

THE ECOLOGY AND BIOGEOGRAPHY OF ATHROTAXIS D. DON.

James by
Philip J. Cullen B.Sc. (Forestry)

submitted in fulfilment of
the requirements for the
degree of
Master of Science

UNIVERSITY OF TASMANIA

HOBART

February 1987

*to be conferred
1988*



DECLARATION

This thesis contains no material which has been submitted for the award of any other degree or diploma in any university and contains no copy or paraphrases of material previously published or writtern by another person, except where due reference is made in the text.

P. J. Cullen.

CONTENTS

	PAGE
ACKNOWLEDGEMENTS	I
ABSTRACT	II
LIST OF FIGURES	IV
LIST OF TABLES	VI
LIST OF PLATES	VIII
CHAPTER 1: INTRODUCTION	1
CHAPTER 2: DISTRIBUTION AND SYNECOLOGY	
2.1 Introduction	8
2.2 Methods	14
2.3 Results and Discussion	
2.3.1 Stand Classification	19
2.3.2 Stand Ordination	32
CHAPTER 3: THE REGENERATION MODES OF <u>ATHROTAXIS</u> <u>CUPRESSOIDES</u> AND <u>ATHROTAXIS SELAGINOIDES</u>	
3.1 Introduction	38
3.2 Methods	
3.2.1 Stand demography	40
3.2.2 Spatial distribution of seedlings	43
3.2.3 Seed dispersal	44
3.2.4 Vegetative reproduction	45
3.3 Results and Discussion	
3.3.1 Size/age correlations	48
3.3.2 Seed production and dispersal	52
3.3.3 Vegetative regeneration	55
3.3.4 Stand demography and seedling distribution of <u>Athrotaxis cupressoides</u>	60
3.3.5 Stand demography and seedling distribution of <u>Athrotaxis selaginoides</u>	82
3.3.6 The presence of <u>Athrotaxis laxifolia</u>	88
3.4 Conclusion	89

CHAPTER 4:	THE RELATIVE FROST RESISTANCE OF <u>ATHROTAXIS CUPRESSOIDES</u> AND <u>ATHROTAXIS</u> <u>SELAGINOIDES</u> SEEDLINGS	
4.1	Introduction	92
4.2	Methods	93
4.3	Results	96
4.4	Discussion	99
CHAPTER 5:	THE EFFECT OF GRAZING ON THE SEEDLING REGENERATION OF <u>ATHROTAXIS CUPRESSOIDES</u>	
5.1	Introduction	107
5.2	Methods	107
5.3	Results	109
5.4	Discussion	111
CHAPTER 6:	DISCUSSION	116
REFERENCES		135
APPENDIX A:	REGENERATION PATTERNS IN POPULATIONS OF <u>ATHROTAXIS SELAGINOIDES</u> D. DON. FROM TASMANIA	150
APPENDIX B:	TWINSpan CLASSIFICATION OF THE 57 SAMPLE STANDS X 114 SPECIES	188
APPENDIX C:	PRELIMINARY INVESTIGATIONS OF THE RELATIVE DROUGHT RESISTANCE AND TOLERANCE TO WATERLOGGING OF <u>A. CUPRESSOIDES</u> AND <u>A. SELAGINOIDES</u> SEEDLINGS	195

ACKNOWLEDGEMENTS

I would like thank Dr. J. B. Kirkpatrick for his excellent supervision of this thesis. I am also in debt to Dr. G. van de Geer for his help and advice, and I would like to thank Sian Smith and Ian Thomas for their continous encouragement and assistance. Thanks must also be directed to Dr. M. J. Brown and J. S. Jarman for their help.

This project was funded by grants from the Australian Heritage Commission to the Tasmanian Conservation Trust and from the University of Tasmania. I am grateful for the assistance I have recieved from the staff of these institutions.

ABSTRACT.

The coniferous tree species Athrotaxis cupressoides and Athrotaxis selaginoides and a probable hybrid, A. laxifolia, form the genus Athrotaxis, which is endemic to Tasmania. These species are found in a wide range of cool temperate rainforest, subalpine scrub, and alpine heath communities in central, western, and southern Tasmania. Athrotaxis species are slow growing, extremely long lived, and very fire sensitive.

The floristic composition, site characteristics, and demographic structure of Athrotaxis populations were investigated at 57 rainforest and subalpine scrub stands dominated by either A. cupressoides or A. selaginoides. The distribution of A. cupressoides largely coincides with those areas occupied by trees where extreme frosts are most common. In areas where both species occur, A. cupressoides is more likely to be found at higher altitudes or in cold valley bottoms. Subsequent trials demonstrated that A. cupressoides seedlings are more frost resistant than A. selaginoides seedlings. Field observations and preliminary experimental investigations indicated that neither differences in drought resistance nor tolerance to waterlogging are important in determining the relative distributions of these two species.

For both species seed dispersal is restricted to areas within a few tens of metres of parent trees, except when seeds fall into flowing water. The demographic structure of Athrotaxis populations is strongly related to the floristic composition of the communities in which they are found. A. selaginoides relies on gap formation or catastrophic disturbance for regeneration opportunities in forests dominated by evergreen species (thamnic and callidendrous rainforests). However, in

forests containing a high proportion of the deciduous tree, Nothofagus gunnii, (implicate rainforests) and in subalpine scrub communities A. selaginoides regenerates continuously. A. cupressoides regenerates continuously in open montane rainforests, often by producing root suckers. This species is also capable of regeneration following catastrophic disturbance. However, stands of A. cupressoides on the Central Plateau of Tasmania have no, or low, numbers of seedling sized individuals. Trials suggest that this regeneration failure is due to grazing by both introduced and native mammals. In undisturbed thamnic and implicate rainforests the species cannot regenerate successfully. Demographic structure and floristic composition of these communities indicates that they are seral stages in a succession from open montane to thamnic and implicate communities without A. cupressoides.

It is probable that the colder conditions and a higher incidence of catastrophic disturbance during full glacial and interstadial climates would have been advantageous to Athrotaxis species. However, the loss of Athrotaxis populations and lack of regeneration in many cases must be attributed to the activities of Europeans in Tasmania and not to an inability to survive under the present climate.

LIST OF FIGURES.

2.1 The distribution of <u>A. cupressoides</u> and effective precipitation.	9
2.2 The distribution of <u>A. selaginoides</u> and effective precipitation.	10
2.3 The ecological ranges of <u>A. cupressoides</u> and <u>A. selaginoides</u> .	13
2.4 The location of sites investigated in this study.	15
2.5 Dendrogram of the TWINSpan classification.	20
2.6 Axis 1 versus axis 2 for the ordination of sample stands using DECORANA.	33
2.7 Score on axis 1 of the ordination versus stand altitude.	34
3.1 The phenology of <u>A. cupressoides</u> and <u>A. selaginoides</u> .	53
3.2 <u>A. cupressoides</u> and <u>A. selaginoides</u> seedling distribution.	54
3.3 Percent frequency versus size class histograms of <u>A. cupressoides</u> .	63
3.4 Percent frequency versus size class histograms of <u>A. cupressoides</u> .	65
3.5 Percent frequency versus size class histograms of <u>A. cupressoides</u> .	67
3.6 Percent frequency versus size class histograms of <u>A. cupressoides</u> .	68
3.7 Percent frequency versus size class histograms of <u>A. cupressoides</u> .	69
3.8 Percent frequency versus size class histograms of <u>A. cupressoides</u> .	71
3.9 Percent frequency versus size class histograms of <u>A. cupressoides</u> .	72
3.10 Profile diagrams of <u>A. cupressoides</u> stands.	74

	V
3.11 Percent frequency versus size class histograms of stands dominated by <u>A. selaginoides</u> not included in Appendix A.	85
4.1 The location of seedling collection sites and climate recording stations.	94
4.2 The distribution of <u>A. cupressoides</u> and temperature efficiency.	102
4.3 The distribution of <u>A. selaginoides</u> and temperature efficiency.	103
5.1 The location of grazing trial study sites.	108

APPENDIX A

Fig. 1 The distribution of <u>A. selaginoides</u> and annual precipitation in Tasmania.	155
Fig. 2 Axis 1 versus axis 2 for the ordination of <u>A. selaginoides</u> sample stands using DECORANA.	163
Fig. 3a Percent frequency versus size class histograms for <u>A. selaginoides</u> .	165
Fig. 3b Percent frequency versus size class histograms for <u>A. selaginoides</u> .	168

APPENDIX C

Fig. 1 Rate of moisture loss of <u>A. cupressoides</u> and <u>A. selaginoides</u> seedlings.	198
--	-----

LIST OF TABLES.

2.1	Stand designation, location, and characteristics of <u>A. cupressoides</u> stands.	16
2.2	Stand designation, location, and characteristics of <u>A. selaginoides</u> stands.	17
2.3	<u>A. cupressoides</u> stands on the Central Plateau. Floristic group, site quality, and average slope.	21
3.1	Age/diameter relationships and mean annual growth rates for <u>A. selaginoides</u> and <u>A. cupressoides</u> .	49
3.2	The relationship between age and diameter for <u>A. cupressoides</u> .	51
3.3	<u>A. cupressoides</u> stands on the Central Plateau ranked according to average no of stems per clump.	59
3.4	Correlation of percent frequency versus size class with the Power Function Model for sample stands of <u>A. cupressoides</u> .	62
3.5	Nearest neighbour distance in open montane rainforests on the Central Plateau.	76
3.6	Correlation of percent frequency versus size class with the Power Function Model for sample stands of <u>A. selaginoides</u> .	84
4.1	Glasshouse temperatures prior to frosting trials.	97
4.2	The survival of <u>A. cupressoides</u> and <u>A. selaginoides</u> following exposure to low temperatures.	98
4.3	Extreme minimum temperatures recorded at stations close to or within the range of <u>A. cupressoides</u> and <u>A. selaginoides</u> .	104
5.1	The effect of grazing on <u>A. cupressoides</u> seedlings.	110
6.1	The distance from extant populations of <u>A. cupressoides</u> in southern and western Tasmania to the nearest area at 200 m a.s.l.	126
APPENDIX A.		
Tab. 1	Stand designation, location, and characteristics of <u>A. selaginoides</u> stands.	157

	VII
Tab. 2 Canopy height and basal area of <u>A. selaginoides</u> stands.	161
APPENDIX B.	
Tab. 1 TWINSpan classification.	194
APPENDIX C.	
Tab. 1 The survival of <u>A. cupressoides</u> and <u>A. selaginoides</u> seedlings following periods of drought.	196
Tab. 2 Root/Shoot ratios of <u>A. cupressoides</u> and <u>A. selaginoides</u> .	199

LIST OF PLATES.

3.1 A root connection between two <u>A. cupressoides</u> stems.	46
3.2 A clump of vegetatively reproduced <u>A. cupressoides</u> stems.	47
3.3 <u>A. cupressoides</u> root suckers.	57
3.4 Lateral roots on <u>A. cupressoides</u> .	58
4.1 Variation in the foliage of <u>A. laxifolia</u> seedlings.	100
5.1 Browsing damage on <u>A. cupressoides</u> sucker regeneration.	114

CHAPTER 1.
INTRODUCTION.

Conifer species are widespread in cool temperate South America, New Zealand, and Tasmania (c 38°S to 55°S). They are found in communities ranging from tall lowland forests, through montane forests, to subalpine woodland and scrub, and alpine heath.

As with other taxa, such as Nothofagus, many of the conifer genera are common to two or all three of the regions. Podocarpus is found in southern South America, New Zealand, and Tasmania, as is Dacrydium (now divided into four genera; Dacrydium, Halocarpus, Lagarostrobos, and Lepidothamnus by Quinn (1982)). Phyllocladus is found in Tasmania and New Zealand. Libocedrus is found in New Zealand with a close relative, Austrocedrus in South America. The genus Fitzroya from South America and Diselma in Tasmania are closely related as are Saxegothaea (South America) and Microcachrys (Tasmania). These taxonomic links have been attributed to the common origins of the genera in the ancient continent Gondwanaland (Raven and Axelrod, 1972; Jardine and McKenzie, 1972; Moore, 1972; Smith, 1975).

Many of these species are slow growing and extremely long lived. In South America, Araucaria araucana (Mol.) C. Koch. can live for more than 1300 years (Veblen, 1982)

and Fitzroya cupressoides (Mol.) Johnston. has been recorded between 2000 to 3000 years of age (Veblen and Ashton, 1982). Conifers over 600 years old are common in New Zealand forests. For instance, Libocedrus bidwillii Hook. f. stems have been aged at between 600 and 700 years by Clayton-Greene (1977). In Tasmania, Athrotaxis species have been recorded in excess of 1000 years (Ogden, 1978), and Lagarostrobos franklinii (Hook.) Quinn. can survive for between 2000 and 3000 years (Davies, 1983).

Schmithusen (1960) considered the southern Andean conifers as relict from the Tertiary period, and now forced to occupy sites of inferior quality (ie. rocky, dry, cold, wet, or low fertility sites) due to an inability to compete with more aggressive broadleaved species under the prevailing climate. Fossil evidence which points to a much wider distribution of the southern conifer genera in the past (Florin, 1963) supports this view.

Holloway (1954) proposed that the New Zealand conifers were unable to regenerate under present climatic conditions, and were in the process of being replaced by hardwood species. Nicholls (1956), Wardle (1963a,b, 1978), Elder (1963), and Grant (1963) produced evidence to support this hypothesis. This view is based on the premise that the New Zealand conifers, if growing under

optimum conditions, will form all-aged populations. In tall lowland forests the general condition of the conifer populations is often one of overmaturity and lack of regeneration or, when regeneration is present, large temporal gaps between regeneration and the next age class. On the other hand, hardwood species in these forests are regenerating continuously. However, recent research in Chile and New Zealand has suggested that at least some species, eg. Araucaria araucana (Veblen, 1982) and Libocedrus bidwillii (Clayton-Green, 1977; Veblen and Stewart, 1982; Norton, 1983), are well-adapted to their contemporary environments. Veblen et al. (1983) discuss the importance of wide scale catastrophic disturbance, resulting from volcanic and seismic activity in a variety of Chilean forest types. Araucaria araucana appears able to survive this type of disturbance and also displays a strategy of gap-phase regeneration. Combined with its longevity, these mechanisms allow it to maintain dominance once established in an area (Veblen, 1982). Investigations of Libocedrus bidwillii show that it takes advantage of both gaps and infrequent catastrophic disturbances for regeneration opportunities (Clayton-Greene, 1977; Veblen and Stewart, 1982; Norton, 1983).

Hutchinson (1932) reported a similar strategy for Dacrydium cupressinum Lamb. It displayed both "selection

life history", regeneration in gaps and "even aged life history", with regeneration occurring over extensive areas after windthrow of the previous forest. In addition to these two species, regeneration following catastrophic disturbance has been reported for a number of other conifers in New Zealand (McKelvey, 1953; Cameron, 1960; Llyod, 1960; Beveridge, 1973; Burke, 1974).

Contrary to the view of Schmithusen (1960), Veblen (1982a) argued, for the South American conifers, that competition avoidance by the occupation of inferior niches may be interpreted as an evolutionary response to exploit these more extreme habitats, rather than evidence of relict status. At least some of the New Zealand conifers found in suboptimal sites show adaptations which favour them in these positions. Halocarpus bidwillii (Hook. f. ex T. Kirk.) Quinn. has developed a high tolerance to low temperatures (Wardle and Campbell, 1976; Sakai et al., 1981). Podocarpus nivalis Hook. has developed a prostrate habit which enables it to withstand damage and colonize active scree slopes (Wardle, 1972). Phyllocladus alpinus Hook. f. exists as distinct ecotypes suited to the varying habitats which it occupies (Wardle, 1969; Sakai et al., 1981). Holloway (1954) saw the invasion of swamp communities by Lagarostrobos colensoi (Hook.) Quinn. and Lepidothamnus intermedius (T. Kirk.) Quinn. and the invasion of existing stands of these

species by D. cupressinum as evidence for a change to a drier climate. Burrows and Greenland (1979) point out that the distribution of these species may relate to edaphic rather than climatic factors and instances of L. colensoi under D. cupressinum have been reported (Franklin, 1968). Edaphic factors also appear to be important in the distribution of Podocarpus dacryioides A. Rich. and Dacrydium cupressinum (Wardle, 1974).

Very little has been published on the regeneration strategies of Tasmanian conifers. Millington et al. (1979) found Lagarostrobos franklinii to be regenerating in areas estimated to have been free from disturbance for around 3000 years. Davies (1983) reports young even-aged stands of L. franklinii that appear to have established following fires. This species has also been observed colonizing riverside shingle and mine tailing deposits (Kirkpatrick, 1977a). Phyllocladus asplenifolius* appears to be well adapted to regenerate following catastrophic disturbance as it is often found colonizing disturbed ground. It has been suggested that birds play an important role in the dispersal of this species and this may be a reason for its apparent rapid post-glacial expansion (Macphail, 1980).

* Species nomenclature follows Curtis (1963, 1967) and Curtis and Morris (1975), except where indicated.

Ogden (1978) has found evidence suggesting discontinuous regeneration in populations of Athrotaxis cupressoides and A. selaginoides, and Kirkpatrick and Harwood (1980) have found similar evidence for A. selaginoides. By contrast, Calais and Kirkpatrick (1983) observed a size structure implying continuous replacement of A. selaginoides in undisturbed forest.

The genus Athrotaxis is now endemic to Tasmania but fossil evidence indicates a wider distribution in the past (Florin, 1963). It is the only member of the family, Taxodiaceae, in the southern hemisphere. Three species have been recognized in the genus Athrotaxis; A. cupressoides (Pencil Pine), A. selaginoides (King Billy Pine), and A. laxifolia. A. cupressoides and A. selaginoides have distinct but overlapping distributions and A. laxifolia is usually found where A. cupressoides and A. selaginoides are growing in close proximity. The distribution, morphology (intermediate between the other two species), and a report of segregation in progenies of A. laxifolia (Clifford and Constantine, 1980) suggest that A. laxifolia is a hybrid (see also Plate 4.1). However, chromosome investigation has not thrown light on this question (Gulline, 1952). Usually A. laxifolia occurs as isolated individuals but on rare occasions it forms populations of varying ages. As these populations are of limited extent the study is confined to the other

two species A. cupressoides and A. selaginoides.

Large areas of A. cupressoides and A. selaginoides have been destroyed by fire since the arrival of Europeans in Tasmania (Jackson, 1973; Kirkpatrick, 1977a) and there appears to be little or no regeneration on many of these sites. The increases in forestry operations, hydro-electricity development, mining exploration, and road building activities associated with these works have increased the chances of many remaining stands being burnt in the future. Also the general upsurge in wilderness recreation has increased the potential threat from fire. Consequently there is concern for the conservation of the genus.

The present study was undertaken to investigate the comparative ecology of A. cupressoides and A. selaginoides, in particular; variations in the floristic composition and structure of forests dominated by these species (Chapter 2); the factors influencing the relative distribution of A. cupressoides and A. selaginoides (Chapters 2 and 4); the regeneration modes of the two species (Chapter 3). Chapter 5 discusses the effect of grazing on the regeneration of A. cupressoides and chapter 6 integrates the preceding chapters. Some of the results of the study are in press and are included as Appendix A. Part of these results have subsequently been verified by Read (1986).

CHAPTER 2

DISTRIBUTION AND SYNECOLOGY.

2.1 Introduction.

Athrotaxis species are confined to high rainfall regions in Tasmania (Figs 2.1, 2.2) where they can be found in a wide range of lowland, montane, and subalpine rainforest, scrub, and heath communities. Many of these communities have not been the subject of detailed investigation. There is a considerable overlap in the distribution of A. cupressoides and A. selaginoides, and on occasions they occur in mixture or in close proximity. However, for the larger part of their ranges the two species have distinctly different distributions (Figs 2.1, 2.2).

Situated between latitudes 41°S and 43°S, Tasmania has a cool temperate maritime climate, dominated by a moist westerly air stream. In the region where Athrotaxis species are found, the climate has been described as cool and cold perhumid (Gentilli, 1972). Due to the high rainfall, cool conditions, and often highly siliceous parent materials soils are likely to be high in organic matter, low in fertility, leached, and acidic (Nicholls and Dimmock, 1965; Bowman et al. 1986).

A. cupressoides has a widespread but discontinuous distribution in central, western, and southern Tasmania,

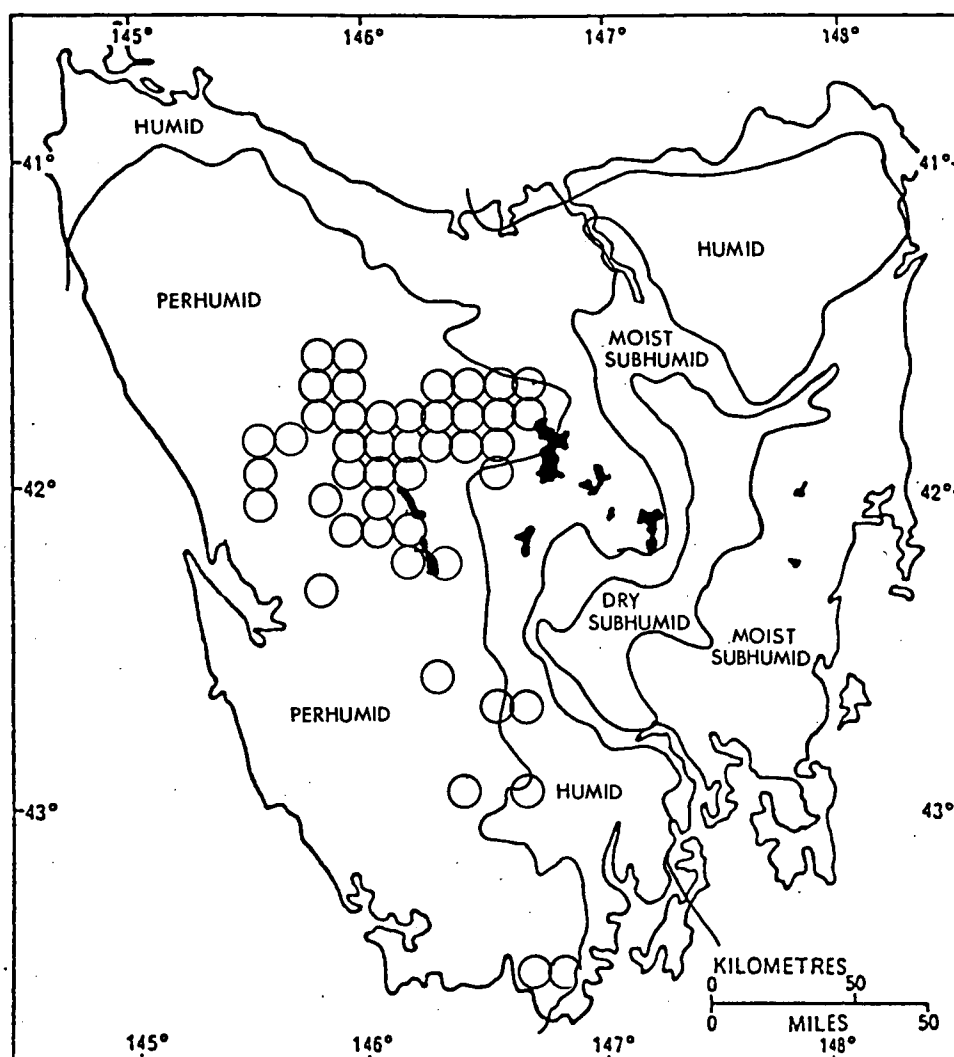


Figure 2.1. The distribution of *A. cupressoides* and effective precipitation. *A. cupressoides* distribution taken from Brown *et al.* (1983) and updated. Precipitation provinces after Gentilli (1972). Circles indicate areas where the species is known to occur. See Appendix A, Fig. 1 for the annual precipitation.

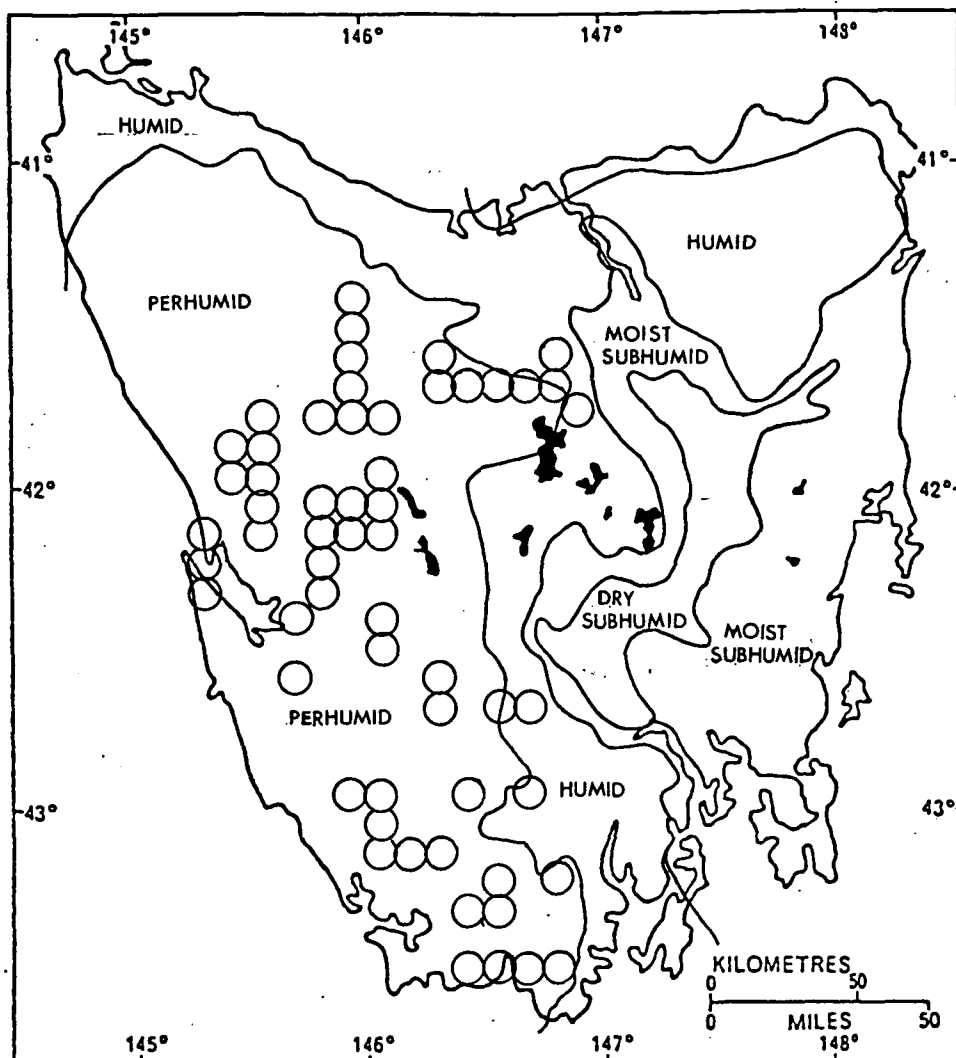


Figure 2.2. The distribution of *A. selaginoides* and effective precipitation. *A. selaginoides* distribution taken from Brown et al. (1983) and updated. Precipitation provinces after Gentilli (1972). Circles indicate areas where the species is known to occur.

at altitudes between c 300 and 1320 m a.s.l. The species usually grows to be an upright tree from 6 and 20+ m in height, with larger individuals having a d.b.h. well in excess of 1m. At high altitudes, and in the more southerly extent of its range, where it is found on some of the higher mountains, A. cupressoides occurs in dwarf or krumholtz form. Extensive stands of A. cupressoides occur on parts of the Central Plateau and in the Central Highlands at around 1000 m a.s.l. Elsewhere it tends to be restricted to small stands around tarns and bog margins, along streams and on dolerite block streams. At its lowest occurrences, A. cupressoides is found beside streams which have transported seed from higher altitude populations. The species may form stands in which it is the sole dominant tree or it may be associated with a variety of rainforest tree species or eucalypts. Jarman et al. (1984) describe open montane and callidendrous rainforests (see Appendix A, page 183) dominated by A. cupressoides but these descriptions are incomplete. Communities containing A. cupressoides are also described in Jackson (1972) and Kirkpatrick (1977b, 1983, 1984a and b).

A. selaginoides has a discontinuous distribution which overlaps that of A. cupressoides (Figs 2.1, 2.2) but it is more common in the west and south of the island. A. selaginoides has an altitudinal range from

just above sea level to 1270 m. The species is most common between c 600 and 1000 m a.s.l. in western and southern Tasmania. At low altitudes and in the north easterly portion of its range A. selaginoides occurs as small isolated stands. It usually occurs as a forest dominant, emerging from a closed canopy of rainforest tree species. In some situations the species can achieve heights of over 40 m and diameters over 2 m. At high altitudes it is found as a stunted tree or in krumholtz form in subalpine scrub and heath communities. Communities dominated by A. selaginoides are described in Kirkpatrick and Harwood (1980), Kirkpatrick (1977b, 1983, and 1984a), Busby (1984), and Jarman et al. (1984).

Ogden (1978) suggested that the distribution of A. cupressoides and A. selaginoides is related primarily to rainfall and altitude (Fig 2.3). However, the factors controlling the relative distributions of A. selaginoides and A. cupressoides are not fully understood.

This chapter has two aims: to investigate the floristic variation in stands of Athrotaxis cupressoides and Athrotaxis selaginoides across their geographical ranges and to consider the forest types encountered with respect to the rainforest classification of Jarman et al. (1984); to investigate the factors influencing the relative distributions of the two species.

