies in the ecology of _Nothofagus cunninghamii_ Oerst. III. Two limiting factors: light intensity and water stress. _Aust. J. Bot_. 21, 93-102.

Howard, T.M. (1973d). Accelerated tree death in mature _Nothofagus cunninghamii_ Oerst. forests in Tasmania. _Vict. Nat._ 90, 343-345.

Howard, T.M. (1974). _Nothofagus cunninghamii_ ecotonal
     stages. Buried viable seed in north-west Tasmania.
     Proc. R. Soc. Vict., 86, 137-142.

Howard, T.M. (1981). Southern closed forests. In:
     Australian Vegetation (Ed. by R.M. Groves), pp. 102-
     120. Cambridge University Press, London.

Howard, T.M. & Ashton, D.H. (1973). The distribution of
     Nothofagus cunninghamii rainforest. _Proc. Roy. Soc._
     Vict. 85, 47-75.

Hsiao, T.C. (1973). Plant responses to water stress.
     A. Rev. Pl. Physiol. 24, 519-570.

Hsiao, T.C., Avecedo, E., Fereres, E. & Henderson, D.W.
     (1976). Stress metabolism. _Phil. Trans. R. Soc. Lond._
     _B._, 273, 479-500.

Humphries, C.J. (1981). Biogeographical methods and the
     southern beeches. In: _The Evolving Biosphere_ (Ed. by
     P.L. Forey), pp. 283-297. Cambridge University Press.

Huston, M.A. (1979). A general hypothesis of species
     diversity. _Amer. Natur._, 113, 81-101.

Huston, M.A. (1980). Soil nutrient and tree species
     richness in Costa Rican forests. _J. Biogeogr._, 7,
     147-157.

Jackson, W.D. (1958). The vegetation of the Lower Pieman
     River region. Unpublished manuscript.

Jackson, W.D. (1965). Vegetation. In: _Atlas of Tasmania_
     (Ed. by J.L. Davies), pp. 30-35. Mercury Press, Hobart.

Jackson, W.D. (1968). Fire, air, water and earth - an
     elemental ecology of Tasmania. _Proceedings of the_
     Ecological Society of Australia, 3, 9-16.

Jackson, W.D. (1973). Vegetation of the Central Plateau.
     In: _The Lake Country of Tasmania_, (Ed. by M.R. Banks),
     pp. 61-86. Royal Society of Tasmania, Hobart.

Jackson, W.D. (1983). Tasmanian rainforest. In: _Tasmania's_
     Rainforest. What Future? (Ed. by R. Blakers &
     P. Robertson), pp. 9-39. Australian Conservation
     Foundation, Hobart.

Jarman, S.J. & Brown, M.J. (1983). A definition of cool

temperate rainforest in Tasmania. <u>Search</u>, 14, 81-87.

Jarman, S.J., Brown M.J. & Kantvilas, G. (1984).
<u>Rainforest in Tasmania</u>. National Parks & Wildlife
Service, Tasmania, Hobart.

Jarvis, P.G. & Jarvis, M.S. (1963). The water relations of
tree seedlings. IV. Some aspects of the tissue water
relations and drought resistance. <u>Physiol. Plant.</u>, 16,
501-515.

Johnston, R.D. & Lacey, C.J. (1983). Multi-stemmed trees in
rainforest. <u>Aust. J. Bot.</u>, 31, 189-195.

Jones, E.W. (1945). The structure and reproduction of the
virgin forest of the northern temperate zone. <u>New
Phytol.</u> 44, 130-148.

June, S.R. & Ogden, J. (1978). Studies on the vegetation
of Mount Colenso, New Zealand. 4. An assessment of the
processes of canopy maintenance and regeneration
strategy in a red beech (<u>Nothofagus fusca</u>) forest.
<u>N.Z. J. Ecol.</u>, 1, 7-15.

Kirkpatrick, J.B. (1977). Native vegetation of the west
coast region of Tasmania. In: <u>Landscape and Man</u> (Ed. by
M.R. Banks & J.B. Kirkpatrick), pp. 55-80. Royal
Society of Tasmania, Hobart.

Kirkpatrick, J.B. & Dickinson, K.J.M. (1983). <u>Vegetation
map of Tasmania, 1:500 000</u>. Forestry Commission,
Hobart.