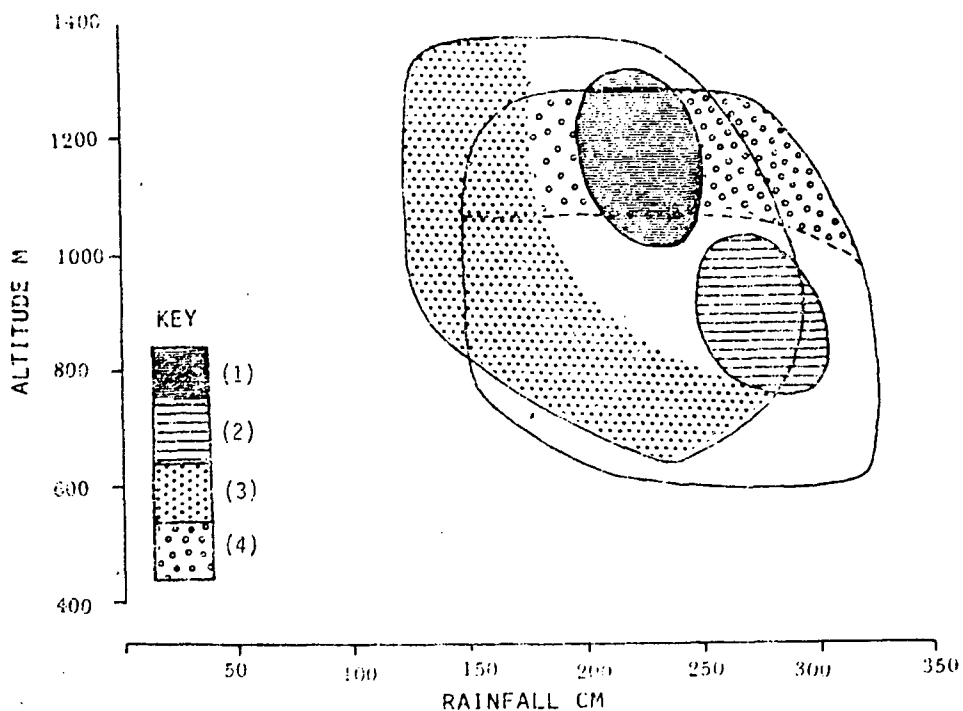


Figure 2.3. The ecological ranges of *A. cupressoides* and *A. selaginoides*: (1) the 'optimum' for *A. cupressoides*; (2) the 'optimum' for *A. selaginoides*; (3) small stands of *A. cupressoides* beside tarns and water courses; (4) krumholtz *A. selaginoides*. From Ogden (1978).

2.2 Methods.

Forests dominated by Athrotaxis species were investigated in 22 locations (Fig 2.4), representing a considerable part of the geographic range of the genus. As A. cupressoides has received less attention in the literature to date, the survey includes more samples of stands dominated by this species than stands dominated by A. selaginoides. A total of 57 stands were sampled. Each stand was subjectively chosen as being representative of the Athrotaxis dominated forest in the area. Sampling was accomplished with transects 3 or 4 m wide and ranging from 15 to 311 m in length, depending upon the nature of the vegetation. The areas sampled are listed in tables 2.1 and 2.2. The start of each transect was located by an over the shoulder toss of a tape measure and the transect was orientated parallel to the contour. The altitude of each stand was taken from a 1:100,000 topographic map, aspect was recorded with a compass, and the average slope was measured with an Abney level. The topographic position was designated as; 1 = top of slope; 2 = middle of slope; 3 = lower slope; 4 = valley floor. The height of Athrotaxis stems and the height of the closed canopy of associated trees (where present) was estimated using an Abney level and tape measure. The pH of the top 10cm of soil (bulked) was measured with a C.S.I.R.O. soil testing kit. Soil parent

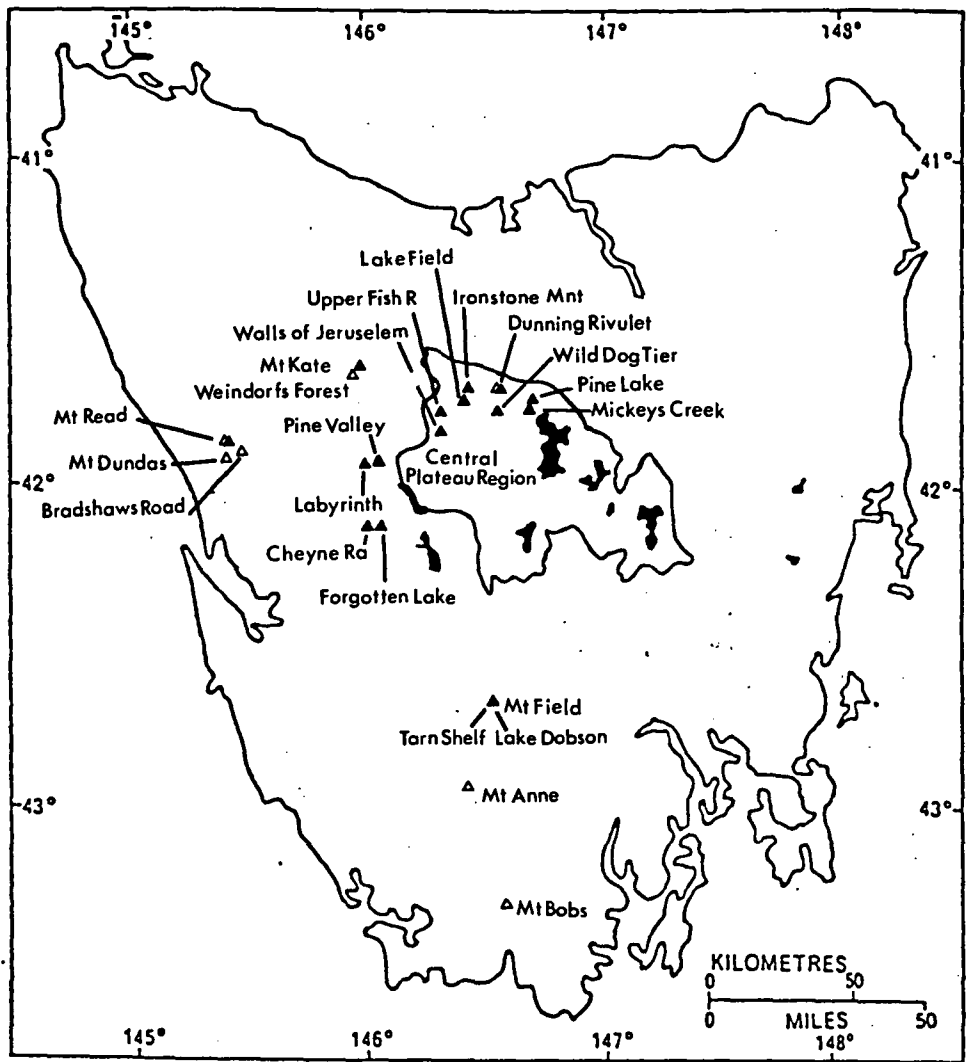


Figure 2.4. The location of sites investigated in this study. ▲ *A. cupressoides* sites. △ *A. selaginoides* sites..

Stand designation	Grid reference	Altitude (m)	Aspect	Slope (°)	Parent material	soil pH top 10cm	Site Quality	Topographic position	Canopy height Athrotaxis	Main canopy	Sample area (m ²)
Pine Lake											
PL1	753788	1200	SW	1.5	Dolerite	4.5	1	4	10	-	1533
PL2	749789	1200	SE	3.5	Dolerite	4	1	3	10	-	450
PL3	729786	1210	SW	2.5	Dolerite	5	2	2	16	-	171
PL4	742783	1190	NW	2	Dolerite	4.5	1	3	10	-	792
Ironstone Mountain											
IM1	548793	1250	SW	3	Dolerite	4	3	4	14	-	180
IM2	554786	1250	SW	2.5	Dolerite	4.5	1	3	10	-	612
Lake Field											
LF1	546754	1220	SW	0	Dolerite moraine	4.5	3	4	14	-	243
LF2	543756	1220	S	5	Dolerite	4.5	2	3	18	-	606
Dunning Rivulet											
DR1	685770	1110	E	10	Dolerite	5.5	2	3	16	-	366
Wild Dog Tier											
WDT1	615707	1200	SE	1.5	Dolerite	4	1	3	12	-	363
WDT2	528651	1170	SE	13	Dolerite	5	2	2	20	-	195
Forgotten Lake											
FL	546754	990	SSW	1	Dolerite	4.5	3	3	16	-	105
Cheyne Range											
CR1	220382	950	S	1	Dolerite	4.5	3	4	18	-	198
CR2	220383	955	S	5	Dolerite	4.5	2	3	18	5	150
CR3	217384	980	SE	5	Dolerite	4	2	1	18	5	240
Labyrinth											
L1	210555	1130	E	7.5	Dolerite	5	2	3	12	3	156
L2	205568	1140	SE	2	Dolerite	5	2	3	19	4	225
Tarn Shelf											
TS1	644768	1130	NNE	7.5	Dolerite	5	2	3	8	-	387
TS2	640767	1140	SSW	11	Dolerite	5.5	2	3	8	-	78
TS3	638763	1180	NNE	12.5	Dolerite	4.5	2	3	14	3	400
Lake Dobson											
LD	664744	960	0	0	Dolerite	4	2	4	16	-	210
Walls of Jerusalem											
WJ1	425688	1290	SSE	6.5	Dolerite and Sandstone till	4	3	2	16	-	504
WJ2	427688	1290	W	3	Dolerite till	4.5	2	2	8	-	111
WJ3	428692	1290	NE	4	Dolerite till	4	2	2	18	-	183
WJ4	397717	1200	S	2.5	Dolerite	4.5	3	4	10	-	150
WJ5	402723	1200	S	3	Dolerite	4.5	2	4	18	-	174
Upper Fish River											
UF1	423745	1160	S	6	Dolerite	5	2	2	10	-	207
UF2	421747	1230	S	11	Dolerite	4.5	2	2	20	-	264
UF3	421449	1290	S	6	Dolerite	4.5	2	1	10	-	249
UF4	427751	1320	S	1.5	Dolerite	4.5	3	4	7	-	186
UF5	418743	1160	SE	1	Dolerite	4	3	4	15	-	162
Hickeys Creek											
HC1	739768	1225	S	2.5	Dolerite	5	3	2	16	-	195
HC2	742768	1220	S	1	Dolerite	4.5	3	4	16	-	150
Pine Valley											
PV1	214566	880	SW	5	Sandstone	5	2	4	21	16	606
PV2	230528	820	N	1.5	Sandstone till	5	2	4	14	-	267
Mt Kate											
MtK1	133910	1000	E	3.5	Quartzite	4	2	4	18	10	150
MtK2	136918	1100	E	2	Quartzite	4	2	1	5	3	264
MtK3	132901	930		6	Quartzite	4	2	2	20	16	385
Mt Read											
MtR2	777662	980	S	3	Mt Read volcanics	4.5	2	4	10	6	92

Table 2.1. Stand designation, locality, and characteristics of A. cupressoides sample stands.

Stand designation	Grid reference	Altitude (m)	Aspect	Slope (°)	Parent material	soil pH top 10cm	Site Quality	Topographic position	Canopy height Athrotaxis	Main canopy	Sample area (m2)
Mt Anne											
A1	538460	1020	SSE	10	Carbonaceous sandstone and siltstone	4.5	2	3	6-8	3-5	252
A2	540465	1000	NW	14	Carbonaceous sandstone and siltstone	4.5	2	2	10	6	252
A3	540467	880	NW	14	Conglomerate	4	2	2	20-22	16	300
A4	540468	820	NW		Conglomerate	4.5	2	2	22-25	18	300
Mt Bobs											
B1	695079	680	NW	5	Sandstone till	4.5	2	3	25-35	15-25	555
B2	693079	660	Valley floor	0	Sandstone till	4.5	3	4	4-6	3-4	222
B3	688082	760	S	9	Sandstone	4.5	2	2	15	10-12	201
B4	688091	680	NW	2.5	Sandstone	4.5	2	2	25-30	20	300
Mt Dundas											
D1	733586	720	SSE	4	Sandstone and mudstone	4.5	2	2	18-20	12-15	303
D2	735592	820	S	2	Sandstone and mudstone	4	2	1	7-8	5-6	105
D3	734601	990	S	7	Dolerite moraine	4	1	2	4	2-3	60
Weindorfs forest											
W1	116899	1040	SE	14	Quartzite	4.5	2	2	8-10	5-7	240
W2	117898	980	SE	12	Quartzite	4	2	2	15-18	8-10	264
W3	118897	930	SE	10	Quartzite	4.5	2	3	25-35	15-25	294
Bradshaws Road											
BR1	808661	750	S	2.5	Glacial clays	4.5	2	4	20-22	15-16	300
BR2	801660	780	SE	7	Mt Read volcanics	4.5	2	2	8-10	5-6	184
Mt Read											
MR1	777662	980	S	1	Mt Read volcanics	4.5	2	4	8-10	5-6	82
Dunning Rivulet											
DR2	683775	980	WNW	17.5	Dolerite	5	1	2	8	12-15	300

Table 2.2. Stand designation, locality, and characteristics of A. selaginoides sample stands.

material was recorded and confirmed with the appropriate geological map, and site quality was evaluated in the following manner; 1 = soil; 2 = rocky soil; 3 = blockfield.

To investigate the floristic composition of stand understories, the projected cover of all major canopy and understorey species occurring along the transect was estimated using the following cover classes: 1=0-5%; 2=5-25%; 3=25-50%; 4=50-75%; 5=75-100%. With the aid of the ecological data base system ECOPAK (Minchin, 1986), the cover information was ordinated using the program DECORANA (Hill and Gauch, 1980) and classified using TWINSpan (Hill, 1979). DECORANA is a program for applying Detrended Correspondence Analysis (D.C.A.) D.C.A. has proved to be a reliable form of ordination for data sets which have a low beta diversity (Kenkel and Orloci, 1986; Minchin, in press). TWINSpan is a polythetic divisive classification program which provides two-way tables of species x sample data using a series of ordinations. The results are less prone to misclassification than monothetic divisive techniques (Kirkpatrick, 1986a).

2.3 Results and Discussion.

2.3.1 Stand classification.

Eleven groups were selected from the TWINSPAN classification (Appendix B). These groups coincide with or complement the rainforest classification of Jarman et al. (1984). A dendrogram of the classification showing the indicator species at each division is presented in figure 2.5.

The primary division of stands in the TWINSPAN classification is between open montane and callidendrous rainforest communities on the left hand side and thamnic and implicate rainforests and subalpine scrub communities on the right. Callidendrous rainforests are represented by only one stand, DR2 (TWINSPAN group 1), and it has been classified with the open montane communities on the presence of Poa in the understorey.

The open montane rainforests are further divided into 5 more groups. Three of them, groups 2, 3, and 4, are restricted to the the Central Plateau and reflect the Eastern Alpine Complex (Kirkpatrick and Dickinson, 1984b). The floristic composition of groups 2, 3, and 4 is strongly influenced by soil (site quality) and drainage (slope) conditions ($p < 0.05$, Kruskal-Wallice H test, Tab. 2.3). The stands belonging to groups 5 and 6 are located further to the west and south.

The thamnic and implicate communities are divided

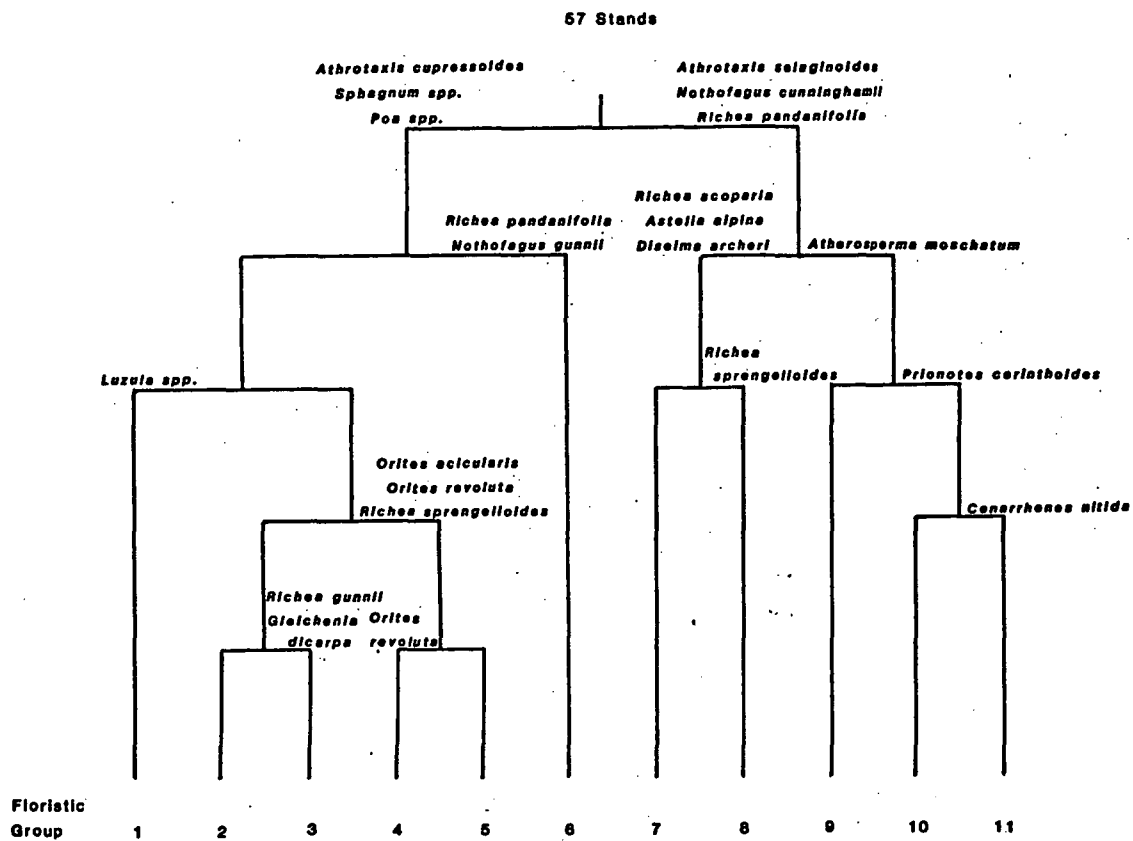


Figure 2.5. Dendrogram of the TWINSpan classification showing the indicator species at each division.

Stand	Floristic group	Site quality *	Slope (°)
PL1	4	1	1.5
PL2	4	1	3.5
PL4	4	1	2
IM2	4	1	2.5
WDT1	4	1	1.5
UF3	4	2	6 (top of slope, dry)
LF2	2	2	5
WDT2	2	2	13
WJ1	2	3	6.5
WJ2	2	2	3
WJ3	2	3	4
WJ5	2	2	3
DR1	2	2	10
PL3	2	2	5
UF1	3	2	6 (slope bottom, wet)
UF2	3	2	11 (slope bottom, wet)
UF4	3	3	1.5
UF5	3	3	1
IM1	3	3	2
LF1	3	3	0
WJ4	3	3	2
MC1	3	3	2
MC2	3	3	1

Table 2.3

A. cupressoides stands on the Central Plateau. Floristic group (TWINSpan), site quality, and average slope.

*Site Quality 3 Block streams
 2 Rocky soil
 1 Soil

into five groups. Group 7 stands are high altitude implicate rainforest and subalpine-scrub communities. Group 8 includes two open subalpine scrub communities near the treeline. Group 9 is comprised of Thamnic rainforests located in the central highlands. Group 10 represents lower altitude thamnic rainforests in the west and south of the island. Stand MTB3 has been wrongly classified in group 10. This stand would be better classified in group 11, low altitude implicate rainforests, because of the presence of Nothofagus gunnii and the low and uneven nature of the canopy.

The essential features of each of group and the relationship of each group to the rainforest classification of Jarman et al. (1984) are discussed below.

1. High altitude callidendrous rainforest with A. selaginoides.

This type is represented by only one stand in the survey (DR2), however it occurs in isolated pockets along the northern margin of the Central Plateau. Although previously unreported, it is very similar to type C2, High altitude callidendrous rainforest, (Jarman et al. 1984). A. selaginoides occurs in small patches or as isolated individuals to 20 m tall and emerges above a closed canopy dominated by N. cunninghamii, to 15 m, with

subordinate Atherosperma moschatum. Phyllocladus aspleniifolius and Pittosporum bicolor are infrequent in the understorey which is very open with few shrubs. These include small N. cunninghamii and A. moschatum, Telopea truncata, Tasmannia lanceolata (Poir.) A.C.Sm. and Coprosma nitida. Ground cover can be comprised of up to 70% litter, moss, and rocks. Poa, Carex, and Luzula species, and the fern Polystichum proliferum are common. On rare occasions individuals of A. cupressoides and A. laxifolia may occur. The former is usually restricted to the banks of water courses which have presumably transported seed from higher altitude populations.

2. Open montane rainforest with A. cupressoides over grassy understories.

This forest type is restricted to the Central Plateau where it is found on sites with well developed soils and good drainage. This group includes forest type OM4 of Jarman et al. (1984) but the group also includes a range of communities occurring on dolerite soils. A. cupressoides can achieve heights of around 20 m in some cases. It is usually the only tree species present, but Eucalyptus coccifera may be present in the canopy on occasions. Canopy cover varies from 25 to 75%. In the more open situations the understorey is dominated by Poa

species (usually P. gunnii) but when the canopy is more complete much of the ground is covered by litter, Sphagnum and other mosses, with isolated patches of Poa and Carex species, ferns, and herbs. Shrubs are uncommon and usually restricted to canopy gaps. Understorey species include Orites acicularis, Orites revoluta, Cyathodes parvifolia, Cyathodes straminea, Richea scoparia, Coprosma nitida, Tasmannia lanceolata, Olearia pinifolia, and Lissanthe montana.

3. Open montane rainforest with A. cupressoides over bog understories.

These stands occupy poorly drained situations on valley floors, moraine hollows, and around the edges of tarns and lakes. There is a heavy accumulation of peat. A. cupressoides individuals can attain heights between 7 and 20 m, depending on exposure. The stems tend to occur in tight clumps and canopy cover varies from 25 to 75%. Where the canopy is closed, litter covers much of the ground surface, with Sphagnum and scattered grasses and herbs, including Poa and Carex species, Uncinia compacta, and Astelia alpina. In places the peat has subsided to reveal a dense tangle of Athrotaxis roots. These depressions are often flooded. At stand edges or in sizable gaps, Sphagnum growth is more profuse. Here the Sphagnum forms deep mounds with emergent Richea gunnii,

Richea scoparia, Gleichenia dicarpa, and Empodisma minus. Shrub species, including Orites acicularis, Orites revoluta, Microcachrys tetragona, and Lissanthe montana are common.

4. Open montane rainforest with A. cupressoides over heath and scrub.

Communities of this type have been described by Jarman et al. (1984) as type OM3. These forests are restricted to dolerite block streams on the Central Plateau and have not been observed outside this region. They are low open communities from 10 to 12 m tall. The canopy is intermittent and rarely exceeds a cover of greater than 25%. The understorey is a mosaic of shrubby heath comprised of such species as Richea sprengelioides, Richea scoparia, Orites acicularis, Orites revoluta, Cyathodes straminea, Coprsma nitida, Leptospermum rupestre, Tasmannia lanceolata, and Lissanthe montana; scrub dominated by Nothofagus cunninghamii; and large areas of dolerite boulders. Eucalyptus coccifera may be present occasionally. Poa species and other grasses and herbs are usually present but they never achieve the abundances common in either group 2 or 3 communities.

5. Open montane rainforest with A. cupressoides over intermediate understoreys.

In the two stands comprising this group A. cupressoides achieves heights of up to 18 m and has a projected canopy cover of between 25 and 50%. Floristically these stands are intermediate between those of the Central Plateau, groups 2, 3, and 4, and group 6 (see Appendix 2). This is probably due to their poorly drained nature. Consequently coniferous or deciduous heaths cannot develop and a community of more tolerant species including Baeckia gunniana, Richea scoparia, Orites acicularis, Empodisma minus, Gleichenia dicarpa, and Astelia alpina has developed.

6. Open montane rainforest with A. cupressoides over deciduous or coniferous heaths.

This group contains a range of communities but the group was not adequately subdivided by TWINSpan. However, there are two basic communities both described by Jarman et al. (1984) as types OM1, with deciduous heath understoreys, and OM2, with coniferous heath understoreys. Stands L1, L2, TS3, MTK2, CR2, CR3, and W1 have deciduous heath understories. In these stands A. cupressoides, up to 19 m tall with a projected canopy cover of between 15 and 25%, emerges from a dense tangled understorey dominated by Nothofagus gunnii, up to 5 m

tall . Nothofagus cunninghamii may also be present in varying quantities. Richea pandanifolia is present as a shrub or palm-like subordinate. Shrubs are scattered through the understorey and included Richea scoparia, Orites acicularis, Orites revoluta, Tasmannia lanceolata, Baeura rubioides, Bellendenia montana, Leptospermum rupestre, Microcachrys tetragona, Diselma archeri, Microstrobus niphophilus, and Telopea truncata. Stand W1 is an odd version of this community with emergent A. selaginoides rather than A. cupressoides. Stand TS1 has a coniferous heath understorey which lacks Nothofagus species and is dominated by Diselma archeri, Microstrobus niphophilus, and Microcachrys tetragona. TS2, LD, and PV2 appear to be successional communities. They are discussed more fully in chapter 3.

7. High altitude implicate rainforest or subalpine-scrub.

Forests of this type are reported in Jarman et al. (1984) as type I2(a). In these communities A. selaginoides (and rarely A. cupressoides) achieves heights of 8 to 10 m with a projected cover of 10 to 20%. Individual trees emerge from an uneven canopy of Nothofagus gunnii, Diselma archeri, and Nothofagus cunninghamii. The dense and tangled species rich understorey is continuous with the canopy and many

Nothofagus gunnii branches contribute to the confusion. Shrub species present can include Tasmannia lanceolata, Richea scoparia, Richea pandanifolia, Coprosma nitida, Podocarpus lawrencii, Cyathodes juniperina, Tetracarpaea tasmanica, Olearia alpina, Archeria hirtella, Archeria eriocarpa, and Trochocarpa gunnii. Ground cover includes Astelia alpina, Uncinea spp, and Luzula spp.

Stand MTD3 must be classified as a subalpine-scrub community on account of the low height of of the canopy and the emergent A. selaginoides (4 m). However, it grades into true high altitude implicate rainforest represented by MTD2.

8. Implicate Nothofagus cunninghamii-Richea scoparia rainforest with A. selaginoides.

This group is comprised of two open subalpine-scrub / rainforest stands. B2 is near an inverted treeline in an intermontane basin at 660 m a.s.l. and A1 is near the treeline at 1020 m a.s.l. The community represented by A1 has been described by Jarman et al. (1984) as type I3a.

Multi-stemmed A. selaginoides individuals up to 10 m tall are scattered throughout a scrub layer dominated by Nothofagus cunninghamii and, at B2, Eucryphia milliganii. These communities are very open and A. selaginoides never contributes more than about 10% canopy cover. They have

a species rich understorey with Richea scoparia common in the gaps. Other species include, Richea sprengelioides, Richea pandanifolia, Tetracarpaea tasmanica, Orites diversifolia, Olearia alpina, Agastachys odorata, Coprosma nitida, Phyllocladus aspleniifolius, Bauera rubioides, Persoonia gunnii, Epacris serpyllifolia, and Tasmannia lanceolata. The ground is covered by dense mat of Astelia alpina, Milligania densifolia, Pentachondra pumila, Carpha alpina, and Empodisma minus where there is break in the canopy.

9. Thamnic rainforest in the Central Highlands.

The stands in this group vary in structure and floristic composition. A. selaginoides up to 35 m tall, but usually around 20 m, or A. cupressoides to around 20 m, emerge from a closed canopy of Nothofagus cunninghamii or a more uneven canopy of N. cunninghamii and Nothofagus gunnii. In some cases A. cupressoides and A. selaginoides occur in mixture, and then occasional Athrotaxis laxifolia stems may be present. Athrotaxis species account for between 15 and 25% of the canopy. Beneath the tallest stands (W3, MTK1, and MTK3) the understorey is open and comprised primarily of Trochocarpa cunninghamii and Trochocarpa gunnii. Richea pandanifolia and Coprosma nitida may be present. In stands containing Nothofagus gunnii the low and more open

nature of the canopy allows a more dense and species rich understorey to develop. The understorey of PV1 lacks the Trochocarpa species common to the other stands and is comprised of species more common in group 10.

10. Thamnic rainforest in the West and South.

These forests are similar in structure to those of group 9 but they are more species rich. A. selaginoides, up to 25 m tall with a projected cover of up to 25%, emerges from a closed canopy of N. cunninghamii, up to 20 m, with Atherosperma moschatum, Eucryphia milliganii, and Phyllocladus aspleniifolius as subordinate tree species. The epiphyte Prionotes cerinthoides is characteristic. The understorey is relatively open and contains palm-like Richea pandanifolia up to 15 m tall. Common shrubs include Trochocarpa gunnii, Trochocarpa cunninghamii, Archeria eriocarpa, Archeria hirtella, and Orites diversifolia. Ground cover is comprised predominantly of litter and moss with occasional patches of Astelia alpina and the ferns Polystichum proliferum or Blechnum wattsi.

Forest types T4c and T5b described in Jarman et al. (1984) are included in this group. Stand B3 has been included in this group by the TWINSpan classification but it would be better placed in group 11, implicate rainforest. It is structurally an implicate rainforest

with A. selaginoides to 15 m emerging from a broken canopy dominated by Nothofagus gunnii and Nothofagus cunninghamii to 12 m.

11. Implicate rainforest.

The height of the forest varies according to site conditions. A. selaginoides up to 20 m tall emerges from an uneven canopy, up to 16 m high, dominated by Nothofagus gunnii, Nothofagus cunninghamii, or Atherosperma moschatum. Phyllocladus asplenifolius and Eucryphia milliganii or Eucryphia lucida may be present. A. selaginoides accounts for 10 to 20% of canopy cover. Prionotes cerinthoides is present on the trunks of the trees. The understorey is continuous with the canopy and is comprised of a dense tangle of Nothofagus gunnii, Anodopetalum biglandulosum and other shrubs. These included Richea pandanifolia, Anopterus glandulosus, and Agastachys odorata. Other species present include Persoonia gunnii, Archeria hirtella, Trochocarpa gunnii, Trochocarpa cunninghamii, Olearia alpina, Coprosma nitida, and Gahnia grandis. The ground is uneven with many moss covered logs. The fern Blechnum wattsii is common.

2.3.2 Stand ordination.

The ordination of the floristic data using the program DECORANA is presented in figure 2.6 with the 11 TWINSpan groups superimposed on the plot. Axes 1 and 2 display most of the variation encountered in the stands studied with 'eigen' values of 0.664 and 0.317 respectively.