Korner, Ch., Scheel, J.A. & Bauer, H. (1979). Maximum
leaf diffusive conductance in vascular plants.
<u>Photosynthetica</u>, 13, 45-82.

Levitt, J. (1980). <u>Responses of Plants to Environmental
Stresses. Vol. II. Water, Radiation, Salt and Other
Stresses</u>. Academic Press, N.Y.

Mayer, A.M. & Poljakoff-Mayber, A. (1982). <u>The germination
of seeds</u>. 3rd Edn. Pergamon Press, Oxford.

McCune, B. & Allen, T.F.H. (1985). Will similar forests
develop on similar sites? <u>Can. J. Bot.</u>, 63, 367-376.

McQueen, D.R. (1976). The ecology of <u>Nothofagus</u> and
associated vegetation in South America. <u>Tuatara</u>, 22,

38-68.

Morisita, M. (1959). Measuring of the dispersion of the dispersion of individuals and analysis of the distributional patterns. Mem. Fac. Sci. Kyushu Univ., 2, 215-235.

Mount, A.B. (1964). Three studies in forest ecology. M.Sc. Thesis, Univ. of Tasmania.

Mount, A.B. (1979). Natural regeneration processes in Tasmanian forests. Search, 10, 180-186.

Noble, I.R. & Slatyer R.O. (1978). The effect of disturbance on plant succession. Proc. Ecol. Soc. Aust., 10, 135-145.

Noble, I.R. & Slatyer, R.O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbance. Vegetatio, 43, 5-21.

Ogden, J. (1978). Investigations of the dendrochronology of the genus Athrotaxis D. Don (Taxodiaceae) in Tasmania. Tree-Ring Bull., 38, 1-13.

Ogden, J. & Powell, J.A. (1979). A quantitative description of the forest vegetation on an altitudinal gradient in the Mt. Field National Park, Tasmania, and a discussion of its history and dynamics. Aust. J. Ecol., 4, 293-295.

Palta, J.P., Levitt, J. & Stadelmann, J. (1977). Freezing injury in onion bulb cells. 1. Evaluation of the conductivity method and analysis of ion and sugar efflux from injured cells. Plant Physiol., 60, 393-397.

Parsons, R.F. (1968). The significance of growth rate comparisons for plant ecology. Amer. Natur., 102, 595-597.

Pedley, J., Brown, M.J. & Jarman, S.J. (1980). A survey of Huon pine in the Pieman River State Reserve and environs. Wild. Divn. Tech. Rept. 83/2, 66 pp., National Parks & Wildlife Service, Hobart.

Prickard, G.J. (1980). Land Systems of Tasmania, Region 4. Goverment Printer, Hobart.

Read, J. (1981). Patterns and processes in the regeneration of cool temperate rainforest in oldfields. Hons. thesis, Univ. of Tasmania.

Read, J. (1985). Photosynthetic and growth responses to different light regimes of the major canopy species of Tasmanian cool temperate rainforest. Aust. J. Ecol., 10, in press.

Read, J. & Hill, R.S. (1982). Rainforest invasion onto Tasmanian old-fields. Aust. J. Ecol., 8, 149-161.

Read, J. & Hill, R.S. (1985). Dynamics of Nothofagus-dominated rainforest on mainland Australia and lowland Tasmania. Vegetatio, 63, 67-78.

Richards, P.W. (1952). The Tropical Rain Forest. Cambridge University Press.

Richley, L.R. (1978). Land Systems of Tasmania, Region 3. Government Printer, Hobart.

Robbins, R.G. (1962). The podocarp-broadleaf forests of New Zealand. Trans. R. Soc. N.Z. (Bot.), 1, 33-75.

Sakai, A., Paton, D.M. & Wardle, P. (1981). Freezing resistance of trees of the south temperate zone, especially subalpine species of Australasia. Ecology, 62, 563-570.

Sakai, A. & Wardle, P. (1978). Freezing resistance of New Zealand trees and shrubs. N.Z. J. Ecol. 1, 51-61.

Sayers, R.L. & Ward, R.T. (1966). Germination responses in alpine species. Bot. Gaz., 127, 11-16.

Slatyer, R.O. (1958). The measurement of diffusion pressure deficit in plants by a means of vapour equilibration. Aust. J. Biol. Sci. 11, 349-365.