The first axis of the ordination represents the transition from Open Montane rainforest dominated by A. cupressoides in the east to Thamnic and Implicate rainforests dominated by A. selaginoides in the west and south of the island.

The scores for each stand on axis 1 of the ordination correlate significantly with the altitude of each stand ($r = -0.855$, $p < 0.001$, see Fig. 2.7). The relationship between altitude and floristic composition is somewhat confused by the variation in the altitude of the treeline across the island (Kirkpatrick, 1982) and by the effects of inverted treelines in many intermontane basins. The other site factors recorded in the study (Tab. 2.1, 2.2) show considerable variation but do not correlate with either axis 1 or axis 2 of the ordination. It is likely that over a large heterogeneous study area, vegetation will be controlled by the complex interaction of environmental factors rather than by the influence of one or a few dominant variables, as is often the case

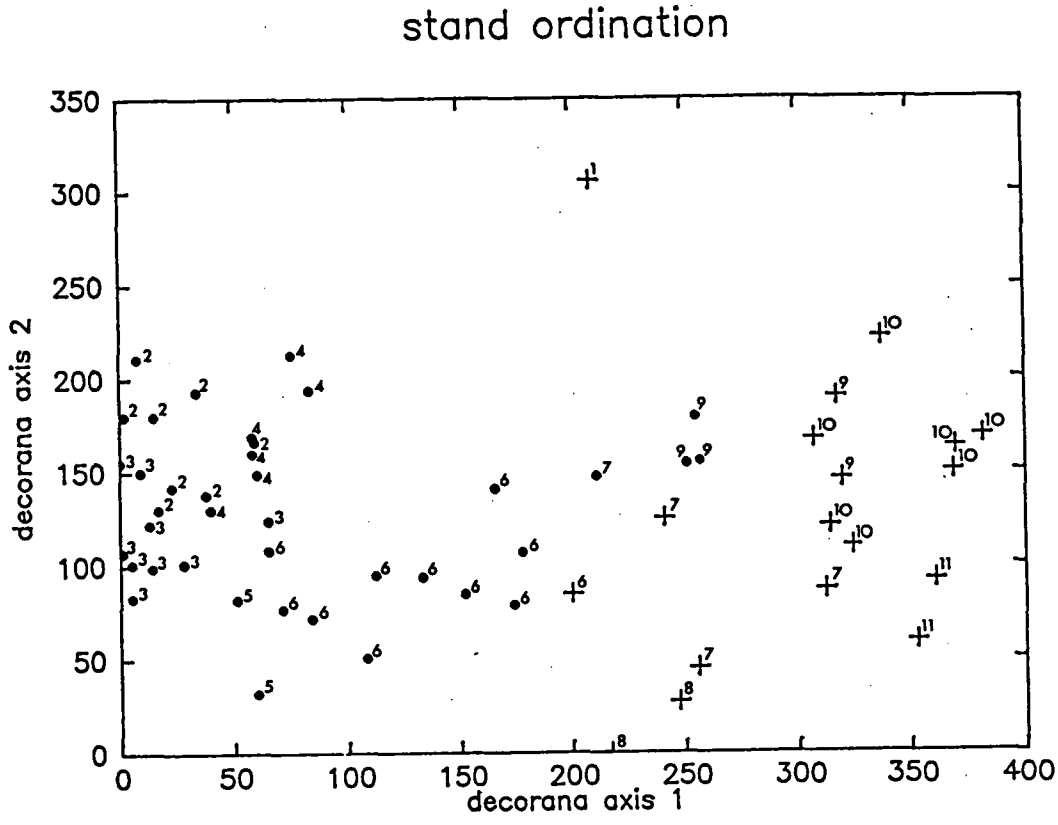
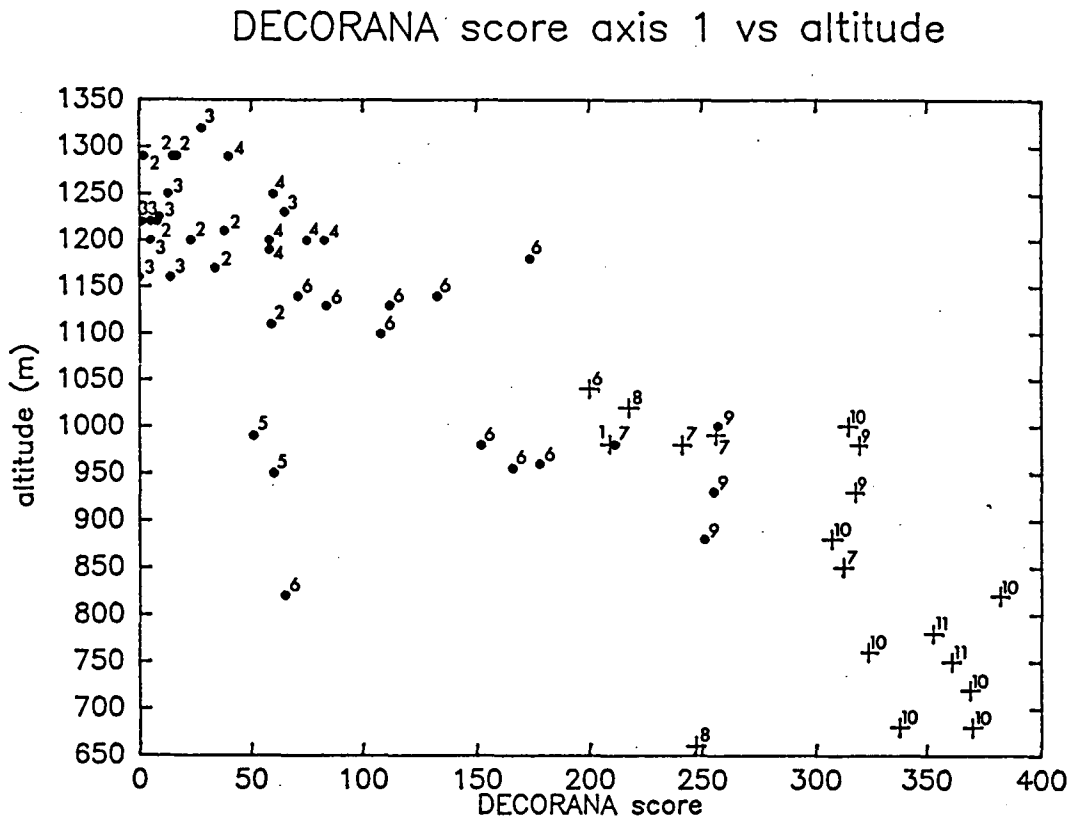


Figure 2.6. Axis 1 versus axis 2 for the ordination of sample stands using DECORANA. Floristic groups (1-11) as selected from the TWINSpan classification are indicated. A. cupressoides stands. • A. selaginoides stands. +



when samples are located in a more restricted area (for example Brown et al., 1984). Temperature, soil depth, soil fertility, drainage, and exposure are all likely to be important and these factors have been related to changes in rainforest communities of the West Coast Range by Kirkpatrick (1984). It is possible that site history also plays an important role in determining the species present at any location.

Due to the lack of suitable precipitation records, no attempt has been made to investigate the effect of annual precipitation on the distribution of the two species. Axis 1 of the ordination should also reflect an increase in precipitation as there is a decreasing precipitation gradient across the island from SW to NE (Fig 2.1). However, A. selaginoides populations extend marginally further east than those of A. cupressoides suggesting that annual precipitation is no more limiting for A. selaginoides than for A. cupressoides. Stand DR2 typifies the forests dominated by A. selaginoides in this area, the northern rim of the Central Plateau. The limited occurrence of A. selaginoides in the eastern portion of its range is probably best explained by increased fire frequencies in these drier areas. Many of the stands are located on fire protected sites such as talus slopes, cliff tops, and wet gullies. On the Central Plateau proper, there is also a tendency for

stands of A. cupressoides to be located on fire protected sites such as bogs, block streams and south facing slopes.

A. cupressoides generally occurs at higher altitudes than A. selaginoides. At most of the study sites where the two species grow in close proximity A. cupressoides forms stands closer to the treeline (or inverted treeline) than A. selaginoides (c.f. Ogden, 1978). Exceptions occur at stands PV1 and MtR2 where the two species grow in mixture on valley floors. These stands appear to be stages in a succession from open montane to implicate or thamnic rainforests.

The tendency for A. cupressoides to occupy valley bottoms could be due to a superior ability to colonize waterlogged sites (see Chapter 3.2.4 and 3.3.2). However, A. selaginoides can be found in equally poorly drained positions, for example stand BR1 and on Mt Anne Shelf near stand A1. It is also found growing in sphagnum bogs and along lake and stream banks. Valley floor stands of A. cupressoides are likely to experience severe frosts. Sakai et al. (1981) have demonstrated that A. cupressoides has a superior tolerance to cold temperatures than A. selaginoides. They report a freezing resistance for A. cupressoides foliage, buds, cortex, and xylem of -20°C and a freezing resistance for A. selaginoides foliage of -17°C , and for buds, cortex,

and xylem -15°C . The increased freezing resistance of A. cupressoides would explain its tendency to be found at higher altitudes than A. selaginoides or in cold valley bottoms. However, other factors such as exposure to wind, snow lie, and waterlogging are may also be important on these sites and would be worthy of investigation.

CHAPTER 3.

THE REGENERATION MODES OF ATHROTAXIS CUPRESSOIDES AND
ATHROTAXIS SELAGINOIDES.

3.1 Introduction.

A study of long lived taxa, such as Athrotaxis, can only hope to record a small proportion of the lives of the individuals. Thus, their life histories have to be deduced from contemporary demographic structure, spatial variation and experimental manipulation.

The mode of regeneration of Athrotaxis species is not fully understood. Evidence for both continuous and discontinuous regeneration in undisturbed communities has been presented for A. selaginoides and A. cupressoides (Calais and Kirkpatrick, 1983; Kirkpatrick and Harwood, 1980; Ogden 1978). The aim of this chapter is to determine the regeneration characteristics of these two species.

Athrotaxis species occur in stands of widely varying floristic composition and structure (see chapter 2). Therefore, they might be expected to show different demographic structures and seedling distributions in response to the different conditions imposed by the subordinate species. Structural variability of this type was hypothesized for Eucalyptus delegatensis populations (but subsequently rejected) by Bowman and Kirkpatrick

(1984).

The successive age classes in the demographic structure of a population can be taken to represent the preceding stages in the development of a single aged group of individuals, as if it was followed from germination through to death. This approach requires certain assumptions: an all-aged age class structure that remains stable over time and negligible influence from allogenic factors. If these criteria are met, the rate of depletion of individuals from one age class to the next can be expected to be a steeply descending or reverse J shaped curve. In a study of climax balsam fir-hemlock communities, Hett and Loucks (1976) found that a power function model of the form $y = y_0 \cdot x^{-b}$ best fitted this relationship (where y = no of individuals in any age class x , y_0 = the initial input of individuals, and b = the mortality rate).

A growing body of literature (for example, West et al., 1981) demonstrates that such factors as large scale disturbances, climatic change, and soil maturation processes make climax forest communities a rarely attained phenomenon. However, the model is still useful because it gives a standard for comparison. By compiling an age class distribution for any stand we can compare it to the idealized reverse J shaped model for a continuously regenerating population. The closeness of

fit to such a idealized curve can supply us with a measure of the all-agedness of the population. This approach has been adopted in the present study.

Departure from the reverse J shaped model is seen as evidence for discontinuous regeneration (Veblen et al., 1979, 1980; Stewart and Veblen, 1982; Bowman and Kirkpatrick, 1984; Read and Hill, 1985). This may not necessarily indicate community instability, as no allowance is made for allogenic influences. It has been demonstrated in North America (Franklin and Hemstrom, 1981), South America (Veblen, 1982; Veblen et al., 1983), and New Zealand (Burke, 1974; Clayton-Greene, 1977; McKelvey, 1953) that disturbances of a catastrophic nature which occur infrequently over a long time period must be considered to be part of the natural order.

3.2 Methods.

3.2.1 Stand Demography.

The following information relating to Athrotaxis populations was recorded along the 57 transects described in chapter 2: the diameter at breast height (d.b.h.) and the position along the transect were noted for all tree species with d.b.h. >1 cm; the position and height of all established seedlings (ie. those greater than 5 cm tall) of Athrotaxis species were noted. Percent frequencies for seedlings and adults of A. selaginoides

in 10cm size classes, and for seedlings and adults of A. cupressoides in 5 cm size classes were determined for each stand. The size classes used were, $1 < 1$ cm d.b.h. (seedlings), 2=1-9.5cm, 3=10-19.5cm, and ensuing 10 cm classes for A. selaginoides and $1 < 1$ cm d.b.h. (seedlings), 2=1-4.9cm, 3=5-9.9cm, and ensuing 5cm classes for A. cupressoides. The use of these size classes takes into account the slower growth rates and generally smaller sizes obtained by A. cupressoides and allows direct comparison with the results of Ogden (1978). Size class-frequency histograms were prepared. They were assessed visually to decide whether each population was all-aged, even-aged, or comprised of a number of even-aged groups, and were also assessed by comparison to the power function model proposed by Hett and Loucks (1976).

Ideally one requires detailed information on the ages of the individuals in the population under study to apply the methods of Hett and Loucks. If diameters are to be used to predict the age of stems, a strong correlation between age and stem diameter must be demonstrated for the species in the stand in question. Lorimer and Krug (1983) and Muller (1982) report diameter distributions which are reverse J shaped in stands of even aged shade tolerant trees which have grown after catastrophic disturbance. When shade tolerant species

are over-topped they are not as likely to die as intolerant species; instead, it is possible for them to accumulate as suppressed individuals in the subcanopy. Lorimer (1985) also reports that it would be difficult to distinguish between the diameter distribution of a balanced all aged stand and that of an old growth even aged stand which has had partial disturbance in recent years (ie heavy wind damage). It is therefore necessary to interpret data based on stem diameter with caution.

Positive relationships between diameter and age have been demonstrated at widely separated sites for A. cupressoides (Ogden 1978) and for A. selaginoides (Ogden, 1978; Cullen, in press, Appendix A). Considering the present concern for the conservation of Athrotaxis, extensive coring of trees was only carried out at 1 stand dominated by A. cupressoides. It was also considered undesirable to cut seedlings or saplings for age determinations. However, the results of Ogden (1978) provide estimates of seedling growth rates for both species. At ten other sites small numbers or single individuals were cored for age determination as a check on the relationship between age and diameter or to provide minimum dates for regeneration events.

Cores were extracted at a point 1 m above the ground. Annual ring formation was assumed for A. cupressoides (Ogden, 1978). A number of problems arose

which made precise aging of the stems difficult. The centre of the trees were not always sampled, either because of inaccurate aiming of the borer or because the radius of the bole was greater than the length of borer. The majority of larger/older trees had rotten centres or substantial sections of their stems missing due to mechanical damage or fire scarring. In many trees the growth rings of the oldest heart wood were very indistinct and it was impossible to count them, even after preparation. Where only small portions of the ring sequence were missing (<3 cm) an estimate of the age was made by applying the average growth rates for the core to the missing section. The relationship between diameter and age was investigated by linear and logarithmic regression.

3.2.2 Spatial distribution of seedlings.

Where windthrow or catastrophic disturbance has created canopy gaps the proportion of seedlings occurring in these gaps is indicated on the size class histograms of each stand. In this case a canopy gap was defined as being formed by the fall or death of one or more trees and seedlings were considered occupants of such gaps if they occurred in positions beyond the projected canopy cover of surrounding adults.

Undisturbed open montane communities dominated by A.

cupressoides on the Central Plateau are often comprised of widely spaced trees or clumps of trees and have low open understories (see Chapter 2.3.1). A. cupressoides is a narrow crowned species and the crowns of individuals do not spread far into unoccupied canopy space. The mean distance between adult nearest neighbours along the sample transects was used as a surrogate measure of the gap space. The high perimeter to sample area ratio associated with belt transects, will cause an edge effect error. The mean distance between nearest stems will be overestimated because the closest neighbour will lie outside the transect in some cases. The interstices between the stems of multi-leader individuals were considered too small to constitute a gap and the distance between discrete individuals was estimated to the nearest 0.5 m. Profiles of selected stands were drawn to illustrate the open nature of these forests.

Mann-Whitney U tests were used to test whether the mean nearest neighbour distance in stands containing seedlings was larger than the mean nearest neighbour distance in stands without seedlings.

3.2.3 Seed dispersal.

The dispersal of seed by A. cupressoides could only be indirectly investigated in this study as there has been a general lack of seed on the species since the

summer of 1982/83. That seed crop produced an abundance of new germinates (cotyledons present). The distribution of these germinates was investigated at three locations, stands MC1, PL2, and MTK3. Initially this was attempted using 1 m wide transects which ran from beneath the canopy to a considerable distance beyond. At MC1 and PL2 this method had to be abandoned because of the lack of germinates in all but isolated patches. At these sites the study degenerated into an intensive search over large areas. At MTK3 the transect proved useful. Seed dispersal of A. selaginoides has been investigated by the Forest Commission of Tasmania (1982).

3.2.4 Vegetative reproduction.

At many stands where A. cupressoides is present in seedling sizes, at least some of the regeneration can be attributed to root suckers. Although it would require massive excavation to ascertain the proportion of regeneration resulting from root suckers in a stand it is often possible to observe root connections between adults which occur in tight clumps (Plates 3.1, 3.2). These clumps vary in size from a few individuals to more than 20. If it is assumed that all the stems in each clump are connected it is possible to make an estimate of the proportion of stems arising vegetatively. Such estimates were prepared for stands on the Central Plateau, where



Plate 3.1. A root connection between two A. cupressoides stems at stand WDT2.



Plate 3.2. A clump of vegetatively produced A. cupressoides stems at stand IM1 (floristic group 3, Open Montane rainforests with bog understories).

the open nature of the understorey enables relatively easy and confident identification of discrete clumps.

3.3 Results and Discussion.

3.3.1 Size/age correlations.

Ogden (1978) found an average age at 1 m high of 42 years for A. selaginoides and 55 years for A. cupressoides. These estimates are used in this study but it is likely that A. selaginoides can increase in height more rapidly on favourable sites. In experimental plantings outside of its natural range A. selaginoides seedlings have been recorded growing at 0.4 m. per annum (Hickey, 1983).

A positive relationship between stem diameter and age ($r = 0.97$, $p < 0.01$) was established at stand B4 (Cullen, in press, see Appendix A). Ogden (1978) found similar results at two other widely separated sites (Table 3.1). He reports differing diameter growth rates for saplings beneath closed canopies and for open grown ones. These results indicate that there can be considerable variations in growth rates between different stands and between different individuals or groups of individuals within stands. Evidence of the suppression of A. selaginoides individuals beneath closed canopies is clearly demonstrated at stand MTK3 where a regression of diameter versus age gave a negative and non-significant

Athrotaxis selaginoides

Location	Altitude (m a.s.l.)	r	p	n	Mean diameter increment (mm/year)
Mt Read	750	0.8996	<0.001	13	1.07
Swifts Creek	880	0.7221	<0.001	23	3.00

Athrotaxis cupressoides

Location	Altitude (m a.s.l.)	r	p	n	Mean diameter increment (mm/year)
Mt Field	1200	0.9557	<0.001	22	1.08
Mt Field	1150	0.8718	<0.001	15	1.24

Table 3.1

Age/diameter relationships and mean annual growth diameter growth rates for Athrotaxis selaginoides and A. cupressoides. Extracted from Ogden (1978).

correlation ($r = -0.07$). Therefore it is necessary to treat the relationship between stem diameter and age for A. selaginoides with some caution.

The relationship between age and diameter for A. cupressoides was investigated at stand MTK1. Nineteen trees were cored and a positive relation between diameter and age was established ($r = 0.78$, $p < 0.001$). Ogden (1978) found stronger relationships at two sites on Mount Field (Table 3.1). Limited numbers of cores were extracted at some other sites and a consistent positive relationship was found between age and diameter (Table 3.2). However, the strength of the relationship varies from site to site and the possibility of significant variations in growth rates between individuals in one stand cannot be ignored. As with A. selaginoides, interpretations based on age/size relationships must be made with some care.

These restrictions mean that large differences in stem diameter can be confidently interpreted as differences in age but where only small diameter differences are involved, for example, from one age class to the next, this relationship might not hold.

Stand	r	p <	n	Mean diameter increment (mm/year)
PL3	0.99	(0.001)	6	1.67
DR1	0.97	(0.001)	8	1.62
PV2	0.97	(0.05)	5	1.56
IM2	0.97	(0.001)	7	0.77
TS3	0.93	(0.01)	5	0.02
IM1	0.93	(0.02)	5	1.31
LF2	0.90	(0.01)	8	1.35
LF1	0.82	(0.05)	6	1.42
MtK1	0.78	(0.001)	19	2.87
MtK3	0.55	---	5	1.80
PV1	-all trees cored in excess of 500 years old-			

Table 3.2

The relationship between diameter and age for
A.cupressoides.

3.3.2 Seed production and dispersal.

Seed production in both species is inconsistent. Large seed crops occur on A. selaginoides once every 5 to 6 years (Calais and Kirkpatrick, 1983). Ogden (1978) considers the phenology of A. selaginoides and A. cupressoides to be similar (Fig 3.1). Mast years appear to be synchronous for both species, the last one occurring in 1982. A. selaginoides can produce light seed crops in the interim years but no seed has been observed on A. cupressoides since 1982. Seeds of A. selaginoides are viable for only 3 to 4 months (Orme in Calais and Kirkpatrick, 1983).

In no case were A. cupressoides germinates found beyond a range of 9 m from parent trees and they were always located on consistently moist sites, eg soaked peat and Sphagnum beds. Germinates were present within the open canopy of stand MC1. Beyond the edge of the stand the vegetation is a low heath and no germinates could be found. At PL2 germinates were restricted to moist Sphagnum mounds located beyond the edge of the canopy. At the edge of MTK3 an old logging track 7 m wide provided a good seed bed for A. cupressoides (Fig 3.2). A. selaginoides germinates were also present in low numbers but all of these appeared to be in an unhealthy condition (see chapter 4). There were no germinates of either species in the grassy vegetation

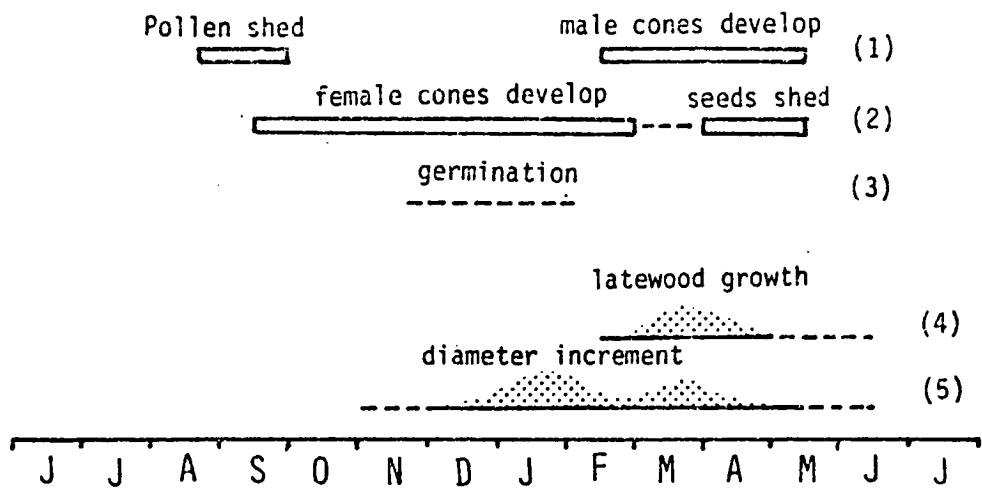


Figure 3.1. The phenology of *A. cupressoides* and *A. selaginoides*. 1, 2, and 3, reproductive schedule in *A. cupressoides*; 4, and 5, wood growth in *A. selaginoides*. Observation suggests that the reproductive behavior and wood growth of the two species is similar, although due to the high altitude of many *A. cupressoides* stands its normal growing season may be shorter than that of *A. selaginoides*. (From Ogden, 1978, Figure 2).

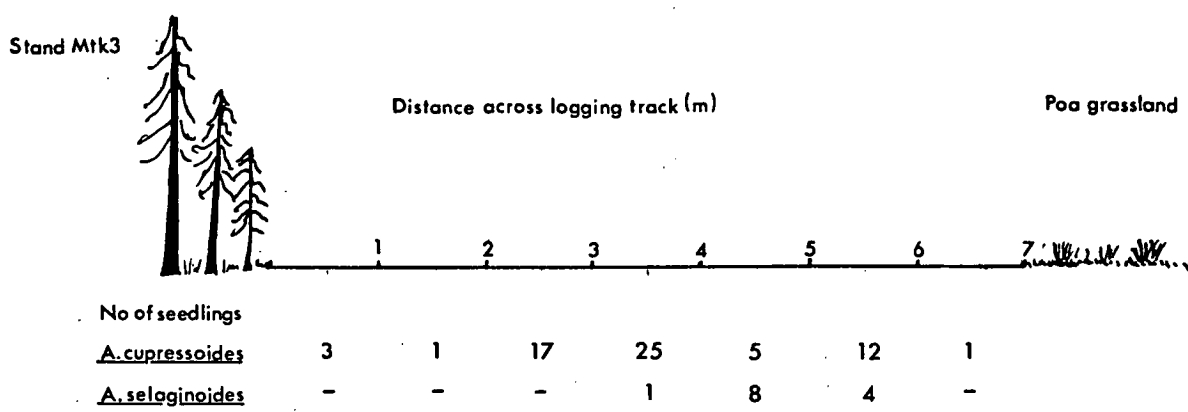


Figure 3.2. The distribution of A. cupressoides and A. selaginoides seedlings across a transect at the edge of stand MtK3.

beyond this track. Competition from the grass, or grazing, may account for their absence. Larger seedlings were absent on the logging track. As this track has been disused since the late 1960's it is probable that previous seedlings have been destroyed by dessication, grazing or some other destructive agent.

The seeds of A. cupressoides are superficially indistinguishable from those of A. selaginoides. Field observations suggest that seeds of A. selaginoides are usually only dispersed for distances up to about 50 m from the parent, unless seeds fall into watercourses. Trials conducted by the Forestry Commission (1982) indicate that effective seed dispersal by A. selaginoides is restricted to areas no further away than twice the height of the parent tree.

Kirkpatrick and Dickinson (1984) found that recovery of Athrotaxis species after fire indicated very poor seed dispersal of these species. However, J.B. Kirkpatrick (pers. comm.) has observed seedling distribution around adult A. cupressoides indicating seed dispersal of about 100 m but this seems to be an exceptional case.

3.3.3 Vegetative regeneration.

A feature previously unreported in A. cupressoides is the capacity of the species to regenerate vegetatively with root suckers. No instances of vegetative

reproduction in A. selaginoides were observed during the study. However, Read (1986) reports limited vegetative regeneration of this species.

Plate 3.3, taken near stands MC1 and MC2, demonstrates the ability of A. cupressoides to produce root suckers. In this example the suckers are concentrated at between 60 and 100 per m² and they are over 50 m from the closest adult trees. At TS2 sucker regeneration extends up to 8 m from the nearest possible parents. At stand IM2 fire has exposed lateral roots of A. cupressoides up to 25 m long (Plate 3.4).

Root suckers seem to be associated with high moisture availability. Small suckers are usually observed growing in very wet positions, often protruding from mounds of Sphagnum. This preference for moisture is also evident for the clumped adult stems. The wettest sites (i.e. bog communities with little or no slope) have the largest clumps of adults, well drained sites with good soils are intermediate, and the block-stream stands have the smallest clumps of adults ($p < 0.001$, Kruskal-Wallis H test, Tab. 3.3).

Many conifer species regenerate vegetatively near the treeline (Tranquillini, 1979) and vegetative regeneration has been reported in a number of cool temperate southern hemisphere conifers. These include Lagarostrobos franklinii (Davies, 1983) in Tasmania,



Plate 3.3. A. cupressoides root suckers near stand MC2. The suckers are concentrated at between 60 and 100 per m² and are over 50 m from the nearest adults.



Plate 3.4. Exposed lateral roots of A. cupressoides at stand IM2. The tape measure is extended 25 m.

Stand	Stems/clump	Floristic group*	Slope (°)
PL2	2.5	4	3.5
PL4	2.7	4	2
PL1	2.9	4	1.5
WDT1	3.3	4	1.5
DR1	3.3	2	10
LF2	3.4	2	5
UF1	3.6	3	6
UF2	3.9	3	11
PL3	4.0	2	5
WDT2	4.1	2	13
IM2	4.1	4	2.5
WJ1	4.3	2	6.5
WJ3	4.4	2	4
UF4	4.4	3	1.5
WJ5	4.7	2	3
UF3	5.4	4	6
MC1	6.2	3	2
WJ2	6.8	2	3
UF5	7.1	3	1
WJ4	8.2	3	2
IM1	8.3	3	2
LF1	8.6	3	0
MC2	10.6	3	1

Table 3.3

A. cupressoides stands on the Central Plateau ranked according to average no stems per clump at each stand.

*4. Blockstreams.

2. Well drained with soil.

3. Poorly drained bogs.

See Chapter 2 for descriptions of these forest types.

Fitzroya cupressoides (Mol.) Johnston. (Veblen and Ashton, 1982) and Araucaria araucana (Veblen, 1982) in southern South America, and a number of New Zealand species including Lagarostrobos colensoi (Hook.) Quinn., Halocarpus biformis (Hook.) Quinn., Agathis australis Salisb., and Phyllocladus alpinus Hook. f. (Wardle, 1963c). In extreme environments vegetative reproduction may confer a distinct advantage. New stems can rely on the parents for nourishment until well established, rather than engage in an unassisted battle with the elements. Regeneration via root suckering can be very important for the regeneration and local dispersal of A. cupressoides. At stand WJ3 at least one new generation has been produced by vegetative regeneration. Here some old live and dead individuals are surrounded by groups of connected smaller diameter stems. It is interesting to note that A. cupressoides appears to be capable of dispersing as far by vegetative means as it can by seedfall, except where water can transport seeds.

3.3.4 Stand demography and seedling distribution of Athrotaxis cupressoides.

The 57 stands sampled have been divided according to forest type, as indicated by the TWINSpan classification (chapter 2). This allows investigation of the effect of subordinate species on the demographic structure and the

distribution of seedlings for each forest type. It is evident from the size class histograms (Figs. 3.3 to 3.9) that stand demography is linked to forest type for both species.

There is a lack of A. cupressoides regeneration in many of the open montane communities on the Central Plateau (groups 2, 3, and 4, Figs. 3.3 to 3.5). However, regeneration is present in open montane rainforests in the west and south of the island. Seedlings and small sized suckers are also absent from beneath the canopies of thamnic and implicate rainforests dominated by this species (groups 7 and 9, Figs. 3.8 and 3.9).

There are no individuals in the first size class (<1 cm d.b.h.) in any of the group 2 stands (open montane rainforests with grassy understoreys, see Fig 3.3) and they show consistantly poor fits to the reverse J shaped model ($r < 0.6$ in all cases, see Tab. 3.4). This represents a prolonged regeneration failure as the time taken to pass through this class would be well in excess of 50 years. In some cases the second size class has depleted numbers indicating that the regeneration failure has extended further back in time. Some group 3 stands, open montane rainforests with boggy understories, have no seedling sized individuals (Fig. 3.4) and consequently low r values (< 0.6 , see Tab. 3.4). The others are all well stocked with seedlings or suckers which account for

Floristic group*	Stand	Equation	r	p <
3	LF2	$\log_{ey}=2.514-0.557.\log_{ex}$	-0.435	0.001
	DR1	$\log_{ey}=2.762-0.746.\log_{ex}$	-0.567	0.001
	PL3	$\log_{ey}=2.678-0.869.\log_{ex}$	-0.589	0.001
	WJ5	$\log_{ey}=2.353-0.628.\log_{ex}$	-0.442	0.001
	WDT2	$\log_{ey}=2.213-0.355.\log_{ex}$	-0.306	0.01
	WJ1	$\log_{ey}=2.535-0.578.\log_{ex}$	-0.534	0.001
	WJ2	$\log_{ey}=2.363-0.450.\log_{ex}$	-0.312	0.01
	WJ3	$\log_{ey}=2.327-0.629.\log_{ex}$	-0.509	0.001
2	LF1	$\log_{ey}=2.516-1.152.\log_{ex}$	-0.341	0.001
	IM1	$\log_{ey}=2.166-0.249.\log_{ex}$	-0.141	---
	UF1	$\log_{ey}=2.869-0.926.\log_{ex}$	-0.521	0.001
	UF2	$\log_{ey}=3.540-1.053.\log_{ex}$	-0.892	0.001
	UF4	$\log_{ey}=3.458-1.137.\log_{ex}$	-0.866	0.001
	UF5	$\log_{ey}=2.261-0.412.\log_{ex}$	-0.309	0.01
	WJ4	$\log_{ey}=0.950-1.374.\log_{ex}$	0.706	0.001
	MC1	$\log_{ey}=3.465-0.999.\log_{ex}$	-0.836	0.001
	MC2	$\log_{ey}=4.107-1.599.\log_{ex}$	-0.987	0.001
4	PL1	$\log_{ey}=3.658-1.152.\log_{ex}$	-0.853	0.001
	PL2	$\log_{ey}=4.102-1.589.\log_{ex}$	-0.801	0.001
	PL4	$\log_{ey}=3.423-1.025.\log_{ex}$	-0.857	0.001
	WDT1	$\log_{ey}=3.625-1.137.\log_{ex}$	-0.842	0.001
	IM2	$\log_{ey}=3.057-0.869.\log_{ex}$	-0.718	0.001
	UF3	$\log_{ey}=3.550-1.113.\log_{ex}$	-0.878	0.001
5	FL	$\log_{ey}=3.856-1.366.\log_{ex}$	-0.912	0.001
	CR1	$\log_{ey}=3.552-1.276.\log_{ex}$	-0.935	0.001
6	L1	$\log_{ey}=3.189-0.926.\log_{ex}$	-0.706	0.001
	L2	$\log_{ey}=3.258-0.941.\log_{ex}$	-0.783	0.001
	TS1	$\log_{ey}=3.253-0.888.\log_{ex}$	-0.806	0.001
	TS2	$\log_{ey}=4.374-2.657.\log_{ex}$	-0.965	0.001
	TS3	$\log_{ey}=3.350-0.992.\log_{ex}$	-0.816	0.001
	PV2	$\log_{ey}=2.674-0.812.\log_{ex}$	-0.585	0.001
	MtK2	$\log_{ey}=3.600-1.125.\log_{ex}$	-0.900	0.001
	CR2	$\log_{ey}=3.853-1.383.\log_{ex}$	-0.914	0.001
	CR3	$\log_{ey}=3.258-1.050.\log_{ex}$	-0.892	0.001
	LD	$\log_{ey}=2.515-0.381.\log_{ex}$	-0.730	0.001
7	MtR2	-Sample too small-		
9	PV1	$\log_{ey}=0.161-0.358.\log_{ex}$	0.285	0.05
	MtK1	$\log_{ey}=3.653-1.137.\log_{ex}$	-0.871	0.001
	MTK3	$\log_{ey}=2.674-0.697.\log_{ex}$	-0.602	0.001

Table 3.4

Regression equations and correlation with the Power Function Model for sample stands of A. cupressoides.

* See Chapter 2 for full descriptions of floristic groups.

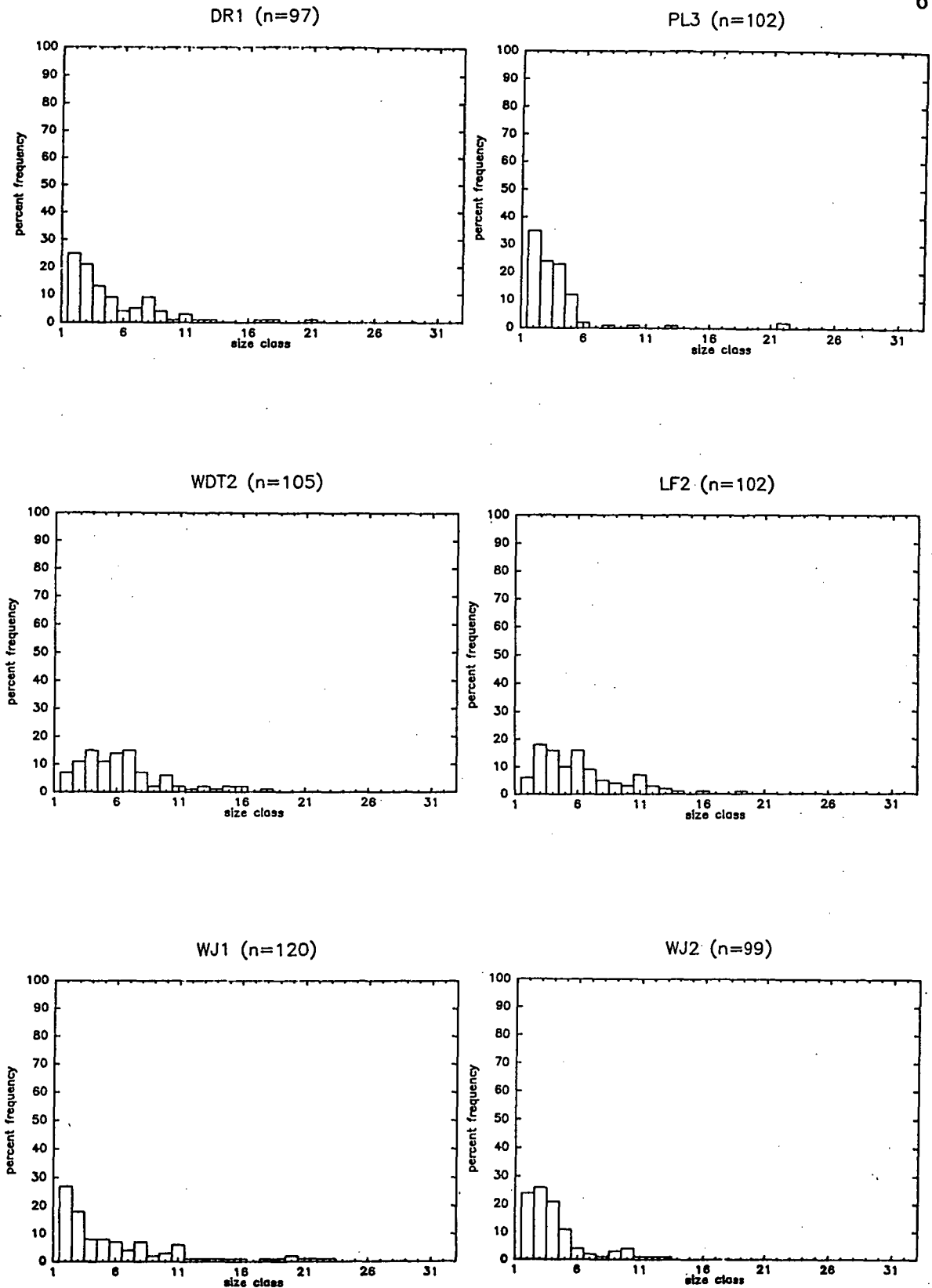


Figure 3.3. Percent frequency versus size class for A. cupressoides in Open Montane rainforests with grassy understories (floristic group 2). Size classes are 1 < 1 cm d.b.h. (seedlings), 2 = 1-4.5 cm, 3 = 5-9.5, 4 = 10-14.5, so on.

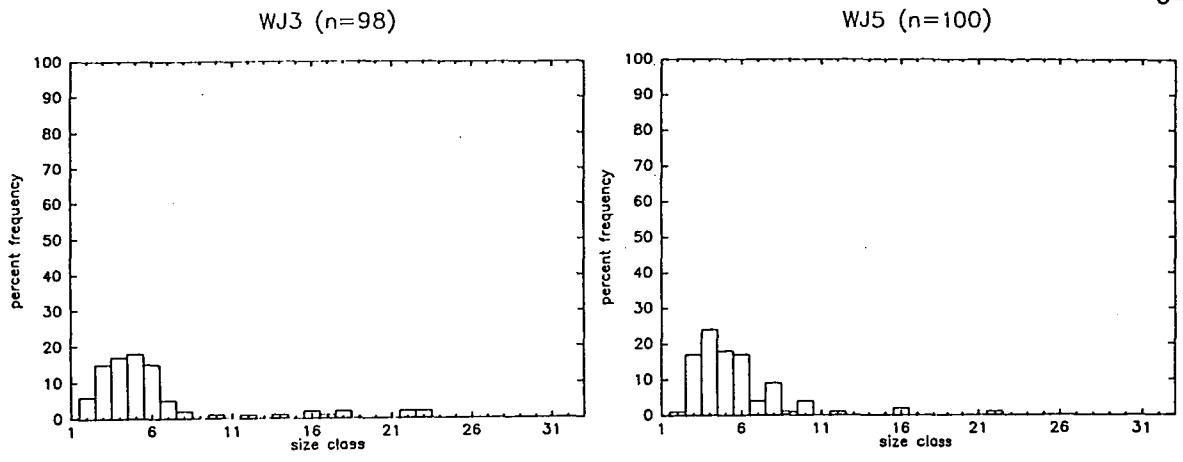


Figure 3.3. continued.

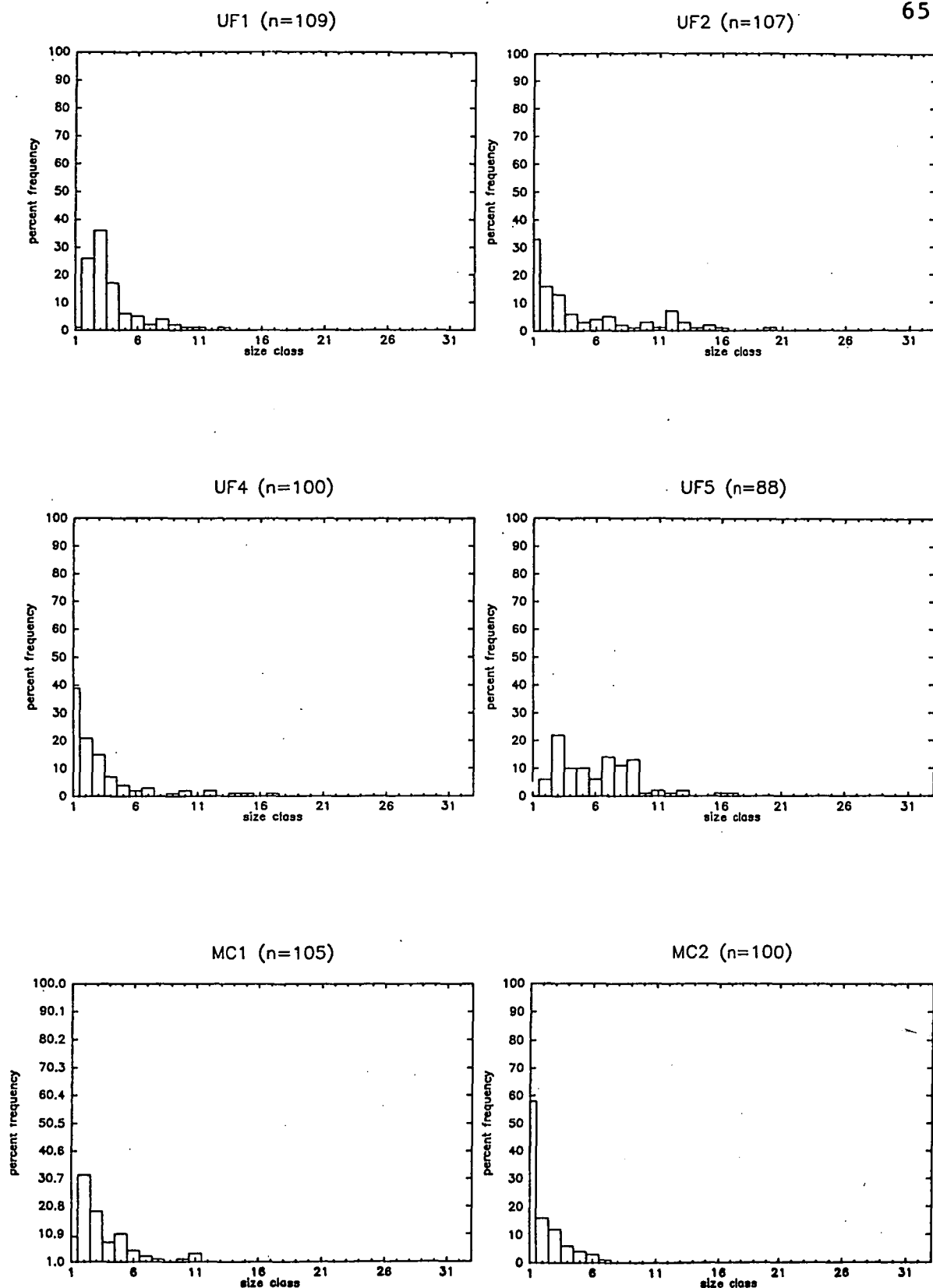


Figure 3.4. Percent frequency versus size class for A. cupressoides in Open Montane rainforests with bog understories (floristic group 3). Size classes are 1 < 1 cm d.b.h. (seedlings), 2 = 1-4.5 cm, 3 = 5-9.5, 4 = 10-14.5, so on.

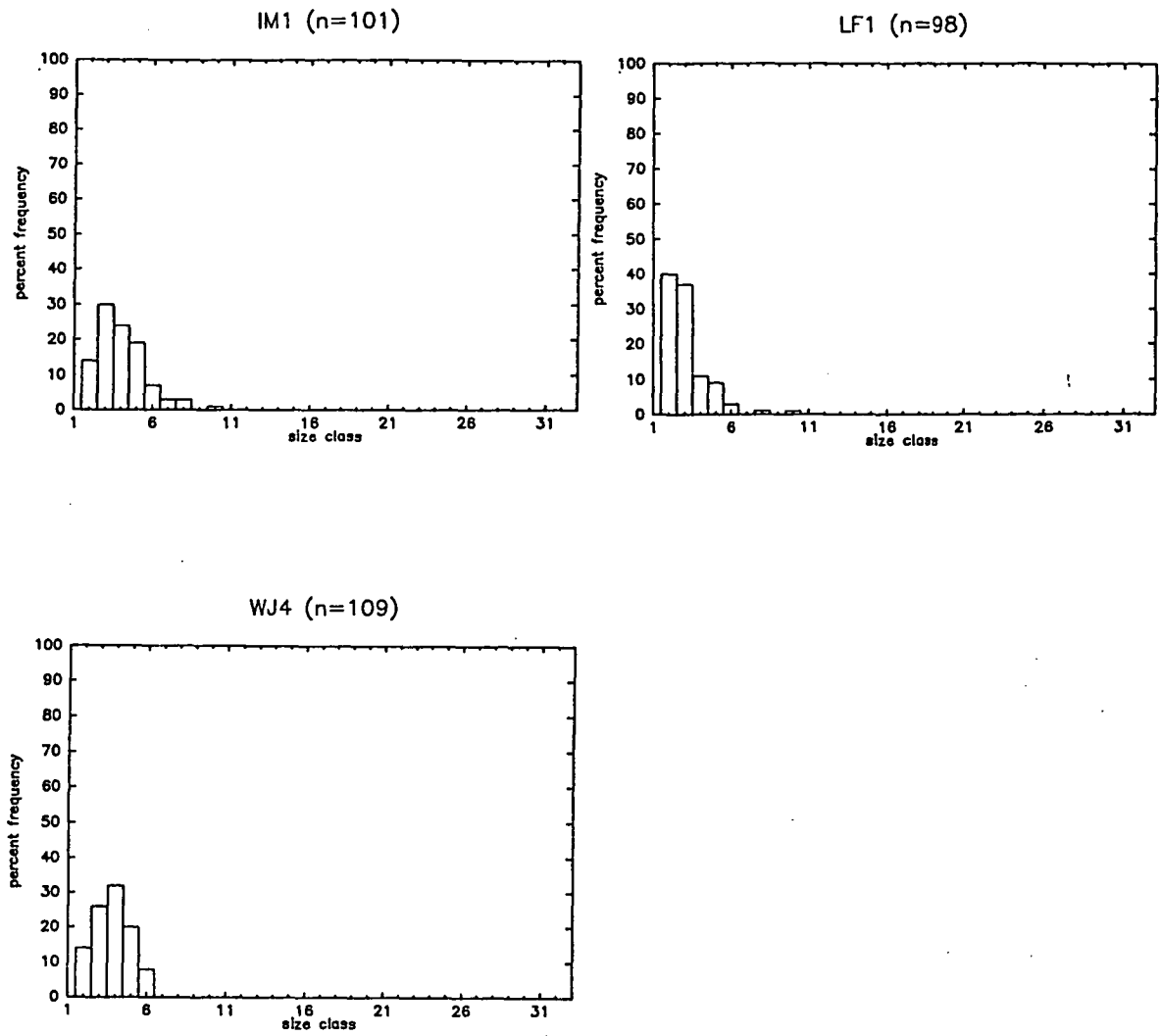


Figure 3.4 continued.

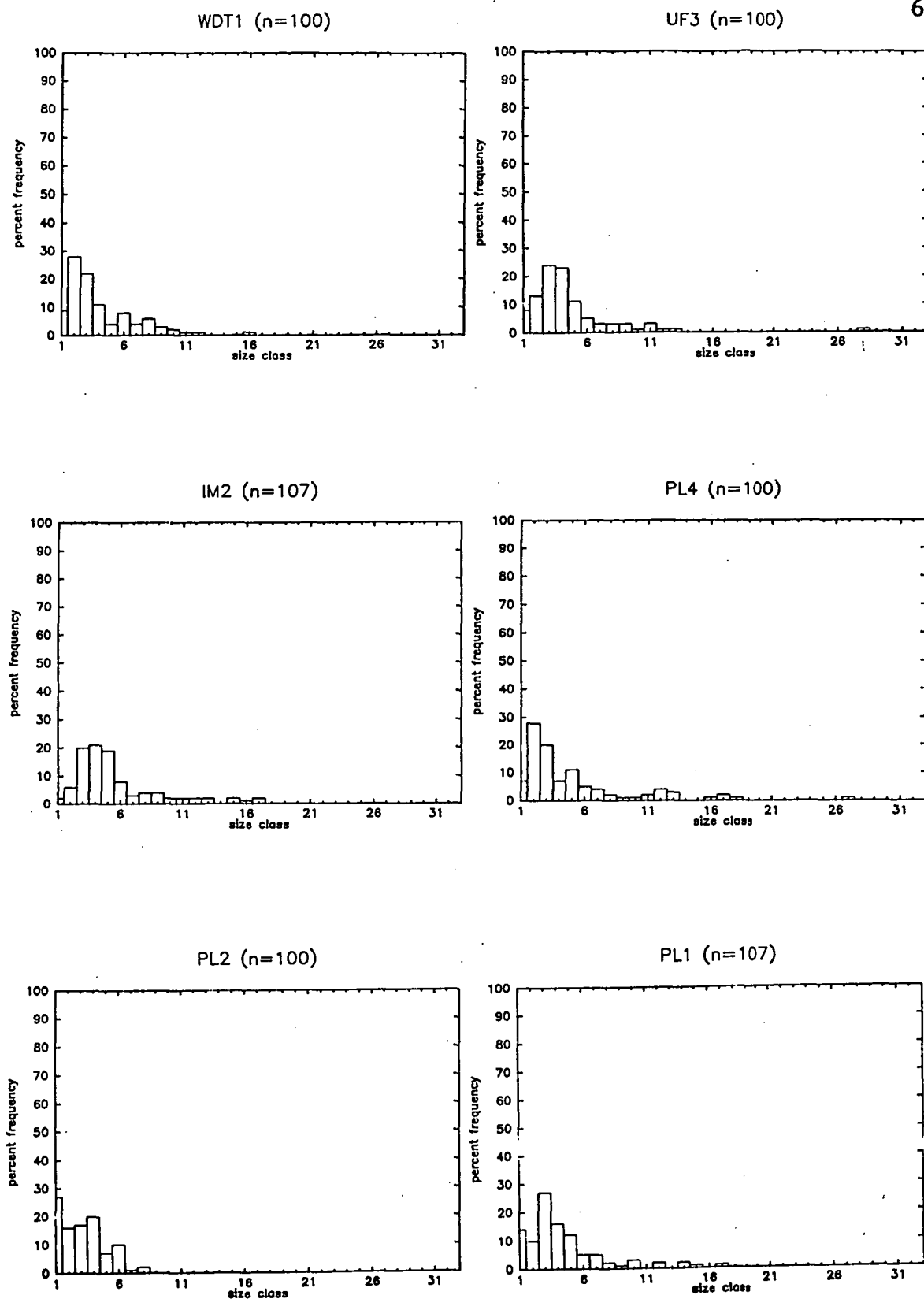


Figure 3.5. Percent frequency versus size class for A. cupressoides in Open Montane rainforests with heath and scrub understories (floristic group 4). Size classes are 1 < 1 cm d.b.h. (seedlings), 2 = 1-4.5 cm, 3 = 5-9.5, 4 = 10-14.5, so on.

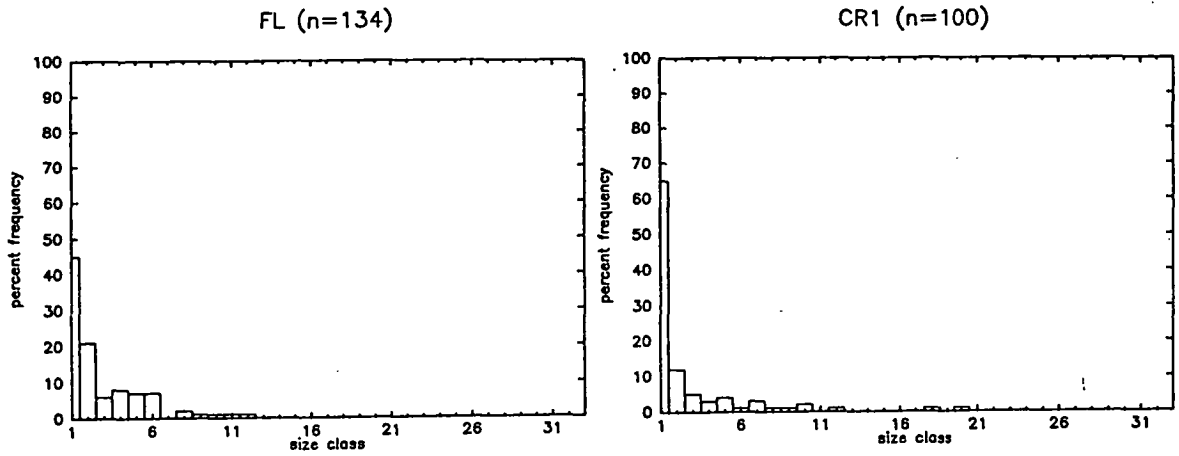


Figure 3.6. Percent frequency versus size class for A. cupressoides in Open Montane rainforests with intermediate understories (floristic group 5). Size classes are 1 < 1 cm d.b.h. (seedlings), 2 = 1-4.5 cm, 3 = 5-9.5, 4 = 10-14.5, so on.

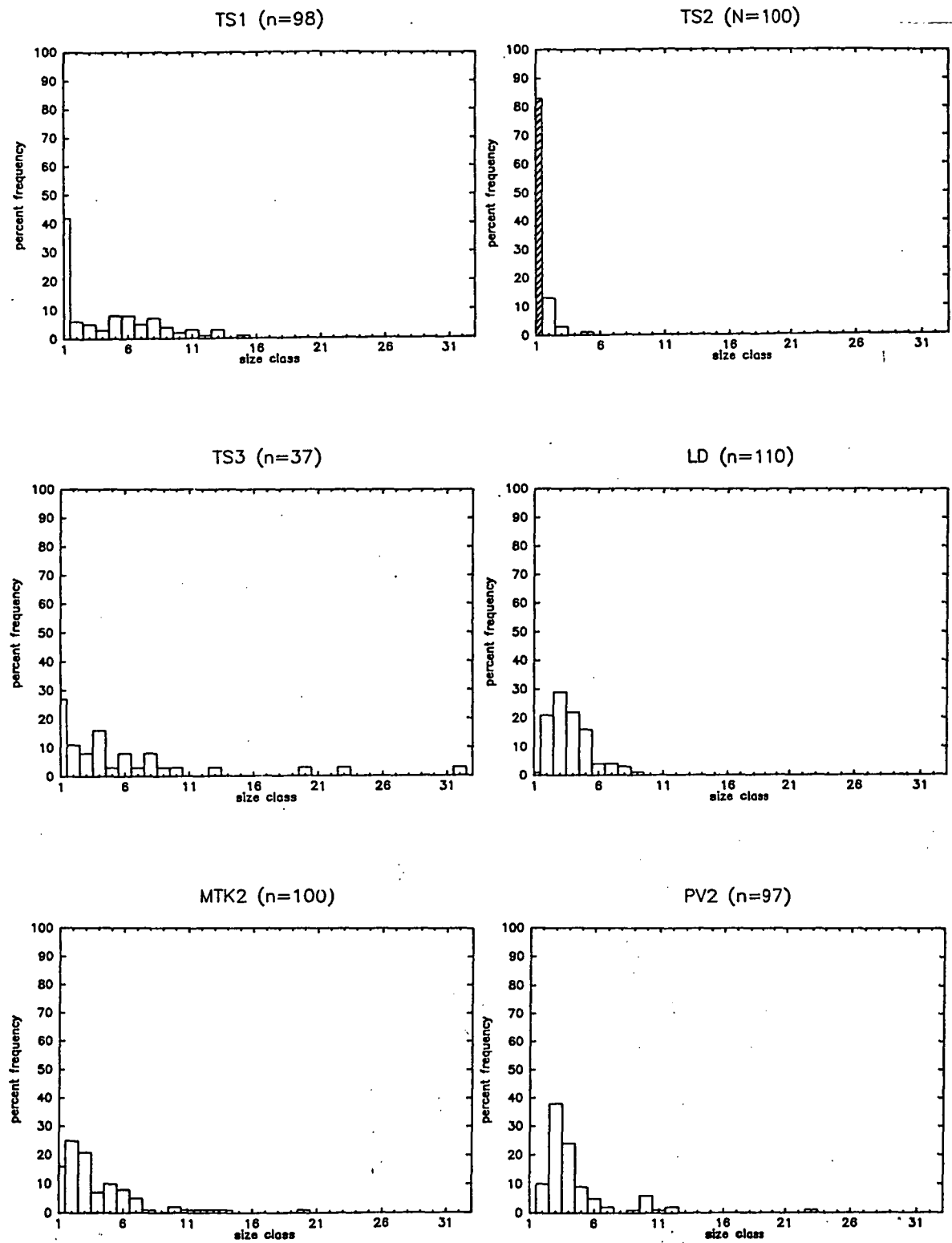


Figure 3.7. Percent frequency versus size class for A. cupressoides in Open Montane rainforests with deciduous or coniferous heath understories (floristic group 6). Size classes are 1 < 1 cm d.b.h. (seedlings), 2 = 1-4.5 cm, 3 = 5-9.5, 4 = 10-14.5, so on. Hatched areas represent the proportion of seedlings located in canopy gaps formed by the death of one or more trees.