Slatyer, R.O. (1961). Internal water balance of Acacia aneura F. Muell. in relation to environmental conditions. In: Plant-Water Relationships in Arid and Semi-Arid Conditions, pp.137-146. Proc. of the Madrid Symposium. UNESCO, PARIS.

Specht, R.L. (1970). Vegetation. In: The Australian Environment (Ed. by G.W. Leeper), 4th Edn (rev.), pp. 44-67. C.S.I.R.O. Australia and Melbourne

University Press, Melbourne.

Turner, J.C. (1976). An altitudinal transect in rain forest in the Barrington Tops area, New South Wales. Australian Journal of Ecology, 1, 155-174.

van den Driessche, R. (1976). Prediction of cold hardiness in Douglas fir seedlings by index of injury and conductivity methods. Can. J. For. Res. 6, 511-515.

Veblen, T.T. (1982). Regeneration patterns in Araucaria araucana forests in Chile. Journal of Biogeography, 9, 11-28.

Veblen, T.T. & Ashton, D.H. (1978). Catastrophic influences on the vegetation of the Valdivian Andes, Chile. Vegetatio, 36, 147-167.

Veblen, T.T., Ashton, D.H. & Schlegel, F.M. (1979). Tree regeneration strategies in a lowland Nothofagus-dominated forest in south-central Chile. Journal of Biogeography, 6, 329-340.

Veblen, T.T., Ashton, D.H., Schlegel, F.M. & Veblen, A.T. (1977a). Distribution and dominance of species in the understorey of a mixed evergreen-deciduous Nothofagus forest in south-central Chile. Journal of Ecology, 65, 815-830.

Veblen, T.T., Ashton, D.H., Schlegel, F.M. & Veblen, A.T. (1977b). Plant succession in a timberline depressed by vulcanism in south-central Chile. Journal of Biogeography 4, 275-294.

Veblen, T.T., Donoso Z., C., Schlegel, F.M. & Escobar, R.B. (1981). Forest dynamics in south-central Chile. Journal of Biogeography, 8, 211-247.

Veblen, T.T., Schlegel, F.M. & Escobar R., B. (1980). Structure and dynamics of old-growth Nothofagus forests in the Valdivian Andes, Chile. Journal of Ecology 68, 1-31.

Veblen, T.T. & Stewart, G.H. (1982). On the conifer regeneration gap in New Zealand: the dynamics of Libocedrus bidwillii stands on South Island. J. Ecol., 70, 413-436.

Wardle, J.A. (1970). The ecology of Nothofagus solandri. 4. Growth, and general discussion to parts 1 to 4. New Zealand Journal of Botany, 8, 609-646.

Wardle, J.A. (1984). The New Zealand Beeches: Ecology, Utilisation and Management. New Zealand Forest Service, Wellington.

Wardle, P. (1964). Facets of the distribution of forest vegetation in New Zealand. N.Z. J. Bot., 2, 352-366.

Wardle, P. (1978). Regeneration of some New Zealand conifers, with particular reference to Libocedrus bidwillii in Westland National Park. N.Z. J. Bot., 16, 471-477.

Wardle, P. (1983). Temperate broad-leaved evergreen forests of New Zealand. In: Temperate Broad-Leaved Evergreen Forests (Ed. by J.D. Ovington),pp. 33-72. Elsevier, Amsterdam.

Weatherley, P.E. (1950). Studies in the water relations of the cotton plant. I. The field measurements of water deficit in leaves. New Phytol., 49, 81-97.

Weatherley, P.E. & Slatyer, R.O. (1957). Relationships between relative turgidity and diffusion pressure deficit in leaves. Nature, 179, 1085-1086.

Webb, L.J. (1959). A physiognomic classification of Australian rainforest. J. Ecol., 47, 551-570.

Williams, J.B. (1982). Checklist of the Rainforest Flora of New South Wales. Dept of Botany and Dept of Continuing Education, Univ. of New England, Armidale.

Williamson, G.B. (1975). Pattern and seral composition in an old-growth beech-maple forest. Ecology, 56, 727-731.

Wilner, J. (1960). Relative and absolute electrical conductance tests for frost hardiness of apple varieties. Can. J. Plant Sci., 40, 630-637.