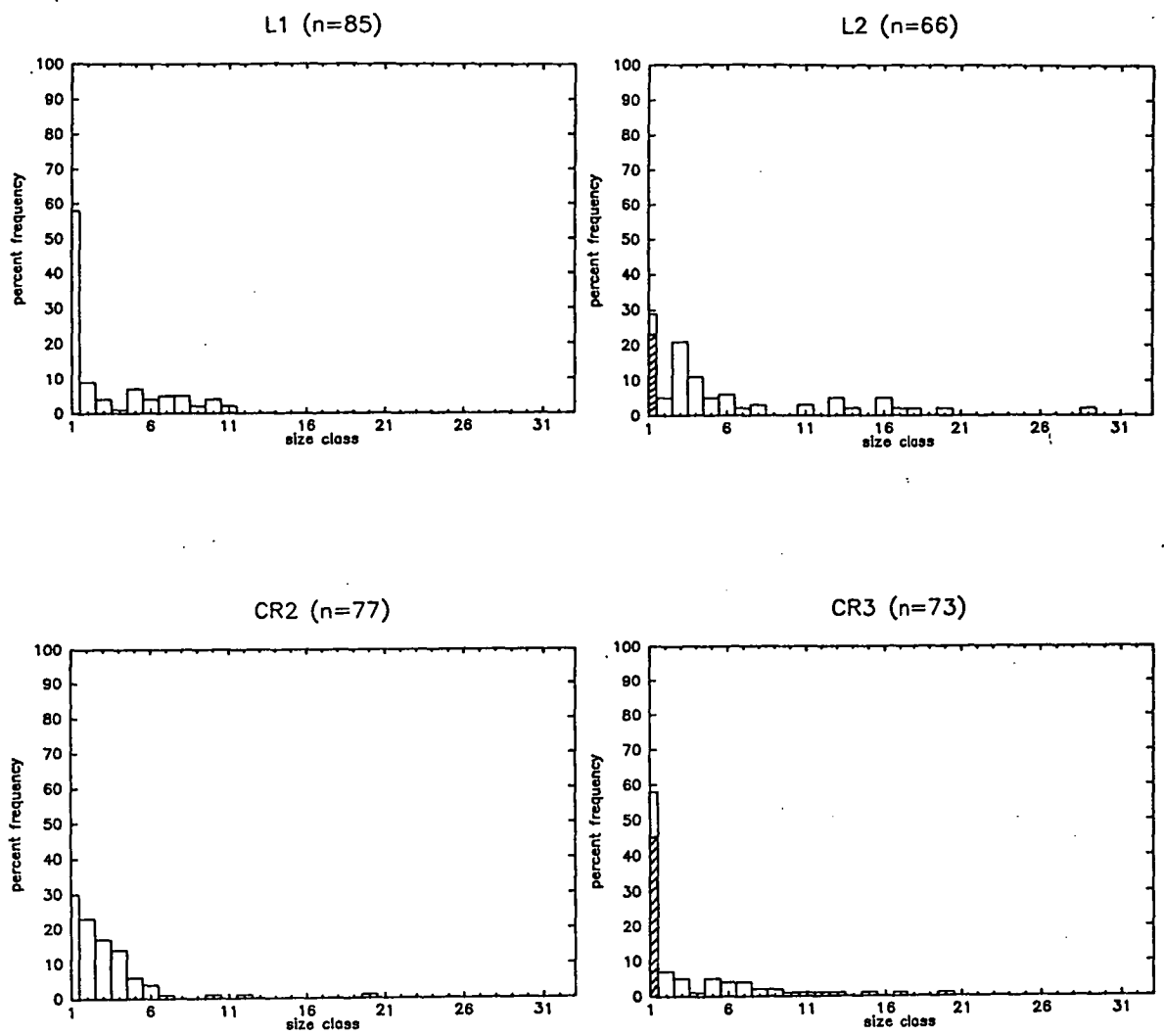


Figure 3.7 continued.

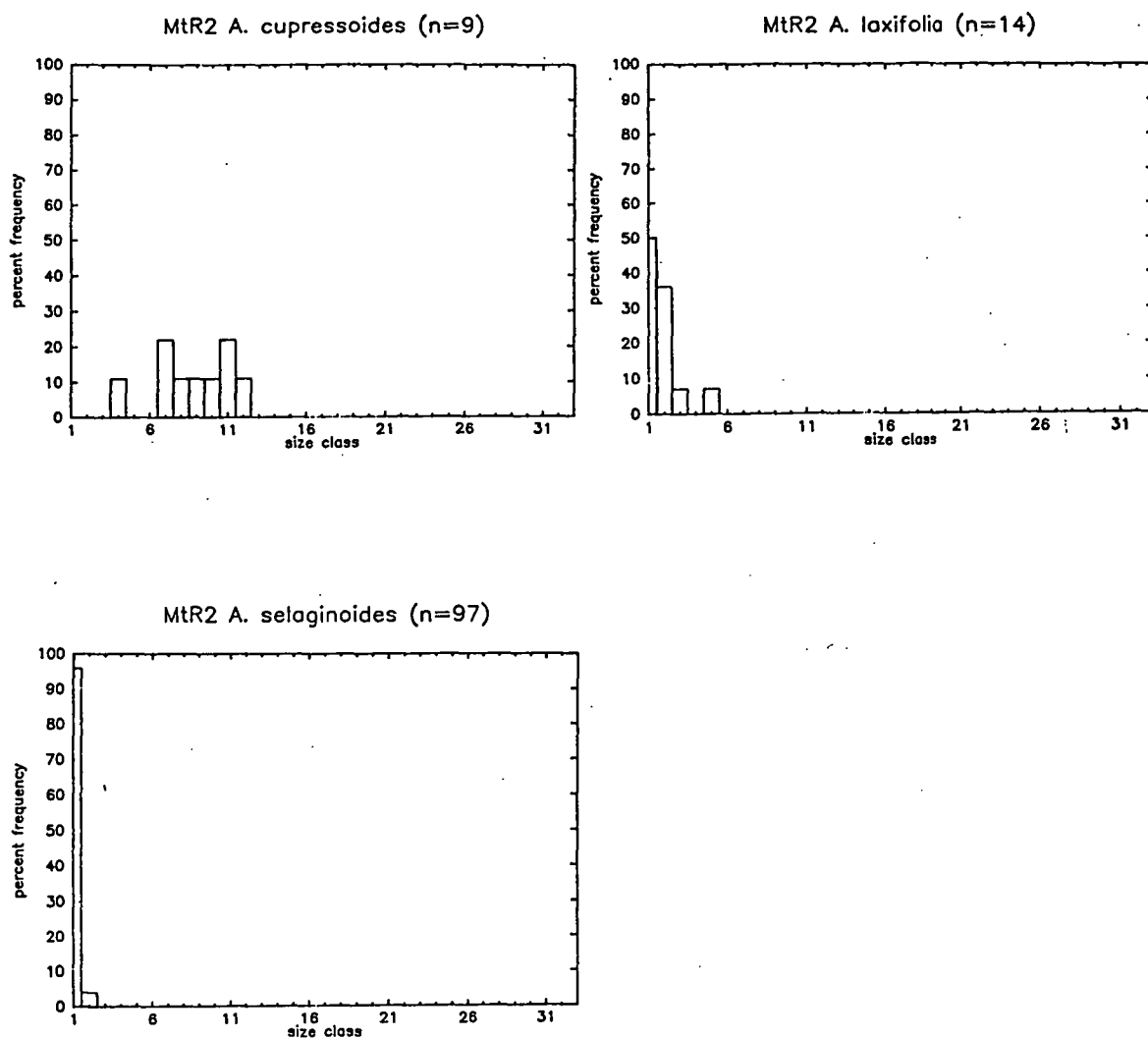


Figure 3.8. Percent frequency versus size class for A. cupressoides, A. selaginoides, and A. laxifolia in high altitude Implicate rainforest with A. cupressoides dominating (floristic group 7). Size classes are 1 < 1 cm d.b.h. (seedlings), 2 = 1-4.5 cm, 3 = 5-9.5, 4 = 10-14.5, so on. Figure 3.3.

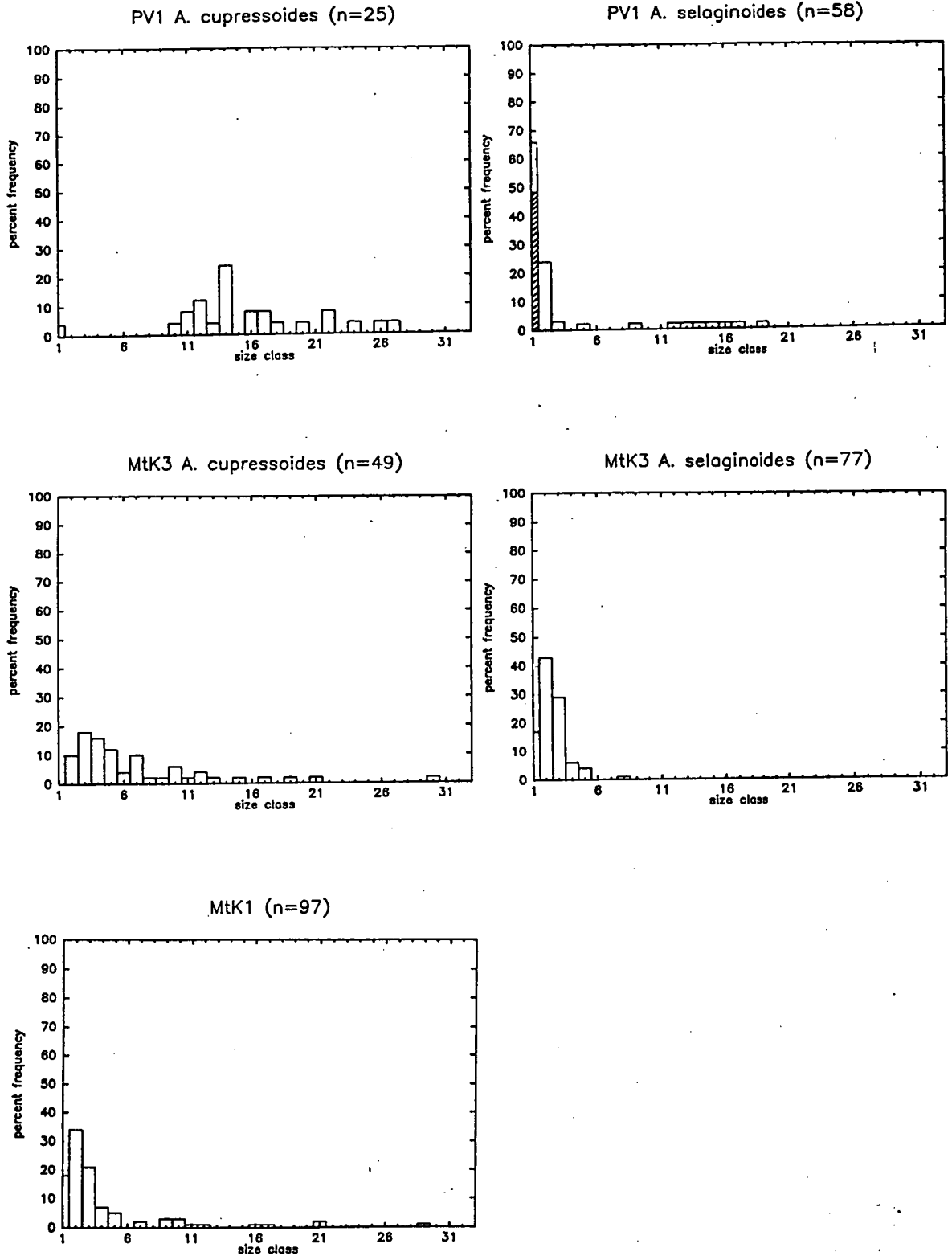


Figure 3.9. Percent frequency versus size class for *A. cupressoides*, and *A. selaginoides* in Central Highlands Thamnic rainforest (floristic group 9). Size classes are 1 < 1 cm d.b.h. (seedlings), 2 = 1-4.5 cm, 3 = 5-9.5, 4 = 10-14.5, so on. Hatched areas represent the proportion of seedlings located in canopy gaps formed by the death of one or more trees.

the closer fits to the reverse J shaped models ($r > 0.8$ in these cases). Group 4 communities, open montane rainforest with heath and scrub understories on dolerite block streams, show a consistently closer fit to the power function curve ($r > 0.7$ in all cases)(Tab. 3.4), with all stands having low numbers of individuals in the first size class (Fig. 3.5). However, in all cases the number of seedlings present falls short of the number of individuals in the second and sometimes third size classes, suggesting that present regeneration is not sufficient to maintain stands at current stocking levels if they were regenerating continuously.

Most of the group 5 and 6 stands, the open montane communities in the west and south of the island, have well stocked seedling size classes and they display close fits to the power function model (Figs. 3.6 and 3.7, Tab. 3.4). With the exception of MTK1 and MTK3, group 7 and 9 stands, the implicate and thamnic rainforest communities, have no or insignificant levels of A. cupressoides regeneration and are poorly fitted to the power function model (Figs. 3.8 and 3.9, Tab. 3.4).

The general lack of regeneration in stands on the Central Plateau cannot be attributed to a lack of gaps as the canopies of these stands are low and open, often contributing less than 50% projected canopy cover (Fig. 3.10). There is no significant difference between the

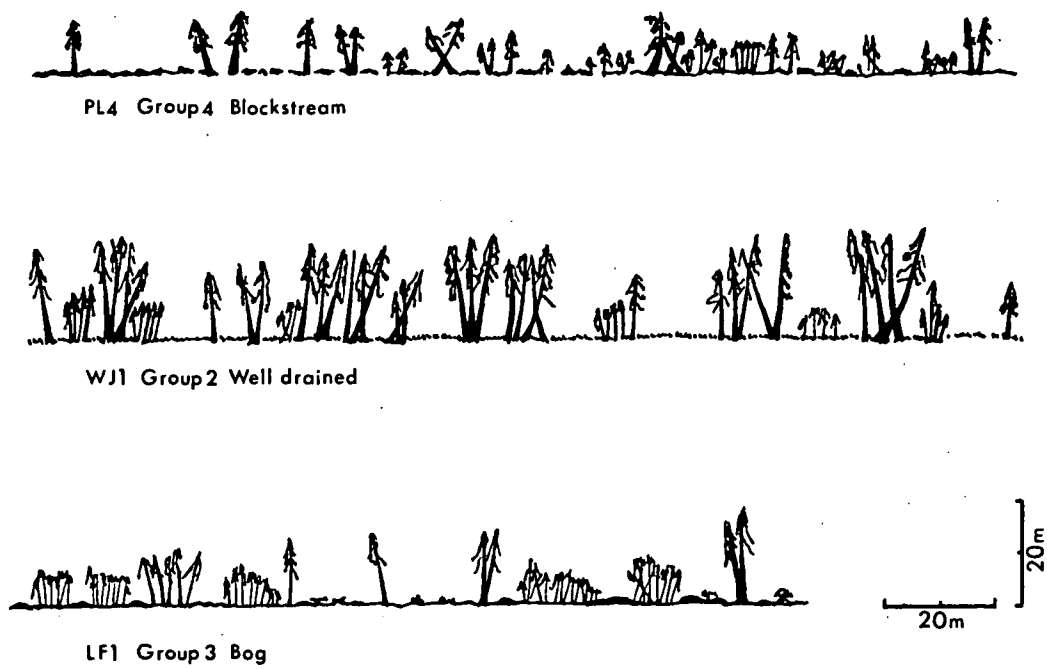


Figure 3.10. Profiles illustrating the open nature of the canopy in three stands on the Central Plateau. Drawn from photographs and data taken from 3 m wide transects.

mean nearest neighbour distance in stands with seedlings and stands without seedlings (Tab. 3.5). This relationship holds for the comparison between group 3 stands with seedlings and group 3 stands without seedlings. Further more, in many of the stands without seedlings the transects crossed the stand edges where conditions suitable for seedling growth could be expected to occur.

Disturbance events are also common, usually fire but in some cases felling of trees for fence building materials. However, no regeneration was observed following any such events which have occurred during, at least, the past fifty years. As regeneration is present in some group 3 and 4 stands it is difficult to attribute the lack of seedling sized individuals to a climatic change. The recent crops of A. cupressoides germinates, which are common to most stands, also suggests that present climates are suitable for the regeneration of this species. Although seed production is intermittent in A. cupressoides, mast seed crops every 5 to 6 years would contribute enough regeneration opportunities to fill the large temporal gap represented by size class 1.

It seems probable that the lack of regeneration has been caused by grazing of seedlings by introduced and native mammals. Sheep and cattle were introduced to the Central Plateau region by 1830 and rabbits were

Floristic group	Stand	Mean nearest neighbour distance (m)	(range) (m)	Seedlings present/absent
2	PL3*	1.9	(0.5-14)	no seedlings (ns)
	WJ5*	2.0	(0.5-4)	ns
	WJ2*	2.2	(1-6)	ns
	DR1*	2.2	(0.5-13)	ns
	WDT2*	2.7	(1-10)	ns
	WJ3*	3.2	(0.5-9)	ns
	LF2*	3.3	(0.5-10)	ns
	WJ1	4.0	(1-15)	ns
3	IM1*	0.8	(0.5-8)	ns
	UF2	1.6	(0.5-5)	seedlings (s)
	UF4*	2.0	(0.5-9)	(s)
	MC1*	2.4	(0.5-10)	suckers at edge
	UF1*	2.4	(0.5-14)	1 seedling
	WJ4*	2.8	(0.5-11)	ns
	MC2*	3.0	(1-6)	suckers at edge
	UF5*	3.4	(1-8)	ns
	LF1*	5.4	(0.5-13)	ns
	PL2*	2.7	(0.5-14)	(s)
4	WDT1*	2.8	(0.5-20)	(s)
	UF3*	3.8	(1-15)	suckers at edge
	PL4*	4.2	(0.5-24)	(s)
	IM2*	4.1	(0.5-26.5)	2 seedlings at edge
	PL1*	6.2	(0.5-33)	ns

Table 3.5.

Nearest neighbour distance in open montane rainforests on the Central Plateau.

* denotes stand edge sampled.

introduced around 1910 (Shepherd, 1974).

A. cupressoides forms more or less all-aged populations in most of the open montane stands in the west and south of the island (Fig 3.6 and 3.7). In these stands the species appears to be replacing itself without canopy disturbance. However, in some stands significant numbers of seedlings are located in canopy gaps or at stand edges where dense shrubberies of Nothofagus and coniferous species have not developed. This suggests that disturbance may enhance the regeneration capability of A. cupressoides provided a seed or root source remains in the immediate vicinity. Examples include stands CR3, L2, and TS2. At CR3 much of the current regeneration is on previously burnt site and the presence of a large diameter, heavily fire scarred stem deep within the intact A. cupressoides-N. gunnii canopy suggests that fire may have been an agent of disturbance in the distant past. Large burnt stumps testify to a past fire at TS2 and the site is now heavily stocked with root suckers. Not far from TS2 a site which was burnt in 1966 had no established regeneration in 1985. Much of the burnt area is within 50 m of an intact A. cupressoides-N. gunnii forest (stand TS3), and the presence of a few germinates on moist sites demonstrates that seed is reaching the site. The north-easterly aspect and steep slope allows this site to dry out at times during the summer. It may

require the development of some initial ground cover to allow conditions suitable for A. cupressoides regeneration to occur, for example, the development of shrub cover to enhance precipitation by fog stripping (Edwards, 1973).

Fire appears to have initiated some new stands on the Central Plateau but stem diameters indicate that this happened long in the past. DK2 has regenerated following fire with large burnt stumps scattered amongst the smaller diameter regrowth. UF1 has regenerated following the burning of part of the forest in which stand UF2 is located.

Except at the edge of stands MTK1 and MTK3, the thamnian and implicate communities investigated do not contain significant levels of A. cupressoides regeneration. However, the other tree species present in these communities are regenerating without canopy disturbance and this suggests that they will develop into thamnian or implicate communities without A. cupressoides in the future.

The present lack of A. cupressoides regeneration in stands MtK1 and MtK3 suggests that the conditions prevailing now are unsuitable for the establishment of A. cupressoides. At MtK1 the two largest A. cupressoides stems are fire scarred but are well within the closed canopy of A. cupressoides and N. cunninghamii. They may

be the remnants of a previous stand which was burnt, thereby creating conditions suitable for A. cupressoides regeneration. A. cupressoides seedlings in stands MtK1 and MtK3 are restricted to the stand edges, where the heathy understorey vegetation and the open nature of the canopy more closely resemble open montane communities than closed thamnic rainforests. However, N. cunninghamii is regenerating within both stands and there are small size stems of A. selaginoides in MTK3.

Early stages of a development from open montane rainforest, with A. cupressoides dominating, to thamnic rainforests, without A. cupressoides, may be represented by stands LD and PV2. In a dendrochronological study of the forest at LD Ogden (1978) concluded that frost damage to early growth rings of some individuals indicated that in the the past the stand was more open and susceptible to severe frosts than it is now. There is very little A. cupressoides regeneration in this stand and N. cunninghamii up to 5 m tall and Richea pandanifolia are common in the understorey. The presence of these species suggests that the stand may develop a closed canopy of N. cunninghamii with A. cupressoides emerging above, as at MTK1. Other rainforest species including A. selaginoides, P. asplenifolius, and A. moschatum are present locally and could conceivably invade in the future. Beyond the margins of the stand, A. cupressoides

is regenerating in open heathy scrub dominated by E. coccifera. This and scattered large E. coccifera individuals in stand LD supports Ogdens interpretation of the stands history.

The stands investigated in Pine Valley also suggest that some open montane communities will develop into thamnic rainforests given enough time. Stand PV2 is an open montane community on grassy creek flats below slopes covered in thamnic rainforest. The lack of seedling sized A. cupressoides at this site may be due to grazing as the stand contains many canopy gaps. Wallabies are common in the area. With the exception of P. aspleniifolius other rainforest tree species are absent. However, a nearby stand of A. cupressoides contains young N. cunninghamii and R. pandanifolia in the understorey and appears to be developing in the same manner as stand LD.

Stand PV1, a thamnic rainforest community, is located further upstream. Here very large stems of A. cupressoides emerge above A. selaginoides, N. cunninghamii, and N. gunnii. A. cupressoides is not regenerating successfully but the other species are present in a range of size classes including seedlings. The largest A. cupressoides stems were dated to a minimum of 500 years but would probably be from 750 to 1000 years old. Similar patches of large sized A. cupressoides

stems can be found scattered throughout thamnic rainforest all along the creek flats in this valley. It is postulated that GC and similar stands arose as open montane communities similar to that represented by PV at present and have since been invaded by thamnic rainforest species.

It appears that the conditions imposed by the subordinate species in the taller and more closed thamnic and implicate rainforests inhibit A. cupressoides regeneration. Evidence suggests that these forests have developed from open montane communities. The relatively slow growth rates of all the species involved means that the process takes many centuries. Presumably it would require canopy disturbance to initiate a new generation of A. cupressoides in these stands. No attempt has been made to discover what factor or factors are limiting A. cupressoides regeneration. On the other hand populations of A. cupressoides in open montane rainforests are regenerating continuously, even when the understorey is comprised of dense shrubberies of Nothofagus or coniferous species. However, canopy disturbance appears to enhance A. cupressoides regeneration in these forests. Where seedlings are absent from open montane stands it is likely that they have been removed by grazing.

The stands with grassy understoreys (group 2) would be most attractive grazing animals and this would explain

the total absence of seedlings in these stands. By contrast the group 4 stands with heath and scrub understoreys on dolerite block fields have reduced amounts of grass and herbs. These stands are probably less attractive to grazing animals and this would explain the low levels of regeneration present. To test the hypothesis that grazing has produced the regeneration failure of A. cupressoides on the Central Plateau trials have been established in the area (see chapter 5).

3.3.5 Stand demography and seedling distribution of Athrotaxis selaginoides.

A wide range of A. selaginoides dominated forest types were encountered in the study (see chapter 2). However, they fall into two broad categories: those forming closed forest with a high component of evergreen tree species, and either a well developed but species-poor shrub understorey (thamnic rainforest, groups 9 and 10), or with only a few scattered shrubs (callidendrous rainforest, group 1); those which are relatively open and have a reduced evergreen component, an increase in the dominance of deciduous N. gunnii, and a dense tangled species-rich understorey (implicate and open montane rainforest, groups 11, 7, and 6, and subalpine scrub, groups 8 and 7).

The demographic structures of the callidendrous and

thamnic communities show poor fits to the power function model ($r < 0.5$ except B4, Tab. 3.6). These stands have either discontinuities in their size (age) structures or no individuals in the smallest size classes, suggesting that these stands are not regenerating continuously (Fig. 3a, Appendix A). On the other hand the implicate and open montane rainforests, and the subalpine scrub communities have size class structures suggestive of continuously regenerating populations (Fig. 3b, Appendix A and Fig. 3.11). Although the numbers of adult individuals in these stands is low, their demographic structures can be interpreted as being reverse J-shaped ($r > 0.8$ in all cases, except stand MtB2, Tab. 3.6).

The distribution of A. selaginoides and adults and seedlings within the stands examined is discussed in Appendix A, page 162. All the thamnic stands, except A2, and W3, show seedling and adult distribution patterns suggestive of gap-phase regeneration whilst seedlings in implicate and open montane rainforests and subalpine scrub communities appear to be continuously regenerating without the need for canopy disturbance. Read (1986) has confirmed the finding that A. selaginoides appears to rely on canopy disturbance for regeneration opportunities in thamnic rainforests. She found that the other tree species common in these forests, namely N. cunninghamii, A. moschatum, and E. lucida, have a competitive advantage

Floristic group	Stand	Equation	r	p <
1	DR2	-Sample too small-		
9	W2	$\log_{ey}=2.543-0.496.\log_{ex}.$	-0.250	0.05
	W3	$\log_{ey}=1.258+0.023.\log_{ex}.$	0.015	---
10	B1	$\log_{ey}=2.277-0.542.\log_{ex}.$	-0.445	0.001
	B4	$\log_{ey}=3.664-1.356.\log_{ex}.$	-0.847	0.001
	A2	$\log_{ey}=0.268+1.330.\log_{ex}.$	0.683	0.01
	A3	$\log_{ey}=1.442+0.287.\log_{ex}.$	0.158	---
	A4	$\log_{ey}=0.732+0.692.\log_{ex}.$	0.450	0.01
	D1	$\log_{ey}=2.327-0.659.\log_{ex}.$	-0.490	0.001
6	W1	$\log_{ey}=3.785-1.833.\log_{ex}.$	-0.898	0.001
7	D2	$\log_{ey}=3.957-1.756.\log_{ex}.$	-0.897	0.001
	D3	$\log_{ey}=4.213-1.759.\log_{ex}.$	-0.996	0.001
	MtR1	-Sample too small-		
8	B2	$\log_{ey}=3.566-1.225.\log_{ex}.$	-0.670	0.001
	A1	$\log_{ey}=4.085-1.590.\log_{ex}.$	-0.803	0.001
11	B3	$\log_{ey}=3.868-1.267.\log_{ex}.$	-0.908	0.001
	BR1	$\log_{ey}=3.397-1.457.\log_{ex}.$	-0.903	0.001
	BR2	$\log_{ey}=3.029-1.331.\log_{ex}.$	-0.814	0.001

Table 3.6

Regression equations and correlation with the Power Function Model for sample stands of A. selaginoides.

* See Chapter 2 for full descriptions of forest types.

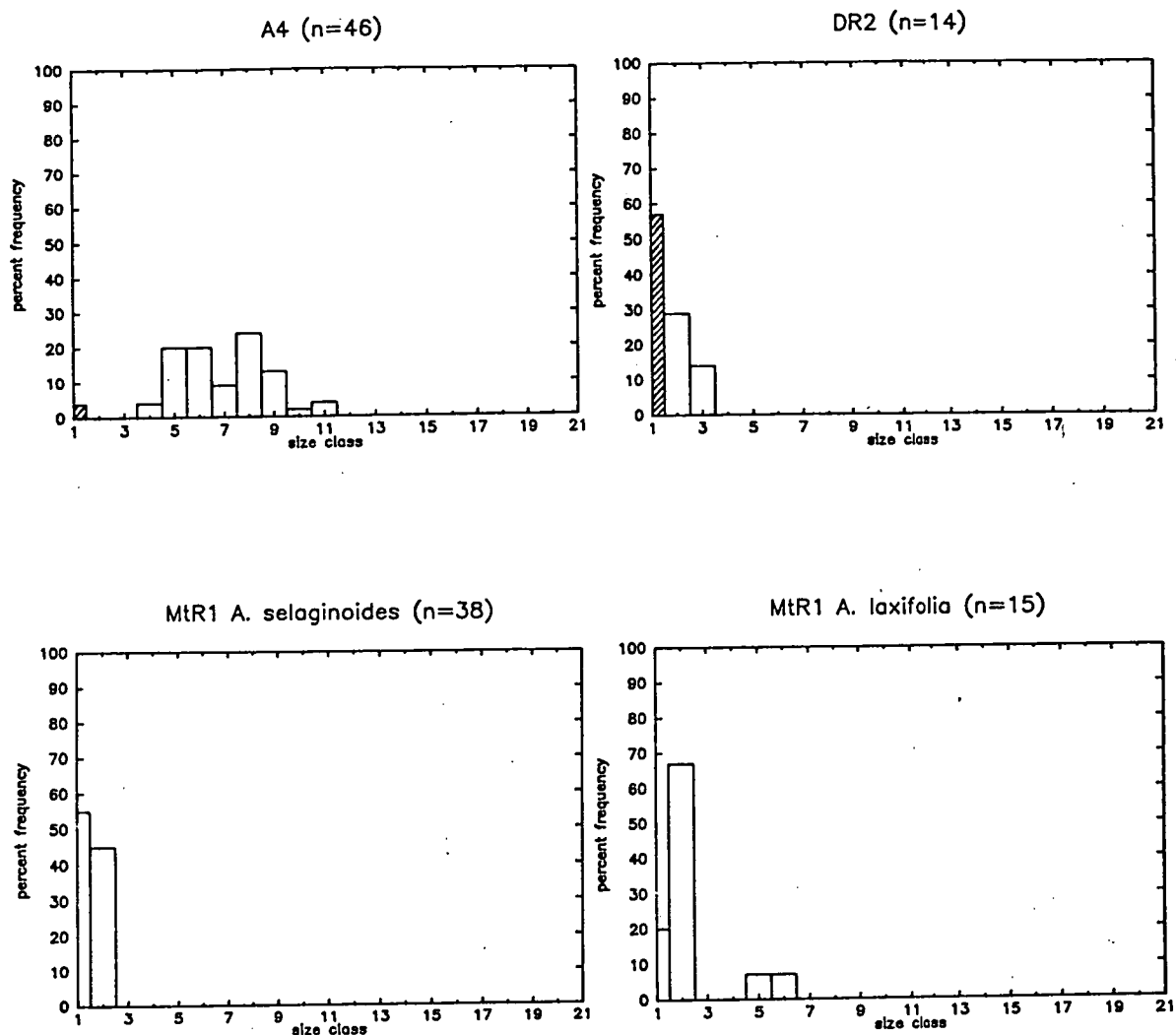


Figure 3.11. Percent frequency versus size class for *A. selaginoides* in sample stands not included in Appendix 1. MtR1 is an Implicate rainforest (floristic group 7), DR2 is a Callidendrous rainforest (floristic group 1), and MtA4 is a Thamnic rainforest (floristic group 10). Size classes are 1 < 1 cm d.b.h. (seedlings), 2 = 1-9.5 cm, 3 = 10-19.5, 4 = 20-29.5, so on. Hatched areas represent the proportion of seedlings located in canopy gaps formed by the death of one or more trees.

over A. selaginoides in small canopy gaps or in undisturbed situations in thamnic rainforest. Therefore it seems that dense stands of A. selaginoides will not be able to replace themselves without major canopy disturbance and in the absence of such disturbance the quantity of A. selaginoides in these stands is likely to decrease.

A. selaginoides is capable of regenerating on catastrophically disturbed sites (see Appendix A, page 167). Further research has yielded another example of such regeneration at stand DR2 and possibly at stand MtA4. Stand DR2 contains A. selaginoides regeneration in a gap created by rock fall. The largest stem in this cohort was aged at a minimum of 33 years (core extracted at ground level), but the site appears to be still open to regeneration of the species. Adjacent to this gap, a group of pole sized A. selaginoides and N. cunninghamii stems occupy an area which appears to have been disturbed over 100 years ago. This area lacks A. selaginoides seedlings. Two A. selaginoides stems yielded minimum ages of 50 and 112 years (cores extracted 1 m above ground level), again indicating a prolonged recruitment period. A burnt site near stand B1 (see Appendix A, page 170) appears to have been open to A. selaginoides regeneration for 60 to 70 years. This suggests that extended periods of seedling recruitment may be normal on

catastrophically disturbed sites.

The necessity for canopy disturbance is clearly demonstrated at stand DR2. Mature A. selaginoides stems overhang the cliffs above and would provide seed to both the gap and to the adjacent closed thamnic rainforest. A. selaginoides regeneration is only present on the disturbed area. The other stands of A. selaginoides in this area may have been initiated in a similar manner. They occur on steep rocky slopes below dolerite crags, are of limited extent, and contain no small sized individuals.

The demography and the spatial distribution of the stems at stand MtA4 are suggestive of past catastrophic disturbance. MtA4 is a dense stand of large pole sized A. selaginoides with subordinate N. cunninghamii. Adjacent to, and down slope the forest is comprised of widely spaced, extremely large diameter A. selaginoides and N. cunninghamii stems. These A. selaginoides individuals represent an older generation (Ogden, 1978) and are probably the parents of the younger generation. The steep slopes and cliffs above may have been the source of a past landslide, or the stand could have been formed by the windthrow of a large patch of forest. J.B. Kirkpatrick and M.J. Brown (pers. com.) report aerial sightings of A. selaginoides forming linear stands, orthagonal to the contours, on steep mountain slopes in

the south of the island. These stands may have formed following landslides or rock falls. A. selaginoides seedlings were also observed on a land slip/erosion gully site in thamnic rainforest at Pine Valley during this study.

3.3.6 The presence of Athrotaxis laxifolia.

Athrotaxis laxifolia occurs in all the stands sampled where A. cupressoides and A. selaginoides grow in mixture (PV1, MtK3, MtR1 and 2). Only one adult stem was found at PV1 and two at MtK3. However seedlings of the species were common on sites disturbed by logging near MtK3. At stands MtR1 and MtR2 Athrotaxis laxifolia is far more common (Figs. 3.8 and 3.11). Conditions favourable for the growth of A. laxifolia seedlings may be present beneath the canopies of the implicate forests at Mt Read which are lower and more open than the canopies of the thamnic rainforests at MtK3 and PV1. Such an explanation is consistent with the presence of A. laxifolia seedlings on disturbed sites at MtK3 but there are many other examples where A. cupressoides and A. selaginoides grow in close proximity in implicate or open montane communities and A. laxifolia occurs only infrequently.

3.4 Conclusion.

As hypothesized, both A. cupressoides and A. selaginoides display different demographic structures and seedling distributions in response to the different conditions imposed by variations in forest structure and floristic composition. However, the variation in demographic structure of open montane communities on the Central Plateau is probably explained by grazing of regeneration over a prolonged period. In other situations open montane forests dominated by A. cupressoides, including those with dense understoreys of Nothofagus gunnii, are regenerating without canopy disturbance. This appears to be due to the very open nature of the canopy in these forests rather than to shade tolerance on behalf of A. cupressoides, because the species fails to regenerate in taller and more closed implicate and thamnic communities. Canopy disturbance in these forests might create conditions suitable for the establishment of a new generation of A. cupressoides. No instances of this have been recorded and A. cupressoides regeneration is restricted to forest edges at the sites investigated. A. selaginoides can regenerate continuously without the need for canopy disturbance in implicate rainforest with a high proportion of N. gunnii and in subalpine scrub communities where it canopy gaps created by disturbance in thamnic and callidendrous communities

with predominantly evergreen canopies.

Where A. selaginoides and A. cupressoides grow together (stands MtK3, PV1, and MtR2) the demographic structures and the distribution of the two species demonstrate the poorer competitive ability of A. cupressoides compared to A. selaginoides and other rainforest tree species. This is well demonstrated at stand MtK3, where A. selaginoides and Nothofagus cunninghamii are present in small sizes beneath the thamnic rainforest canopy but A. cupressoides is only regenerating at the stand edge and beyond. On the other hand the few A. selaginoides seedlings recorded outside of the stand appear to be in an unhealthy condition. These seedlings, growing outside of the shelter of the canopy would be exposed to colder radiation frosts than those within the forest. Bowman (1984) has demonstrated that during frosts temperatures may be 6°C lower on cleared areas than beneath adjacent E. delegatensis forests in Tasmania. Similar temperature differences would be expected between sites beneath thamnic rainforests and those on adjacent open areas.

As discussed in chapter 2, Sakai et al. (1981) has demonstrated that adult A. cupressoides branches are more frost resistant than those of A. selaginoides and N. gunnii, and, by inference from the work of Read (1986), A. cupressoides is likely to be more frost resistant than

N. cunninghamii, A. moschatum, E. lucida, and P. aspleniifolius. An increased frost tolerance for A. cupressoides would allow it to colonize sites in advance of other rainforest tree species. Once established, a stand of A. cupressoides could ameliorate temperatures so that less frost tolerant tree species could establish. In turn they would preclude A. cupressoides regeneration.

CHAPTER 4.

THE RELATIVE FROST RESISTANCE OF ATHROTAXIS CUPRESSOIDES
AND ATHROTAXIS SELAGINOIDES SEEDLINGS.

4.1 Introduction.

Many studies have demonstrated that the frost resistance of trees can play an important role in their distribution (for example, Wardle and Campbell, 1976; Harwood, 1980). The resistance displayed by a species often reflects the minimum temperatures to which it is likely to be exposed in its natural range (Sakai et al., 1981). In Chapters 2 and 3 of this study it is suggested that temperature plays a significant role in controlling the relative distributions of A. cupressoides and A. selaginoides. This view is supported by the research of Sakai et al. (1981) who have demonstrated that adult A. cupressoides is more frost resistant than adult A. selaginoides.

Conifer seedlings have been found to be considerably less frost resistant than adults of the same species (Tranquillini, 1979) and this phenomenon has been demonstrated for A. selaginoides (Read, 1986). The relative distributions of A. cupressoides and A. selaginoides (Chapters 2 and 3) suggest that seedlings of A. cupressoides are likely to be exposed to more severe radiation frosts than those of A. selaginoides. Thus,

the seedlings of A. cupressoides should be more frost resistant than the seedlings of A. selaginoides, if resistance to cold temperatures is important in determining the relative distributions of these two species. The results of an investigation into the relative frost resistance of A. cupressoides and A. selaginoides seedlings, using experimental means, are reported in this chapter. These results are discussed in the context of the frost climate experienced in the natural habitat of both species.

4.2 Methods.

The methods adopted in this investigation broadly follow those of Harwood (1980). As it was not possible to obtain seed from A. cupressoides, recent germinates (cotyledons present) of A. cupressoides from Mickeys Creek and A. selaginoides from the Cracroft Hills (see Fig 4.1 for locations) were collected in Autumn 1984. A limited number of seedlings (cotyledons present) of both species were collected from Mt Kate (Fig 4.1) where the two species are growing in mixture (see chapter 3 for discussion). These seedlings provide a check on the possibility of provenance variation between populations. The seedlings were transplanted to mixture of peat moss and sand (50-50 ratio) and raised in a glasshouse in Hobart for approximately three months.

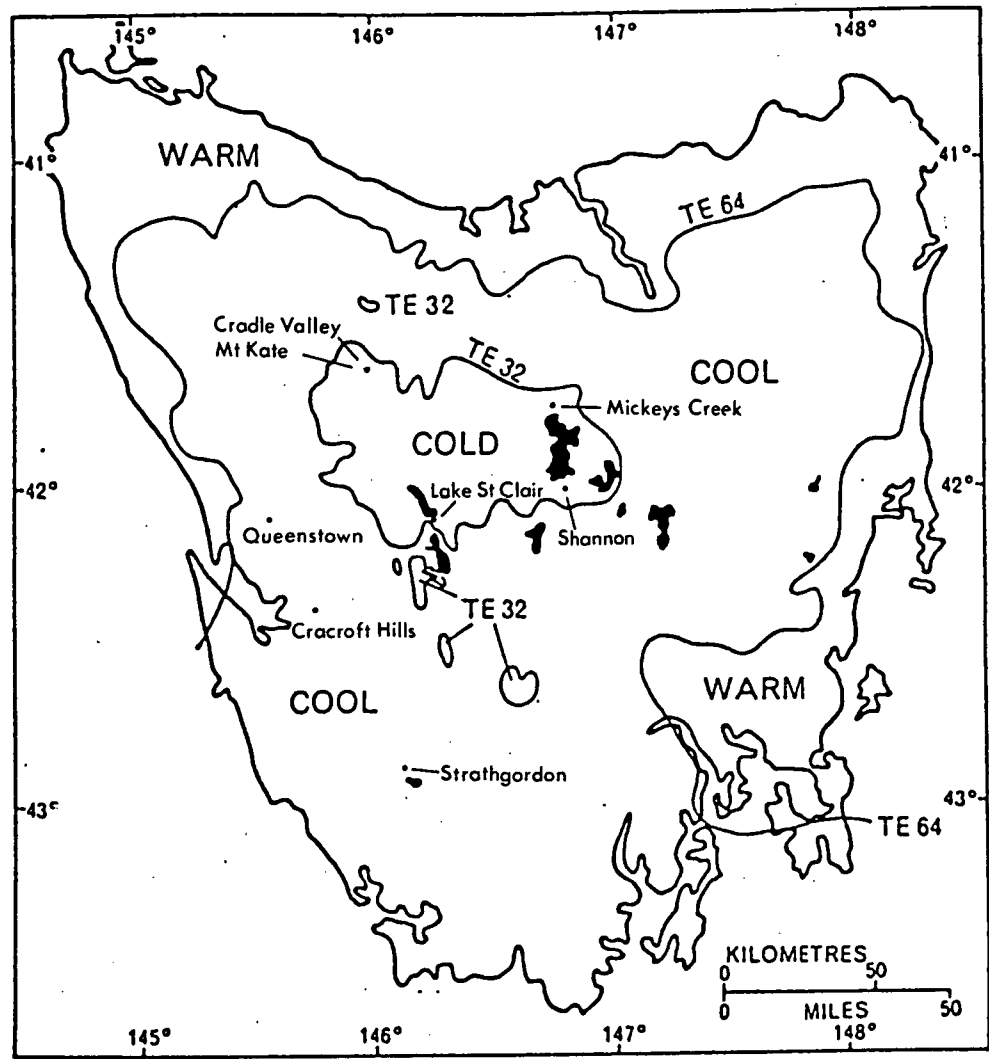


Figure 4.1. The location of seedling collection sites and climate recording stations. Temperature efficiency provinces after Gentilli (1972).

Simulated frost conditions of -5°C , -7.5°C , and -10°C were achieved using a Sanyo controlled temperature cabinet. Daily maximum and minimum temperatures in the glasshouse were recorded prior to the frost experiments. Forty seedlings of each species were chosen at random from the main stock. Twenty were exposed to the desired minimum temperature and a further 20 were reserved for control purposes. Before each frosting trial the pots were packed in loose dry peat moss to prevent the soil from freezing and consequent damage to roots. As a check on the effectiveness of this precaution, one replicate was performed at -10°C with uninsulated pots. Frost simulation proceeded as follows: the seedlings were placed in the frost cabinet after nightfall, the temperature was rapidly reduced to 2°C and was then lowered at a rate of 2°C per hour until the desired minimum temperature was reached. The minimum temperature was maintained for two hours. The seedlings were then returned to the glasshouse.

Freezing injury to the seedlings was assessed visually after five, ten, and twenty days. Browning of the stems and foliage (scales) was used as the criterion for damage. In nearly all cases seedlings either survived undamaged or were killed outright. For the partially damaged seedlings, those with damage to more than 50 % of total shoot length were counted as

fatalities and those with less as survivors.

4.3 Results

Glasshouse temperatures prior to the trials (Tab 4.1) would be expected to produce frost hardening to some degree. Read (1986) found that exposure to night time temperatures of 4°C produced hardening in A. selaginoides seedlings, and night time temperatures of 4°C also induced hardening in Eucalyptus pauciflora seedlings (Harwood, 1980).

The precaution taken to prevent the soil in the pots from freezing proved to be effective (Tab 4.2). There was a significant difference in the survival rates of A. cupressoides for insulated and uninsulated treatments at -10°C ($p < 0.01$, Fisher exact probability test). As the soil in the uninsulated pots was frozen solid, and the soil in the insulated pots remained soft, the increased damage can be attributed to root damage sustained as a result of freezing. There was no difference between treatments for A. selaginoides suggesting that a temperature of -10°C was lethal to the aerial parts of most of the A. selaginoides seedlings.

The results of the frosting trials indicate there is a difference in the frost resistance of hardened A. cupressoides and A. selaginoides seedlings ($p < 0.05$, χ^2 test for 2x7 contingency table of all trials, Tab

Date	Maximum (°C)	Minimum (°C)
4/6/1985	29.0	7.0
	27.0	5.0
	22.0	7.0
	23.0	2.0
	28.5	1.5
	22.0	6.0
	23.0	3.0
	23.0	4.0
	29.0	4.0
	24.5	2.0
	24.0	1.0
	25.0	2.0
	20.0	0.0
	18.0	4.0
	12.0	4.0
19/6/1985	18.0	2.0

Table 4.1

Temperature regime of the glasshouse during June in the 16 days prior to frost trials.

Frost temperature (°C)	Seedling survival					Control
	-10.0	-7.5	-5.0	-10.0*	-7.5#	
<u>A. selaginoides</u>	6	4	19	4	7	20
<u>A. cupressoides</u>	18	15	20	5	13	20

Table 4.2.

The survival of A. cupressoides and A. selaginoides seedlings following exposure to low temperatures.

* Uninsulated pots.

Seedlings collected from Mt Kate.

4.2). At temperatures of -7.5 and -10.0°C A. cupressoides survival rates were significantly greater than those of A. selaginoides ($p < 0.01$, $p < 0.01$, respectively, Fisher exact probability tests) but at -5.0°C there was no significant difference between the performance of A. cupressoides and A. selaginoides. Although there is no significant difference (Fisher exact probability test) in the survival rates of A. cupressoides and A. selaginoides collected from the same locality at Mt Kate, the results of this trial conform to the overall trends. However, the possibility for provenance variation in both species exists. This variation may be the result of genetic exchange between the two species as hybrid A. laxifolia individuals are common in the area where the seedlings were collected. The range in foliage of A. laxifolia individuals supports this suggestion (Plate 4.1).

4.4 Discussion.

These results confirm that Athrotaxis seedlings respond in the same way as the adults tested by Sakai et al. (1981) and support the view that temperature is an important factor controlling the relative distribution of A. cupressoides and A. selaginoides, as discussed in chapters 2 and 3.

The demonstrated difference in frost resistance of

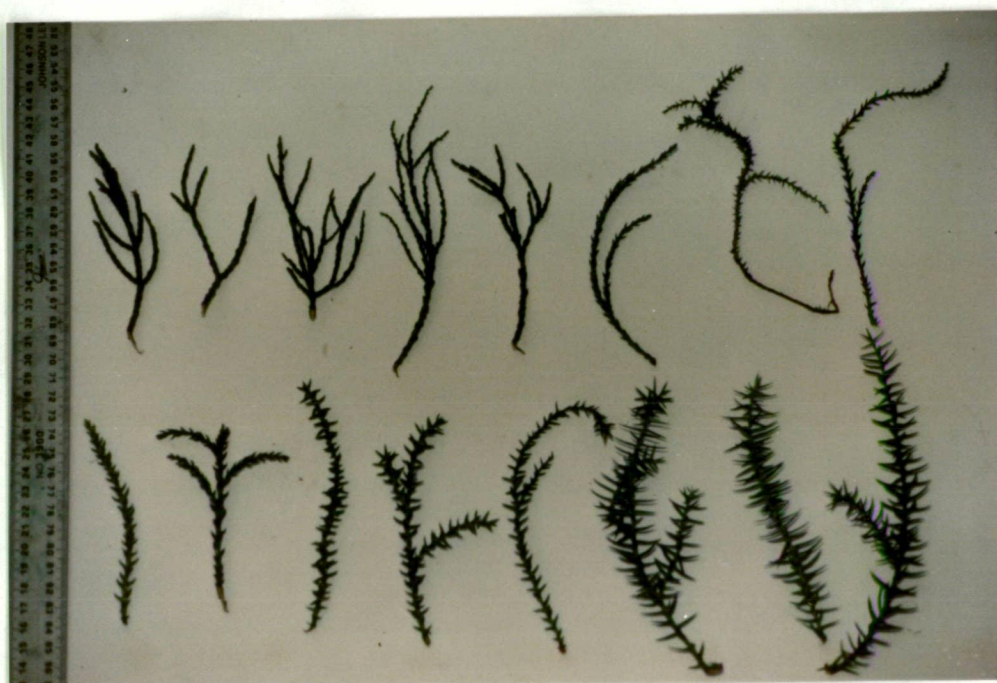


Plate 4.1. Variation in the foliage of A. laxifolia seedlings collected at Mt Kate (stand MtK3). The most extreme variants closely resemble A. cupressoides (top left) and A. selaginoides (bottom right).

these species correlates well with climate likely to be experienced in their respective natural ranges. The Central Plateau and Central Highlands of Tasmania (where A. cupressoides is most common) are the coldest regions of Tasmania and with the exception of some isolated mountain peaks (some of which support small populations of A. cupressoides, see Fig 4.2) the temperatures experienced to the west and south are likely to be considerably less extreme (see Fig 4.2 and Tab 4.3) and it is in these regions that A. selaginoides is most common (Fig 4.3).

It is from the Central Plateau and Central Highlands of Tasmania that we have records of extreme frost and resulting damage to forests. Calder (1850) describes extensive areas of the lower Central Plateau region where large tracts of Eucalyptus forest were killed by an extreme frost during the winter of 1837. Calder reported that the effects of this frost were only evident for around 5 or 6 miles west of Lake St Clair. This distance corresponds roughly with the south western margin of the Central Highlands. Col. Legge (1887) also comments on the common occurrence of frost killed Eucalyptus trees in the Lake Country (Central Plateau). The frequency and extent of such severe frosts is not well documented. A. cupressoides appears able to with stand the low temperatures imposed by these catastrophic frosts. At

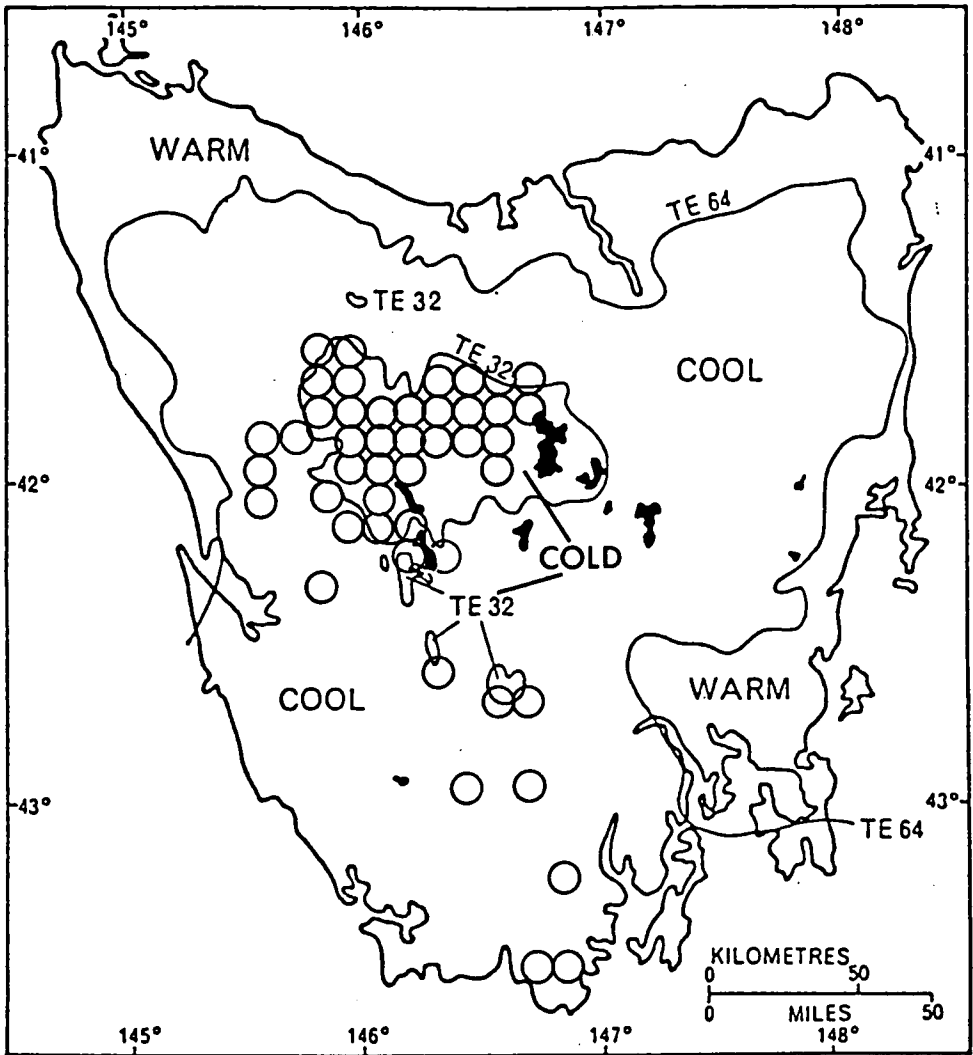


Figure 4.2. The distribution of *A. cupressoides* and temperature efficiency. *A. cupressoides* distribution taken from Brown *et al.* (1983) and updated. Temperature efficiency provinces after Gentilli (1972). Circles indicate areas where the species is known to occur.

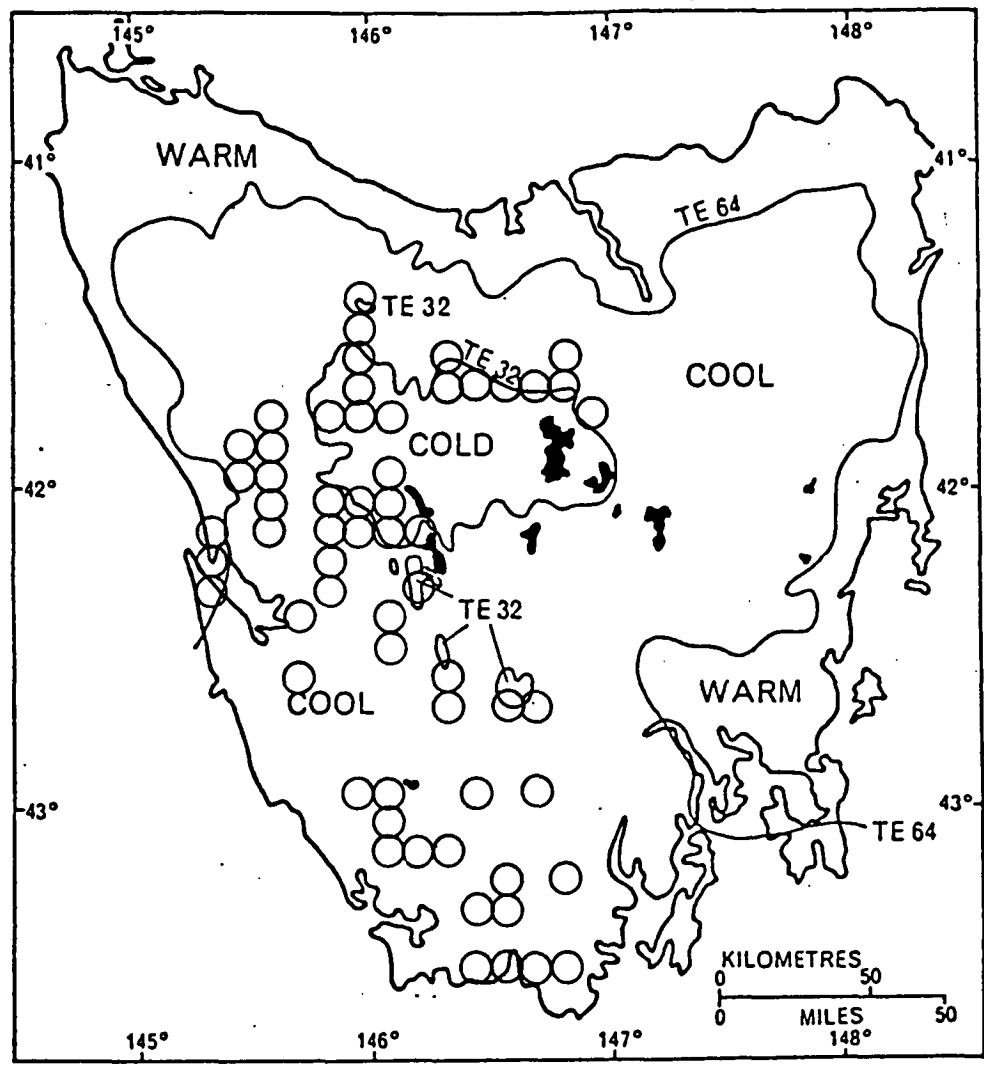


Figure 4.3. The distribution of *A. selaginoides* and temperature efficiency. *A. selaginoides* distribution taken from Brown *et al.* (1983) and updated. Temperature efficiency provinces after Gentilli (1972). Circles indicate areas where the species is known to occur.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Shannon												
Min	-2.2	-3.8	-3.9	-7.0	-8.3	-13.0	-10.2	-11.0	-6.1	-6.7	-5.2	-3.4
Year	1965	1980	1967	1963	1958	1983	1982	1974	1969	1966	1978	1948
										/67		/79

Cradle Valley												
Min	-3.0	-1.9	-2.8	-4.0	-8.3	-8.3	-7.8	-8.5	-8.0	-5.0	-3.9	-5.0
Year	1930	1936	1934	1975	1968	1972	1970	1974	1972	1974	1933	1938
		/70	/40									

Lake St Clair												
Min	-2.0	-1.4	-3.5	-6.7	-5.3	-11.7	-10.0	-8.5	-5.0	-4.7	-4.0	-2.2
Year	1976	1955	1973	1953	1971	1983	1983	1974	1959	1971	1978	1961

Queenstown												
Min	0.0	0.0	-1.1	-2.6	-6.0	-6.2	-6.7	-5.5	-3.1	-3.3	-1.5	-0.6
Year	1965	1966	1966	1965	1974	1973	1978	1974	1967	1965	1974	1965
										/68		/66

Strathgordon												
Min	2.8	1.5	1.3	0.6	-1.1	-4.0	-2.5	-3.1	-1.5	-1.2	1.0	1.8
Year	1970	1970	1971	11971	1970	1972	1983	1974	1977	1970	1974	1969
											/81	

Table 4.3

Extreme minimum temperatures recorded at stations close to or within the range of A. cupressoides and A. selaginoides. See Fig 4.1 for the localities of climate stations.

present many examples can be seen on the Central Plateau where dead Eucalyptus coccifera occur amongst live A. cupressoides, suggesting death by frost. These examples would not date back to the great frost of 1837. In 1983 temperatures of -20°C were recorded by Davidson and Read (1985) and in the same year frost damage was noted on Eucalyptus delegatensis. Nearby A. cupressoides growing on a valley bottom remained undamaged.

Frosts can be experienced at any time during year in the montane regions of Tasmania (Bureau of Meteorology, 1985). During the summer growing season frost hardness of trees and seedlings is likely to be reduced and for suitably sensitive species a relatively mild frost occurring at this time can cause more damage than a frost which occurs during winter, when individuals have been hardened by the gradually decreasing temperatures of autumn. Damage of this nature has been reported in Australia (Slatyer, 1976) and in New Zealand (Wardle and Campbell, 1976). However, Read (1986) found that A. selaginoides had a frost resistance in the order of -5°C for unhardened seedlings. Climatic records for Tasmania suggests that frosts of this magnitude could occur during summer in the highland areas of Tasmania (Tab 4.3). The frost resistance of unhardened A. cupressoides seedlings has not been investigated but they would be expected to be hardier than those of A. selaginoides. If so, the

occurrence of extreme summer frosts may be important in determining the relative distributions of the two species.

Frost damage may not be the only aspect of cold temperature effects governing the relative distributions of A. cupressoides and A. selaginoides. Germination and growth rates can also differ between species at low temperatures. A. selaginoides has a greater photosynthetic tolerance and displays more rapid germination at low temperatures than N. cunninghamii, A. moschatum, and E. lucida (Read, 1986). A similar trend for A. cupressoides compared to A. selaginoides would also contribute to observed differences in their distributions.

A. cupressoides has a far better developed capacity for vegetative reproduction than A. selaginoides and in many cases vegetative regeneration can account for a considerable proportion of the regeneration in a stand (see chapter 3). Vegetative regeneration is an important factor determining the distribution of timberline tree species (Tranquillini, 1979) and some species can persist on sites which are environmentally unsuitable for sexual reproduction. This may be the case for A. cupressoides, as cones were never observed on the highest krumholtz individuals but were common on this species at lower elevations in the same locality.

CHAPTER 5.

THE EFFECT OF GRAZING ON THE SEEDLING REGENERATION OF
ATHROTAXIS CUPRESSOIDES.

5.1 Introduction.

Chapter 3 demonstrates that there is little or no regeneration of A. cupressoides in many stands on the Central Plateau region of Tasmania (Fig 5.1). Field observations suggested that this regeneration failure could be the result of grazing by either introduced or native mammals, rather than the effect of a climatic change. The demographic structures of A. cupressoides showed that the regeneration failure has lasted approximately 100 years. A period which coincides with the introduction of sheep and cattle to the region (Shepherd, 1974). This chapter reports the results of experiments designed to test the impact of grazing on A. cupressoides regeneration.

5.2 Methods.

A series of 6 enclosures were established at Mickeys Creek, stand MC2, and Pine Lake, stand PL2 (Fig. 5.1). Each enclosure consisted of a chicken-wire cage measuring 1 m x 1 m x 0.3 m. The location of each cage was subjectively chosen, as patches of seedlings were of limited extent. The seedlings were all recent germinates

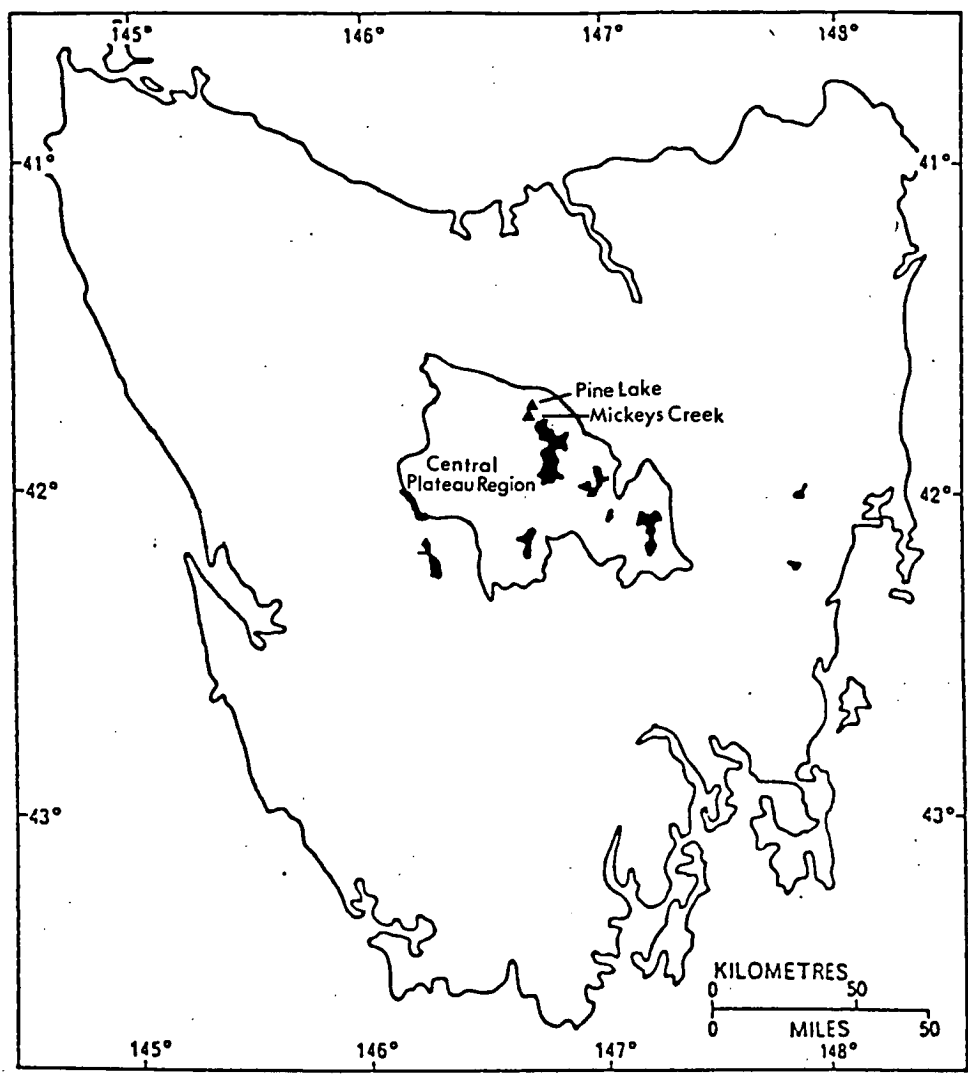


Figure 5.1. The location of grazing trial study sites.

still in the cotyledonary stage. The cages were sited so that a variety of micro-environments were included. Four cages were placed at MC1 and two were placed at PL2.

At the onset of the trial, the number of seedlings present inside each cage and on an adjacent, similar, unenclosed 1 m x 1 m plot were counted. Animal scats were collected from the enclosed and the open plots and identified. Seedling numbers were monitored every 3 to 6 months for approximately 18 months. At the finish of the trial animal scats were again collected for identification.

The percentage change in the numbers of seedlings for each plot was calculated and the statistical significance of the results was tested using the Mann-Whitney U test.

5.3 Results.

The protective effect of the enclosures is demonstrated in table 5.1. In all cases the numbers of unprotected seedlings decreased by greater amounts than the number of seedlings inside the enclosures. A one tailed Mann-Whitney U test indicated that these results are statistically significant ($p < 0.02$). It appears that the A. cupressoides seedlings were consumed at random along with the other vegetation, rather than preferentially, as many seedlings remain on the

Location	Mickeys Creek				Pine Lake	
Plot no	1	2	3	4	1	2
Enclosed seedlings						
No seedlings start	80	50	270	11	36	37
No seedlings finish	75	54	67	241	41	25
% change	-6.25	+8.00	-75.18	+111.40	+13.89	-32.43
Unenclosed seedlings						
No seedlings start	59	92	241	132	44	44
No seedlings finish	13	56	50	97	20	17
% change	-77.97	-39.13	-79.25	-26.52	-54.55	-61.36

Table 5.1

The effect of grazing over an eighteen month period on
A. cupressoides seedlings on the Central Plateau.

unprotected plots. Scats of both rabbits and wallabies were collected on all the unprotected plots.

5.4 Discussion.

The results of this trial confirm the view that regeneration of A. cupressoides is suffering from grazing in this area. As seed production occurs only once every 5 to 6 years for this species, it is probable that grazing would eliminate all seedlings in the period between successive crops of germinates. Root suckers are likely to suffer the same fate. Heavily grazed suckers have been observed in the area.

The distribution of A. cupressoides seedlings in stands on the Central Plateau also supports the view that regeneration is being lost through grazing. The stands with grassy understoreys (group 2, see chapter 2) have no seedling sized individuals (see chapter 3). They would be the most attractive to grazing animals. By contrast the stands growing on dolerite block fields with heath and scrub understoreys and with reduced amounts of grass and herbs (group 4) would be less attractive to grazing animals. In all cases these stands contain some regeneration.

The scat collections reveal that both rabbits and wallabies are responsible for the grazing at the 2 sites investigated, and no sheep were seen in the area during

the study. However, flocks of sheep are still grazed in the area during the summer and they might also contribute to the problem. In the past the numbers of sheep and cattle grazing on the Central Plateau were much higher. Shepherd (1974) estimated that each year approximately 350,000 head of sheep and 6,000 head of cattle were sent to the region in the late 1800's and some of the flocks remained over winter, even on the highest areas. He reports- "the numbers were kept high in order to produce 'hunger-fine' wool". Therefore it is reasonable to assume that grazing pressure during this period was very intense. Rabbits arrived on the Central Plateau around 1910 (Shepherd, 1974) and their rapid rise to plague proportions would have maintained and possibly increased the grazing pressure. They are still thought to be responsible for considerable damage to the vegetation of the region (Jackson, 1973).

The only animal to have been directly observed grazing on the foliage of A. cupressoides is the red-necked wallaby (Rufus macrocarpus). Wallabies have been observed foraging on A. cupressoides after heavy snow falls which bury most of the vegetation. The snow provides an elevated surface which accounts for the high browsing (1-2 m) on many A. cupressoides trees. However, most snow falls in Tasmania are relatively light compared to Australian mainland mountain areas and snow cover is

intermittent. Observations indicate that, except after the heaviest storms, snow is likely to be shallow and not persistent beneath stands of A. cupressoides, presumably because much of the snow is intercepted by the canopy. In Europe, falls of up to 10 cm have been completely intercepted by fir thickets (Geiger, 1965) and canopy interception accounts for reduced periods of snow lie beneath evergreen Nothofagus betuliodes (Mirb.) Oerst. in Chile (Veblen et al., 1977). During and after snow falls on the Central Plateau, grazing animals would seek the protection and fodder afforded by stands of A. cupressoides. Locals report that wallaby populations on the Central Plateau appear to be increasing (Shepherd, 1974). Plate 5.1 illustrates heavy grazing damage to A. cupressoides sucker regeneration near Pine Lake.

As noted previously, the onset of the regeneration failure of A. cupressoides broadly coincides with the introduction of sheep and cattle to the region. This event also coincides with the destruction of the Tasmanian hunting and gathering culture. Archeological evidence (Kiernan et al., 1983) and historical accounts (Cosgrove, 1984) indicate that wallabies formed an important proportion of the diet of the Tasmanian aborigines. The aborigines frequented the Central Plateau on a regular basis, probably for about the last



Plate 5.1. Browsing damage on A. cupressoides sucker regeneration near Pine Lake. The undamaged stems in the centre of the clump are beyond the reach of herbivours.

10,000 years (Cosgrove, 1984; Thomas, 1984). Their activities may have kept a check on wallaby numbers in the region.

In the absence of further evidence, the loss of A. cupressoides regeneration through grazing must be attributed to the combined effects of sheep, cattle, rabbit, and wallaby populations rather than to any one species. The role played by these species has most certainly varied through time. Sheep and cattle numbers have declined where as the numbers of rabbits and most probably wallabies have risen during this century. Consequently, the pressure on populations of A. cupressoides seedlings has probably been maintained.

The effect of grazing on the regeneration of A. cupressoides is undoubtedly intensified by the intermittent seed production and extremely slow growth rates of the species. These factors, combined with the increase in wildfires since the arrival of Europeans and the dramatic up turn in the use of the Central Plateau for recreational purposes may place A. cupressoides populations in this area in long term danger of mass depletion.

CHAPTER 6.

DISCUSSION.

The results of the present study suggest that the ability of A. cupressoides to withstand the effects of low temperatures is an important factor controlling the relative distribution of A. cupressoides and A. selaginoides. Through greater frost tolerance, superior vegetative regeneration, and perhaps better germination and growth rates at low temperatures, A. cupressoides is more likely to be found at higher altitudes, or in cold valley bottoms than A. selaginoides. The relative resistance of Athrotaxis species to waterlogging and drought resistance has not been thoroughly investigated using experimental means. However, preliminary trials (see Appendix C) suggest that neither A. cupressoides or A. selaginoides possess an advantage in either drought or waterlogging resistance. Field observations support these results, as both species extend to areas of approximately the same annual rainfall on the eastern Central Plateau and both species can be found occupying poorly drained sites.

The lower distributional limit of A. cupressoides appears to be determined by its inability to compete with more aggressive rainforest tree species, including A. selaginoides, which prevail as a consequence of the

warmer temperatures experienced at these elevations. The factors affecting the lower altitudinal limit of A. selaginoides are not completely understood. Read (1986) suggests that decreased competitive ability under warmer temperatures, drought susceptibility, and intolerance of fire are important. This view is supported by the very limited occurrence of the species at low altitudes and in the drier, more fire prone portion of its range.

Where A. cupressoides or A. selaginoides occur in open montane and implicate rainforest or in subalpine scrub they can regenerate without canopy disturbance. Both species demonstrate the ability to regenerate following minor disturbance and it appears that A. selaginoides relies on canopy disturbance for regeneration opportunities in thamnic and callidendrous rainforests.

A. selaginoides has been observed regenerating following fire, windthrow, landslides and rockfalls. Damage caused by exceptionally heavy snow falls has also been observed in Tasmania. Old, large crowned Nothofagus cunninghamii trees are most susceptible to such damage. It is quite probable that narrow crowned A. selaginoides individuals are less prone to snow damage and can survive to take advantage of gaps created in this manner. A. cupressoides has been observed colonizing burnt sites and is tolerant of extreme frosts which can kill associated

tree species. The frost-kill of competing canopy species could create conditions suitable for the regeneration of A. cupressoides.

Man made fire is now the most widespread and frequent form of catastrophic disturbance in Tasmania (Bowman and Jackson, 1981). The role of fire in the Tasmanian environment before the arrival of Europeans is not well understood. However, evidence suggests that long term vegetation changes are the result of climatic variation and not fire (Macphail, 1980; Colhoun and van de Geer, in press, a). The present rate of loss of fire sensitive communities within the range of Athrotaxis species indicates that since the arrival of Europeans the fire regime has been severely altered (Kirkpatrick and Dickinson, 1984a). If the Aborigines were deliberately or inadvertently burning these regions then their activities must have produced a different fire pattern.

The Tasmanian Aborigines are often credited with having an active burning policy which has produced a variety of vegetation disclimaxes (Jones 1969, 1975). However, there is only slim evidence of Aborigines setting fires for the purpose of range management and it can be argued that this evidence is derived from a period when the Aboriginal population was under great stress (Thomas, 1984). If the Aborigines used fire as a management technique then it is not unlikely that they

practiced a sophisticated program of burning. In northern Australia, traditional Aborigines use fire for range management in a very precise manner, including the deliberate protection of fire sensitive monsoon rainforests. These practices produce a result which is far different from that produced by the firing habits of Europeans (Haynes, 1985).

The size of the canopy gap required to create conditions suitable for the regeneration of A. selaginoides is related to forest structure and composition (Appendix A, page 173). In thamnic rainforest the gap size requirement increases with canopy height, closure, and the proportion of evergreen tree species in the stand. Therefore, A. selaginoides would place a greater reliance on large scale (i.e. catastrophic) disturbance events for regeneration opportunities in tallest and most closed thamnic rainforests and callidendrous rainforests which prevail at lower altitudes. A similar relationship may hold for A. cupressoides but due to its poor competitive ability it is largely restricted to open montane communities and the only recorded instances of A. cupressoides regeneration associated with implicate or thamnic communities are at the stand edges.

The past frequency and extent of catastrophic disturbances, other than fire, which could create

conditions suitable for the regeneration of A. selaginoides are not known. However, they are not likely to be as frequent or widespread as in either southern South America or New Zealand where volcanic and seismic activity are common and much of the terrain is more mountainous. In Tasmania, events such as rockfalls, landslides, windstorms, and heavy snowfalls are likely to be more common in mountain environments than at lower altitudes, and a lack of disturbance opportunities suitable for A. selaginoides regeneration at lower altitudes may be a contributing factor controlling the distribution of the species.

The results of this study and that of Read (1986) suggest that Athrotaxis species would be well suited to colder full glacial and interstadial climates in Tasmania. Interstadial conditions prevailed from ca 50,000 to 25,000 BP. During this period temperatures appear to have been 4.5°C to 5°C colder than at the present and the treeline was probably lowered by around 700 m to 800 m (Colhoun, 1985; Colhoun and van de Geer, in press, a, b). Full glacial conditions occurred from around 25,000 to 10,000 BP and mean annual temperatures on the West Coast Range were probably depressed by around 6.5°C at this time. Temperature depression of a similar order could have been expected in the Central Highlands. With these conditions prevailing over much of Tasmania,

the treeline would be reduced to elevations at or below 200 m a.s.l. (Kiernan 1980, 1985; Colhoun 1985).

At low altitudes in the south and west of Tasmania the cool moist climate prevailing during the last glacial and interstadial would have favored Athrotaxis species for the following reasons. The lower temperatures would have been advantageous to A. selaginoides because the species has higher growth rates at low temperatures than Nothofagus cunninghamii, Atherosperma moschatum, Phyllocladus asplenifolius, and Eucryphia lucida. A. cupressoides may have been advantaged in a similar manner. The frequency of extreme frosts would be increased providing favourable conditions for A. cupressoides and to a lesser extent A. selaginoides. Even if precipitation was half that of today, the precipitation would have been ample for Athrotaxis species, especially as lower temperatures would have made the precipitation more effective. The incidence of disturbance events suitable for the regeneration of A. selaginoides in thamnic and callidendrous rainforest is likely to have been much higher during colder climates than at present. Glacial climates produced greater slope instability than occurs now or during most of the Holocene (Kiernan 1985). In the Cascade Range of North Western U.S.A., Oliver et al. (1985) found that the alternating advance and retreat of a glacier, rockfalls,

avalanches, and other events caused widespread disturbance in forested areas adjacent to the glacier. Wardle (1973, 1980) has investigated similar phenomena in relation to recent glacial activity the South Island of New Zealand. The glaciers on the West Coast Range of Tasmania, and possibly further inland, would have been similar to those found in New Zealand and Patagonia at present (Keirnan, 1980, 1985). It is reasonable to assume that the glaciers in Tasmania extended down to and below the treeline on occasions, creating conditions similar to those reported by Oliver et al. (1985) and Wardle (1973). Disturbance caused by heavy snow falls and avalanches is also likely to be increased during a colder climate. Macphail and Colhoun (1985) suggested that Phyllocladus asplenifolius was able to invade glacial debris left in the wake of retreating ice. It is highly probable that A. selaginoides and A. cupressoides could do likewise.

Ogden (1978) points out that the present distribution of A. cupressoides closely coincides with that of ice during the last glaciation. This is not true for all stands but those in the south and west of Tasmania confirm to this pattern (see Fig. 4.2). These stands suggest that the species was widespread at lower altitudes in southern and western Tasmania during the last glacial and preceeding interstadial period, as it is

extremely unlikely that these stands have established through long distance seed dispersal. Since the last glaciation (post 10,000 BP) A. cupressoides must have been retreating upslope in response to the increasing temperatures which have allowed the treeline to rise. In turn less cold tolerant but more shade tolerant species, including A. selaginoides, would have invaded areas occupied by open montane forest in the manner described in chapter 3.

Evidence from pollen investigations in western Tasmania supports the inference that A. cupressoides formed stands at low altitudes in the past. Interstadial pollen records (ca 50,000 to 25,000 BP) from the King River (c 200 m)(Colhoun and van de Geer, in press, b), Henty Bridge (c 120 m)(Colhoun, 1985b), and Tullarbardine Dam (c 200)(Colhoun and van de Geer, in press, a) and late last glacial pollen (preceeding 11,420 +/- 770 BP) from Poets Hill (c 600 m)(in Colhoun and van de Geer, in press, a) contain pollen assemblages which are indicative of open montane and implicate communities containing Athrotaxis species or Diselma archeri.

Unfortunately A. cupressoides, A. selaginoides, and Diselma archeri pollen is indistinguishable and this pollen type may be under-represented in the pollen record due to poor dispersal or infrequent flowering (G. van de Geer pers comm.). Where Athrotaxis-Diselma type pollen

is recorded it is more often associated with N. gunnii than N. cunninghamii pollen (Macphail, 1986). Other pollen types such as Microstrobis, Drimys, Compositae, Gramineae, Epacridaceae, and Podocarpus lawrencii regularly occur with Athrotaxis-Diselma pollen (Macphail, 1986). This suggests that these communities are open montane or implicate rainforests with either A. cupressoides or A. selaginoides rather than thamnic or callidendrous communities with A. selaginoides. The lack of Athrotaxis-Diselma type pollen in assemblages which suggest thamnic or callidendrous rainforest may be due to the irregular distribution of A. selaginoides in these forest types and perhaps poor dispersal through these tall and dense forests.

The limited seed dispersal ability of both Athrotaxis species, the early appearance of Athrotaxis-Diselma pollen at high altitude sites in southern and western Tasmania, and the location of extant A. cupressoides populations in this region, supports the view of Kirkpatrick (1986b) that the treeline in southern and western Tasmania, during the last glaciation, was variable, and suggests that A. cupressoides existed at altitudes above the proposed treeline of 200m or less. Athrotaxis-Diselma type pollen is first recorded at Adamsons Peak (c 960 m), The Denison Range (c 980 m), and the Tyndall Range (c 840 m) in the early Holocene, and at

Ooze Lake in the Southern Range (c 880 m) in the middle Holocene (Macphail, 1986). All of these sites are close to extant populations of A. cupressoides. The distance from these populations to the nearest area at 200 m a.s.l., and the migration rates necessary for the species to travel these distances in the last 18,000 years, since the last glacial maximum when the treeline was at its lowest, are listed in table 6.1.

Detailed data concerning the seed dispersal ability of A. cupressoides is lacking. However, observations during this study and by Kirkpatrick and Dickinson (1984a) indicate that effective seed dispersal for A. cupressoides is limited to within a few metres of the parent trees but the species can achieve dispersal of up to 100 m on rare occasions (see Chapter 3). However, an intensified westerly air stream (Bowden, 1983) and a higher occurrence of disturbance events may have increased the migration rate of A. cupressoides considerably in late glacial times. However, it is very doubtful whether A. cupressoides could have reached the Denison Range site in the 18,000 years available, if the species was restricted to areas below 200 m a.s.l. during the last glacial maximum. The necessary migration rate of 85 m every 100 years would be improbable as a 100 year old tree would be only about 2 m tall. Trees of this size would be incapable of producing large seed crops and

Mountain	Distance to 200m contour (km)	Migration rate (m/100 years)
Pindars Peak	3.5	19
Mt Anne	7.5	42
Snowy Range	5.4	30
Frenchmnas Cap	5.9	33
Mt Read	5.0	28
Denison Range	15.3	85

Table 6.1

The distance from extant populations of A. cupressoides in southern and western Tasmania to the nearest area at 200m a.s.l. and the migrations rate necessary for the species to travel this distance in the 18,000 years since the last glacial maximum.

seed dispersal ability would be very limited due to the low crown heights. For these reasons it is likely that migration would be less than 50 m in 100 years (9 km in 18,000 years).

If A. cupressoides was growing at altitudes above 200 m a.s.l. during the last glacial maximum, then problems of long distance dispersal would have been avoided. Kirkpatrick (1986) considers that the treeline in south west Tasmania during the last glaciation was likely to be highly variable, increasing in altitude in inland valleys where the climate would have been more continental. Ogden and Powell (1979) have suggested that species such as Nothofagus cunninghamii, Nothofagus gunnii, A. cupressoides, A. selaginoides and Diselma archeri existed as krumholtz populations on sites with stable soils below the limits of glaciation but well above the limits of periglacial activity. Krumholtz communities of these species grow up to 300 m above the treeline in southern and western Tasmania today (Macphail, 1975).

A. cupressoides is absent from many mountain peaks in southern and western Tasmania, including Mt Owen, Mt Jukes, the Franklin Range, the Arthur Range, Mt Picton, Mt Bobs and the Boomerang. All these mountains appear to have sites which would be suitable for the species. There are two possible explanations for the lack of A.

cupressoides on these peaks: 1) A. cupressoides was never present; 2) the species has been eliminated by fire. The second possibility seems the most likely. Most mountains without A. cupressoides are as close to low altitude sites as are those with the species and it is likely that A. cupressoides occupied their slopes at some time in the past. Gibbs (1920) recorded A. cupressoides at the Hartz Mountains but the species has since been eliminated by fire. At Lake Skinner on the Snowy Range an A. cupressoides population has been badly damaged by fire and the remaining stems could easily be killed by one more fire. On Mt Read the species is being replaced by A. selaginoides and other implicate rainforest species and nearby on Mt Dundas there is no A. cupressoides despite very suitable sites. The adjacent Tyndall Plateau is a relatively extensive high altitude area and it supports populations of A. cupressoides (Kirkpatrick, 1977b). The extent of these populations would make them more resilient to disturbance. On the other hand the remnant populations at Mt Anne, Pindars Peak, Lake Rhona, and Frenchmans Cap are so small that they could easily be eliminated by a single fire.

Pollen evidence also suggests that there have been past local extinctions of A. cupressoides. The disappearance of Athrotaxis-Diselma and N. gunnii pollen from the record at Upper Lake Warawina cirque in the

Denison range are associated with peaks in charcoal particles (Macphail, 1986). However the species are still present about one kilometer away (Kirkpatrick and Dickinson, 1984). At Adamsons Peak (Macphail, 1986) Athrotaxis-Diselma pollen disappears abruptly from the record in the middle Holocene. N. gunnii terminates in a similar manner near the present, almost certainly as a result of fire (Macphail, 1986).

From pollen evidence Colhoun and van de Geer (in press, a) consider that there is a marked time lag in the establishment of major forest associations in response to warmer climates but taxa appear to terminate abruptly, almost immediately, upon climatic deterioration. Athrotaxis species could be expected to respond to such temperature changes in a way which would contribute to this observed pattern.

As temperature increases the frequency of disturbance events, except fire, would decrease and cold tolerant species such as A. cupressoides and A. selaginoides would have to be replaced through the slow processes of forest succession. A. cupressoides could persist on a site for over 1000 years after regeneration has ceased (see Chapter 3). Other species such as Nothofagus gunnii and Diselma archeri are likely to be equally long lived (J.B. Kirkpatrick pers. comm.) and therefore a very long time would expire before

replacement species growing in the shade or in small canopy gaps could assume dominance on a broad scale. A. selaginoides is similarly long lived and its ability to regenerate in canopy gaps in thamnic or callidendrous rainforest could ensure its persistence for more than one generation under warmer climates which are favourable to other rainforest tree species. Dense stands of A. selaginoides, which are probably the result of catastrophic disturbance, appear to undergo a self-thinning process. The fall of dead and weak stems at this stage is likely to create large canopy gaps suitable for further A. selaginoides regeneration (see Appendix A, page 164). Further senescence of trees will create more gaps, and regeneration opportunities for A. selaginoides will occur if these gaps are large enough. The overall trend will be from a dense stand of A. selaginoides to a forest containing progressively more shade tolerant angiosperm tree species with isolated individuals or small clumps of A. selaginoides (as is the case in many thamnic rainforests). In the long term A. selaginoides might be eliminated. If the elimination of A. selaginoides was complete in only three generations the time involved could still be in the order of 3000 years. During this period the occurrence of catastrophic disturbance, other than a fire, can provide conditions suitable for the regeneration of dense stands of A.

selaginoides.

When temperatures are decreasing the frequency of disturbance events and extreme frosts will increase and less cold tolerant species are likely to be abruptly terminated. In these circumstances widely scattered individuals or small cohorts of A. selaginoides in thamnic or callidendrous rainforest would be better adapted to expand into newly formed canopy gaps and disturbed areas because the species has an increased competitive ability at lower temperatures. A. cupressoides would be likewise favoured at higher altitudes and in frost prone valleys. For this species, dispersal of seed down streams and from individuals already in place on stream banks at low altitudes would increase the rate of spread. The potential for this type of event is demonstrated at Warners Sugar Loaf (c 300 m a.s.l.), the lowest known occurrence of the species. Here, stream side A. cupressoides and Podocarpus lawrencii (the most frost tolerant Australian species tested by Sakai et al., 1981) could expand to invade surrounding areas given the onset of a more suitable (colder) climate.

The Quaternary period has seen repeated cycles of cold glacial and warm interglacial climates, but colder climates than those prevailing at present have been normal (Singh, 1982). Cool to cold, wet mountain

environments would have been common in the cool temperate region of the southern hemisphere during colder glacial and interstadial periods. Therefore, Athrotaxis species can be seen as well adapted to the commonly prevailing conditions.

Species with extremely long life expectancies only require very infrequent opportunities for regeneration to ensure survival. The 10,000 year period of the Holocene could be negotiated by as few as ten generations of A. selaginoides and major canopy disturbance need only occur very infrequently to perpetuate the species in thamnic and callidendrous rainforests. Viewed in a long term perspective, the presence of A. selaginoides in these forest types maintains a wide geographical range during interglacial periods, and allows rapid expansion of the species upon a return to cooler conditions.

There are similarities in the physiologies and life histories displayed by Athrotaxis species and other conifers from the cool temperate region of the southern hemisphere. The similarities include: extremely slow growth and longevity (see Chapter 1); the ability to regenerate following catastrophic disturbances, a feature shared with such species as Araucaria araucana from southern South America, and Libocedrus bidwillii and some of the podocarps from New Zealand (see Chapter 1); the ability to tolerate low temperatures (by southern

hemisphere standards) (see Sakai et al., 1981 for comparable species); a capacity for vegetative regeneration (see Chapter 3). As discussed for Athrotaxis species, such features can be seen as well suited to the commonly prevailing climates of the Quaternary. However, they have served to place their possessors at an extreme disadvantage in the environments imposed by human societies.

In Tasmania the activities of humans, certainly Europeans and perhaps Aborigines, have had a dramatic impact on Athrotaxis populations. These activities include increases in the number of fires, logging, and grazing by exotic herbivores. A similar fate has befallen at least some of the conifer species in southern South America and New Zealand. Populations of Fitzroya cupressoides and Austrocedrus chilensis (D. Don.) Florin. from Chile and Argentina have been depleted by fires, logging, and grazing of regeneration (Veblen and Ashton, 1982; Veblen et al., 1976; Thomasson, 1959; Erikson 1975, in Veblen et al., 1976). Burning and clearing firstly by the Maoris and then by Europeans have wiped out large tracts of podocarp forest from New Zealand and the introduction of exotic herbivours has had a large impact upon forest ecosystems (Burrows and Greenland, 1979)

If firing, grazing of regeneration, and loss of habitat for other reasons ceased it would be many

thousands of years before Athrotaxis species could reoccupy the areas in which they occurred at the time of the arrival of Europeans. The present construction of new hydro-electricity schemes, forestry and mining operations, recreational activities, grazing, and arson will place the remaining populations of these species at a greater risk from fire. Unless there is a rapid change in the perception of the natural environment by the Tasmanian Government and public further destruction of Athrotaxis species is likely to occur in the near future.

REFERENCES.

Beveridge, J.L. (1973) Regeneration of podocarps in central North Island podocarp forests. Proc. N.Z. Ecol. Soc. 11,48-55.

Bowden, A.R. (1983) Relict terrestrial dunes: legacies of a former climate in coastal northeastern Tasmania. Z. Geomorph. N.F. Suppl-Bd. 45,153-174.

Bowman, D.M.J.S. (1984) The ecology and silviculture of Eucalyptus delegatensis R.T. Baker. on dolerite in Tasmania. Unpublished PhD thesis, University of Tasmania.

Bowman, D.M.J.S. & Jackson, W.D. (1981) Vegetation succession in Southwest Tasmania. Search. 12,358-362.

Bowman, D.M.J.S. & Kirkpatrick, J.B. (1984) Geographic variation in the demographic structure of stands of Eucalyptus delegatensis R.T. Baker on dolerite in Tasmania. J. Biogeogr. 11,427-437.

Bowman, D.M.J.S., MacLean, A.R. and Crowden, R.K. (1986) Vegetation-soil relations in the lowlands of south-west Tasmania. Aust. J. Ecol. 11,141-153.

Brown, M.J., Kirkpatrick, J.B. & Moscal, A. (1983) An Atlas of Tasmania's endemic flora. Tas. Cons. Trust Inc., Hobart, Tasmania.

Brown, M.J., Ratkowsky, D.A. & Minchin, P.R. (1984) A comparison of detrended correspondence analysis and principal co-ordinates analysis using four sets of Tasmanian vegetation data. Aust. J. Ecol. 9,273-279.

Burke, W.D. (1974) Regeneration of podocarps on Mt Tarawera, Rotorua. N.Z. J. Bot. 12,219-226.

- Burrows, C.J. and Greenland, D.E. (1979) An analysis of the evidence for climatic change in New Zealand in the last thousand years: evidence from diverse natural phenomena and from instrumental records. J. Roy. Soc. N.Z. 9:321-373.
- Bureau of Meteorology. (1985) In Tasmanian year book no 19. Australian Bureau of Statistics.
- Busby, J.R. (1984) Nothofagus cunninghamii (Southern Beech) vegetation in Australia. Australian flora and fauna series. Number 1. A.G.P.S. Canberra.
- Calder, J.E. (1850) Some account of the country between Hamilton and the Frenchman's Cap. The Hobart Town Courier, September 21.
- Calias, S.S. & Kirkpatrick, J.B. (1983) Tree species regeneration after logging in temperate rainforest, Tasmania. Pap. Proc. Roy. Soc. Tasmania. 117,77-83.
- Cameron, R.J. (1960) Natural regeneration of podocarps in the forests of the Whirinaki River Valley. N.Z. J. For. 8,337-364.
- 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.
- Clifford, H.T. & Constantine, J. (1980) Ferns, fern allies, and conifers of Australia. A laboratory manual. University of Queensland Press.

- Colhoun, E.A. (1985a) Glaciations of the West Coast Range, Tasmania. Quat. Res. 24,39-59.
- Colhoun, E.A. (1985b) Pre-last glacial maximum vegetation at Henty Bridge, western Tasmania. New Phytol. 100,681-690.
- Colhoun, E.A. & van de Geer, G. (in press, a) Holocene to middle last glacial vegetation history at Tullarbardine Dam, western Tasmania. Proc. Roy. Soc. Lond.
- Colhoun, E.A. and van de Geer, G. (in press, b) Pre-last glacial maximum vegetation history at Crotty Road, western Tasmania. Pap. Proc. Roy. Soc. Tas.
- Cosgrove, R. (1984) Aboriginal economy and settlement in the Tasmanian Central Highlands. National Parks and Wildlife Service Occasional Paper No. 8. National Parks and Wildlife Service, Hobart, Tasmania.
- Curtis, W.M. (1963) The student's flora of Tasmania, Part II. Government Printer, Tasmania.
- Curtis, W.M. (1967) The student's flora of Tasmania, Part III. Government Printer, Tasmania.
- Curtis, W.M. & Morris, D.I. (1975) The student's flora of Tasmania, Part I. Government Printer, Tasmania.
- Davidson, N.J. & Read, J.B. (1985) Frost as a factor influencing the growth and distribution of subalpine eucalypts. Aust. J. Bot. 33,657-667.

- Davies, J. (1983) Huon Pine Survey. Tasmania National Parks and Wildlife Service, Wildlife Division Technical Report No 83/2.
- Elder, N.L. (1963) Evidence of climatic change from the vegetation of the North Island. Proc. N.Z. Ecol. Soc. 2,143-171.
- Florin, R. (1963) The distribution of conifer and taxad genera in time and space. Acta. Hort. Bergiani. 20,121-312.
- Forest Commission of Tasmania. (1982) Internal report.
- Franklin, D.A. (1968) Biological flora of New Zealand 3. Dacrydium cupressinum Lamb. (Podocarpaceae) Rimu. N.Z. J. Bot. 6,493-513.
- Franklin, J.F. & Hemstrom, M.A. (1981) Aspects of succession in the coniferous forests of the Pacific Northwest. In: West, D.C., Shugart, H.H. & Botkin, D.B. (Eds.) Forest succession: Concepts and Applications. Springer-Verlag, New York.
- Geiger, R. (1965) The climate near the ground. Harvard University Press, Cambridge, Massachusetts.
- Gentilli, J. (1972) Australian climatic patterns. Nelson, Melbourne, Victoria.
- Gibbs, L.S. (1920) Notes on the phytogeography and flora of the mountain summit plateaux of Tasmania. J. Ecol. 8,1-17,90-117.

- Grant, P.J. (1963) Forests and recent climatic history of the Huiarau Range, Urewera region, North Island. Trans. Roy. Soc. N.Z. 82,329-410.
- Gulline, H.F. (1952) The cytology of Athrotaxis. Pap. Proc. Roy. Soc. Tas. 86,131-136.
- Harwood, C.E. (1980) Frost resistance of subalpine Eucalyptus species. 1 Experiments using a radiation frost room. Aust. J. Bot. 28,587-99.
- Haynes, C.D. (1985) The pattern and ecology of munwag: traditional Aboriginal fire regimes in north-central Australia. Proc. Ecol. Soc. Aust. 13,203-214.
- Hett, J.M. & Loucks, O.L. (1976) Age structure models of balsam fir and eastern hemlock. J. Ecol. 64,1029-1044.
- Hill, M.O. (1979) TWINSpan - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University.
- Hill, M.O. & Gauch, H.G. (1980) Detrended correspondence analysis: an improved ordination technique. Vegetatio 42,47-58.
- Holloway, J.T. (1954) Forests and climates of the South Island of New Zealand. Trans. Roy. Soc. N.Z. 82,329-410.
- Hutchinson, F.E. (1932) The life history of the Westland rimu bush. Te Kura Ngahere. 3:54-61.

- Jackson, W.D. (1973) Vegetation. In Banks, M.R. (Ed.):
The lake country of Tasmania. Royal Society of
Tasmania, Hobart, Tasmania.
- Jardine, N. and McKenzie, D. (1972) Continental drift and
the dispersal and evolution of organisms. Nature.
235:20-24.
- Jarman, S.J. & Brown, M.J. (1983) A definition of cool
temperate rainforest in Tasmania. Search. 14,81-87.
- Jarman, S.J., Brown, M.J., & Kantvilas, G. (1984)
Rainforest in Tasmania. National Parks and Wildlife
Service Tasmania.
- Jones, R. (1969) Fire-stick farming. Aust. Nat. History.
16,224-228.
- Jones, R. (1975) The neolithic, palaeolithic and the
hunting gardeners: man and land in the Antipodes. In
Suggate, R.P. & Cresswell, M.M. (Eds.) Quaternary
studies. Roy. Soc. N.Z., Wellington.
- Kenkel, N.C. & Orloci, L. (1986) Applying metric and
nonmetric multidimensional scaling to ecological
studies: Some new results. Ecology. 67,919-928.
- Kiernan, K. (1980) Pleistocene glaciation of the central
West Coast Range, Tasmania. Unpublished Honours
thesis, University of Tasmania.
- Kiernan, K. (1985) Late Cainozoic glaciation and mountain
geomorphology in the Central Highlands of Tasmania.
Unpublished PhD thesis, University of Tasmania.

- Kiernan, K., Jones, R. & Ranson, D. (1983) New evidence from Fraser Cave for glacial age man in south-west Tasmania. Nature. 301,28-32.
- Kirkpatrick, J.B. (1977a) The impact of man on the vegetation of the West Coast region, Tasmania. In Banks. M.R. and Kirkpatrick. J.B. (Eds): Landscape and Man. Royal Society of Tasmania, Hobart. 151-156.
- Kirkpatrick, J.B. (1977b) Native vegetation of the West Coast region of Tasmania. In Banks. M.R. and Kirkpatrick. J.B. (Eds): Landscape and Man. Royal Society of Tasmania, Hobart. 55-80.
- Kirkpatrick, J.B. (1982) Phytogeographical analysis of Tasmanian alpine flora. J. Biogeog. 9,255-271.
- Kirkpatrick, J.B. (1983) Treeless plant communities of the Tasmanian high country. Proc. Ecol. Soc. Aust. 12,61-77.
- Kirkpatrick, J.B. (1984a) Altitudinal and successional variation in the vegetation of the northern part of the West Coast Range, Tasmania. Aust. J. Ecol. 9,81-91.
- Kirkpatrick, J.B. (1984b) Tasmanian high mountain vegetation 2 - Rocky Hill and Pyramid Mountain. Pap. Proc. Roy. Soc. Tas. 118,5-20.
- Kirkpatrick, J.B. (1986a) Conservation of plant species, alliances, and associations of the treeless high country of Tasmania, Australia. Biol. Cons. 37,43-57.

- Kirkpatrick, J.B. (1986b) Tasmanian alpine biogeography and ecology and interpretations of the past. In Barlow, B.A. (Ed.) Flora and fauna of alpine Australasia. Ages and Origins. C.S.I.R.O., Melbourne, Victoria.
- Kirkpatrick, J.B. & Dickinson, K.J.M. (1984a) The impact of fire on Tasmanian alpine vegetation and soils. Aust. J. Bot. 32,613-629.
- Kirkpatrick, J.B. & Dickinson, K.J.M. (1984b) Vegetation of Tasmania (Map) Forest Commission of Tasmania, Hobart.
- Kirkpatrick, J.B. & Harwood, C.E. (1980) Vegetation of an infrequently burned Tasmanian mountain region. Proc. Roy. Soc. Victoria. 91,79-107.
- Legge, Col.W.V. (1887) The highlands of Lake St Clair. Pap. Proc. Roy. Soc. Tas. 114-133.
- Lloyd. R.C. (1960) Growth study of regenerated Kauri and podocarps in Russell Forest. N.Z. J. For. 8,341-355.
- Lorimer, C.G. (1985) Methodological considerations in the analysis of forest disturbance history. Can. J. For. Res. 15,200-213.
- Lorimer, C.G., & Krug, A.G. (1983) Diameter distributions in even-aged stands of shade-tolerant and midtolerant tree species. Am. Midl. Nat. 109,331-345.

- Macphail, M.K. (1975) Late Pleistocene environments in Tasmania. Search. 6,295-300.
- Macphail, M.K. (1980) Regeneration processes in tasmanian forests. A long term perspective based on pollen analysis. Search. 11:184-190.
- Macphail, M.K. (1986) "Over the top": Pollen-based reconstructions of past alpine floras and vegetation in Tasmania. In Barlow, B.A. (Ed.) Flora and fauna of alpine Australasia. Ages and origins. C.S.I.R.O. Melbourne, Victoria.
- Macphail, M.K. & Colhoun, (1985) E.A. Late last glacial vegetation, climates and fire activity in southwest Tasmania. Search. 16,43-45.
- McKelvey, P.J. (1953) Forest colonization after recent volcanicity at West Taupo. N.Z. J. For. 6,435-448.
- Millington, R.J., Jones, R., Brown, D., & Vernon, B. (1979) Huon Pine - Endangered? Environmental Studies Occasional Paper 9. Board of Environmental Studies, University of Tasmania, Hobart.
- Minchin, P.R. (1986) How to use ECOPAK: An ecological database system. Technical Memorandum 86/6. C.S.I.R.O., Canberra.
- Minchin, P.R. (In press) An evaluation of the robustness of techniques for ecological ordination. Vegetatio.

- Moore, D.M. (1972) Connections between cool temperate floras with particular reference to southern South America. In Valentine, D.H. (ed.) Taxonomy, Phytogeography, and Evolution. Academic Press, London-New York.
- Muller, R.N. (1982) Vegetation patterns in the mixed mesophytic forest of eastern Kentucky. Ecology. 63, 1901-1917.
- Nicholls, J.L. (1956) The historical ecology of the indigenous forest of the Taranaki upland. N.Z. J. For. 7, 17-34.
- Nicolls, K.D. and Dimmock, G.M. (1965) Soils. In Davies, J.L. (ed.) Atlas of Tasmania. Dept. Lands and Survey, Hobart, Tasmania.
- Norton, D.A. (1983) The population dynamics of subalpine Libocedrus bidwillii forests in the Cropp River valley, Westland, New Zealand. N.Z. J. Bot. 21, 127-134.
- Ogden, J. (1978) Investigations of the dendrochronology of the genus Athrotaxis D. Don. (Taxodiaceae) in Tasmania. Tree-Ring Bulletin. 38, 1-13.
- Ogden, J & Powell, J.A. (1979) A quantitative description of the forest vegetation on an altitudinal gradient in the Mount Field National Park, Tasmania, and a discussion of its history and dynamics. Aust. J. Ecol. 4, 293-325.
- Oliver, C.D., Adams, A.B. & Zasoski, R.J. (1985) Disturbance patterns and forest development in a recently deglaciated valley in the northwestern Cascade Range of Washington, U.S.A. Can. J. For. Res. 15, 221-232.

Quinn, C.J. (1982) Taxonomy of Dacrydium Sol. ex Lamb. emend de Laub. (Podocarpaceae). Aust. J. Bot. 30,311-320.

Raven, P.H. and Axelrod, D.I. (1972) Plate tectonics and Australasian paleobiogeography. Science. 176,1379-1386.

Read, J. (1986) The dynamics of Nothofagus cunninghamii rainforest associations in Tasmania - an ecophysical approach. Unpublished PhD thesis. University of Tasmania.

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

Read, J. (1985) Photosynthetic and growth responses to different light regimes of the major canopy species of Tasmanian cool temperate rainforest. Aust. J. Ecol. 10,327-334.

Runkle, J.R. (1982) Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology. 63,1533-1546.

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

Schmithusen, J. (1960) Die nadelholzer in den waldgesellschaften der sudlichen Anden. Vegetatio. 9,313-327.

- Shepherd, R.R. (1974) The Central Plateau of Tasmania: A resource survey and management plan. Unpublished M.Sc. thesis, University of Tasmania.
- Shirely, J.E. (1980) Tasmanian seismic activity-natural and reservoir-induced. Bull. Seismol. Soc. Am. 70,2203-2220.
- Singh, G. (1982) Environmental upheaval. The vegetation of Australasia during the Quaternary. In Smith, J.M.B. (Ed) A history of Australian vegetation. McGraw-Hill, Sydney, New South Wales.
- Slatyer, R.O. (1976) Water deficits in timberline trees in the Snowy Mountains of south-eastern Australia. Oecologia. 24,357-366.
- Smith, J.M.B. (1975) Living fragments of the flora of Gondwanaland. Aust. Geog. Stud. 13,3-12
- Stewart, G.H. & Veblen, T.T. (1982) Regeneration patterns in southern rata (Metrosideros umbellata) - kamahi (Weinmannia racemosa) forest in central Westland, New Zealand. N.Z. J. Bot. 20,55-77.
- Sutherland, L. (1980) A tale of two continents. Aust. Nat. Hist. 20,49-56.
- Thomas, I. (1984) Liawenee Moor: The post-glacial history of a Tasmanian alpine grassland. Unpublished Honours thesis, Australian National University.

- Thomasson, K. (1959) Nahuel Huapi: Plankton of some lakes in an Argentine national park, with notes on terrestrial vegetation. Acta. Phytogeographica Suecica. 42
- Tranquillini, W. (1979) Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. Springer-Verlag, Berlin, Heidelberg, New York.
- Veblen, T.T. (1982) Regeneration patterns in Araucaria araucana forests in Chile. J. Biogeogr. 9,11-28.
- Veblen, T.T. & Ashton, D.H. (1982) The regeneration status of Fitzroya cupressoides in the Cordillera Pelada, Chile. Biol. Cons. 23,141-161.
- Veblen, T.T., Ashton, D.H., Schlegel, F.M. & Veblen, A.T. (1977) Distribution and dominance of species in the understorey of mixed evergreen-deciduous Nothofagus forest in south-central Chile. J. Ecol. 65,815-830.
- Veblen, T.T., Ashton, D.H. & Schlegel, F.M. (1979) Tree regeneration strategies in a lowland Nothofagus dominated forest in south-central Chile. J. Biogeogr. 6,329-340.
- Veblen, T.T., Delmastro, R.J. & Schlatter, J.E. (1976) The conservation of Fitzroya cupressoides and its environment in southern Chile. Environ. Cons. 3,291-301.

- Veblen, T.T., Schlegel, F.M. & Escobar, R.B. (1980)
Structure and dynamics of old-growth Nothofagus
forests in the Valdivian Andes, Chile. J. Ecol.
68,1-31.
- Veblen, T.T., Schlegel, F.M. & Oltremari, J.V. (1983)
Temperate broad-leaved evergreen forests of South
America. In Ovington, J.D. (Ed.) Temperate
broad-leaved evergreen forests. Elsevier Scientific
Publishers, Amsterdam.
- 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, P. (1963a) The regeneration gap of the New
Zealand gymnosperms. N.Z. J. Bot. 1,301-315.
- Wardle, P. (1963b) Vegetation studies on Secretary
Island, Fiordland. Part 5. Population structure and
growth of rimu, (Dacrydium cupressinum). N.Z. J. Bot.
1,208-214.
- Wardle, P. (1963c) Growth habits of New Zealand subalpine
shrubs and trees. N.Z. J. Bot. 1,18-47.
- Wardle, P. (1969) Biological flora of New Zealand. 4.
Phyllocladus alpinus Hook. f. (Podocarpaceae). N.Z. J.
Bot. 7,76-95.
- Wardle, P. (1972) Plant Succession on greywacke gravel
and scree in the subalpine belt in Canterbury, New
Zealand. N.Z. J. Bot. 10,387-398.

- Wardle, P. (1973) Variations of the glaciers of Westland National Park and the Hooker Range, New Zealand. N.Z. J. Bot. 11,349-388.
- Wardle, P. (1974) The kahikatea (Dacrycarpus dacryioides) forests of South Westland. Proc. N.Z. Ecol. Soc. : 21,62-71.
- 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. (1980) Primary succession in Westland National Park and its vicinity, New Zealand. N.Z. J. Bot. 18,221-232.
- Wardle, P. & Campbell, A.D. (1976) Seasonal cycle of tolerance to low temperatures in three native woody plants, in relation to their ecology and post-glacial history. Proc. N.Z. Ecol. Soc. 23,85-91.
- West, D.C., Shugart, H.H. & Botkin, D.B. (1981) (Eds.) Forest succession: Concepts and Applications. Springer-Verlag, New York.

APPENDIX A.

REGENERATION PATTERNS IN POPULATIONS OF ATHROTAXIS
SELAGINOIDES D. DON., FROM TASMANIA.

P.J. Cullen

Geography Department, University of Tasmania, G.P.O. Box
252C, Hobart, Tasmania. 7001.

Submitted to the Journal of Biogeography in October 1985,
accepted 26th June 1986.

ABSTRACT

Athrotaxis selaginoides is an emergent tree in cool temperate rainforests of western and southern Tasmania. The species is found growing with evergreen tree species and the deciduous tree Nothofagus gunnii, in a variety of rainforest communities. The regeneration strategy of A. selaginoides is investigated through an examination of the demographic structure and the floristic composition of fifteen widely located stands throughout Tasmania.

A. selaginoides relies on gap formation or catastrophic disturbance for regeneration opportunities in forests dominated by evergreen tree species. However, in forests containing a high proportion of the deciduous tree, N. gunnii, A. selaginoides regenerates continuously. It appears that low light levels beneath undisturbed evergreen rainforest canopies inhibit the regeneration of the species, while the lower, more open, forests dominated by N. gunnii allow greater light penetration to the forest floor.

INTRODUCTION

Conifer species are common in the cool temperate rainforests of southern South America, New Zealand, and Tasmania. Until recently the southern conifers have received relatively little attention in the ecological literature.

Schmithusen (1960) considered the southern Andean conifers as relict from the Tertiary period, and now forced to occupy sites of inferior quality (ie. rocky, dry, cold, wet, or low fertility sites) due to an inability to compete with more aggressive broadleaved species under the prevailing climate. Fossil evidence which points to a much wider distribution of the southern conifer genera in the past (Florin, 1963) supports this view.

In New Zealand, Holloway (1954) proposed that the conifers were unable to regenerate under present climatic conditions, and were in the process of being replaced by hardwood species. Nicholls (1956), Wardle (1963a,b, 1978), Elder (1963), and Grant (1963), produced evidence to support this hypothesis. However, recent research in Chile and New Zealand has suggested that at least some species, eg. Araucaria araucana (Mol.) C. Koch. (Veblen, 1982) and Libocedrus bidwillii Hook. f. (Clayton-Green, 1977; Veblen and Stewart, 1982; Norton 1983), are well-adapted to the environments in which they occur. Veblen et al. (1983) discuss the importance of wide scale catastrophic disturbance, resulting from volcanic and seismic activity in a variety of Chilean forest types. Araucaria araucana appears able to survive this type of disturbance and also displays a strategy of gap-phase regeneration. Combined with its longevity, these

mechanisms allow it to maintain dominance once established (Veblen, 1982). In New Zealand, Libocedrus bidwillii takes advantage of both gaps and catastrophic disturbances for regeneration opportunities (Clayton-Greene, 1977; Veblen and Stewart, 1982; Norton, 1983). In addition to these two species, regeneration following catastrophic disturbance has been reported for a number of other conifers in New Zealand (McKelvey, 1953; Cameron, 1960; Llyod, 1960; Beveridge, 1973; Burke, 1974).

Very little has been published on the regeneration strategies of Tasmanian conifers. Millington et al. (1979) found Lagarostrobos franklinii (Hook.) Quinn. to be regenerating in areas estimated to have been free from disturbance for around 3000 years. Davies (1983) reports young even-aged stands of L. franklinii that appear to have established following fires. This species has also been observed colonizing riverside shingle and mine tailing deposits (Kirkpatrick 1977b). Ogden (1978) and Kirkpatrick and Harwood (1980) have found evidence suggesting discontinuous regeneration in both Athrotaxis cupressoides* and Athrotaxis selaginoides. By contrast, Calais and Kirkpatrick (1983) observed a size structure

* Species nomenclature follows Curtis (1963,1967) and Curtis and Morris (1975) except where indicated.

implying continuous replacement of A. selaginoides in undisturbed forest.

This present study was undertaken to investigate the regeneration strategies of A. selaginoides and to determine whether it is reliant upon either gap formation or catastrophic disturbance for regeneration opportunities. The genus Athrotaxis is now endemic to Tasmania but fossil evidence indicates a wider distribution in the past (Florin, 1963). Athrotaxis is comprised of three species, A. selaginoides, A. cupressoides and A. laxifolia. All three are noted for their longevity and individuals of A. selaginoides and A. cupressoides over 1000 years old have been recorded (Ogden, 1978).

A. selaginoides has a wide but discontinuous distribution in areas of high rainfall, ranging from altitudes just above sea level to 1270 m (Fig. 1). It occurs as a forest dominant, emerging from a closed canopy of rainforest tree species. In some situations the species can achieve heights of over 40m and diameters over 2m. At high altitudes it is found as a stunted tree or in krumholtz form in subalpine scrub communities.

A. selaginoides is found growing with the evergreen tree species Nothofagus cunninghamii, Atherosperma moschatum, Eucryphia lucida, E. milliganii, and, on occasions, Eucalyptus subcrenulata. It is also commonly

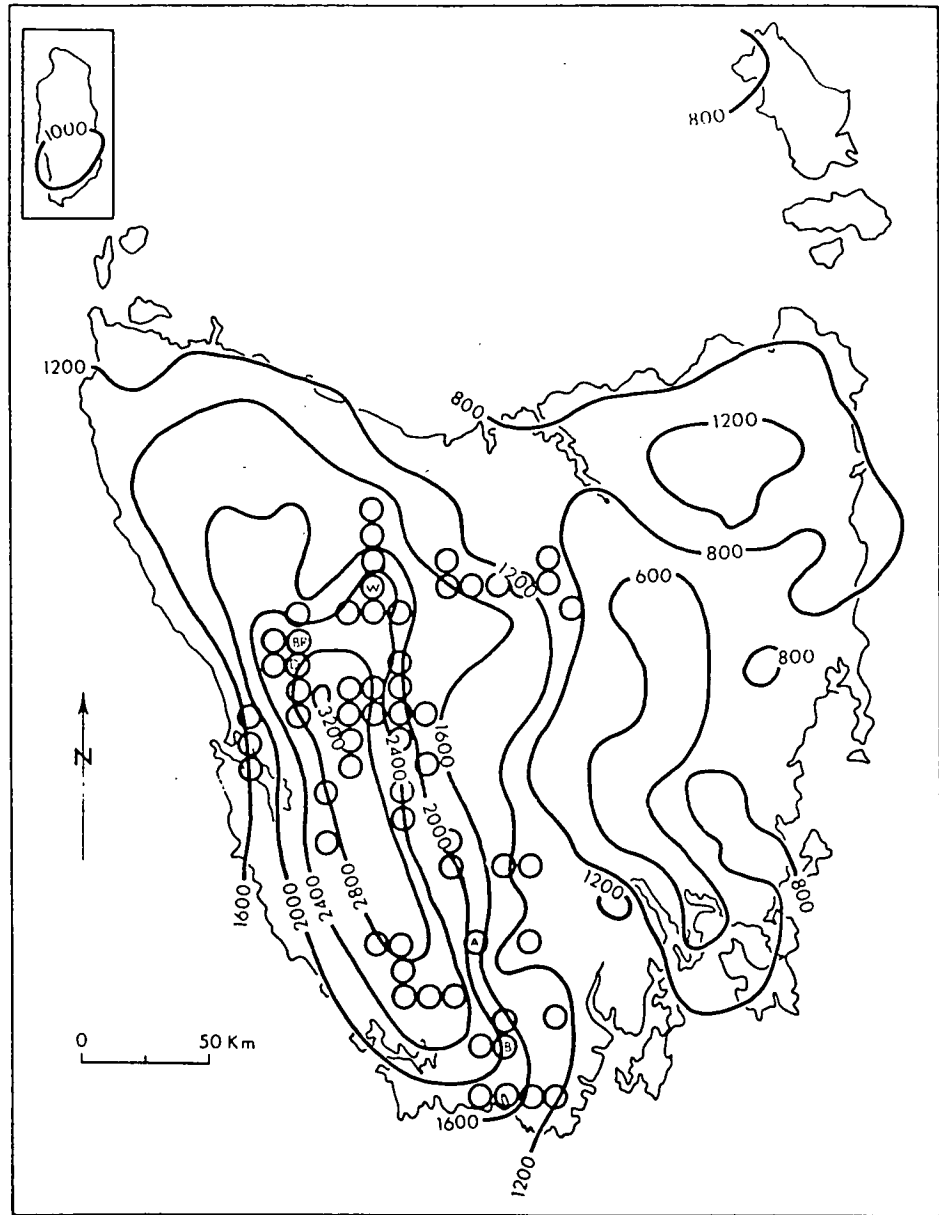


FIG. 1. The distribution of *A. selaginoides* and annual precipitation in Tasmania. Circles indicate where the species occurs, letters indicate the location of study sites (see Table 1). Isohyets are in mm.

associated with the deciduous tree Nothofagus gunnii. A number of these communities are described in Kirkpatrick and Harwood (1980), Kirkpatrick (1977, 1980, 1983, and 1984), and Jarman et al. (1984).

Being present in a variety of forest communities A. selaginoides might be expected to show different demographic structures in response to the different conditions imposed by the subordinate species. Structural variability of this type was hypothesized for Eucalyptus delegatensis populations (but subsequently disproved) by Bowman and Kirkpatrick (1984). This hypothesis is examined for A. selaginoides.

METHODS

Old-growth forest and subalpine scrub dominated by A. selaginoides was investigated at five locations (Table 1) which span a considerable part of the geographic range of the species. A total of fifteen stands were sampled. Each stand was subjectively chosen as being representative of the A. selaginoides dominated vegetation in the area. Sampling was accomplished with transects 3 or 4 m wide and ranging from 15 to 185 m in length, depending upon the nature of the vegetation. The areas sampled are described in table 1. The start of each transect was located by an over the shoulder toss of

TABLE 1

Stand designation	Grid reference	Altitude (m)	Aspect	Slope (°)	Parent material	Soil pH, top 10 cm	Area (m ²)
Mt Anne							
A1	538460	1020	SSE	10	Carbonaceous sandstone and siltstone	4.5	252
A2	540465	1000	NW	14	Carbonaceous sandstone and siltstone	4.5	252
A3	540467	880	NW	14	Conglomerate	4	300
Mt Bobs							
B1	695079	680	NW	5	Sandstone till	4.5	555
B2	693079	660	Valley floor	0	Sandstone till	4.5	222
B3	688082	760	S	8-10	Sandstone	4.5	201
B4	688091	680	NW	2-3	Sandstone	4.5	300
Mt Dundas							
D1	733586	720	SSE	3-5	Sandstone and mudstone	4.5	303
D2	735592	820	S	2	Sandstone and mudstone	4	105
D3	734601	990	S	7	Dolerite moraine	4	60
Weindorfs forest							
W1	116899	1040	SE	14	Quartzite	4.5	240
W2	117898	980	SE	12	Quartzite	4	264
W3	118897	930	SE	10	Quartzite	4.5	294
Bradshaws Road							
BR1	808661	750	S	2-3	Glacial clays	4.5	300
BR2	801660	780	SE	7	Mt Read volcanics	4.5	184

Table 1. Stand designation, location, and characteristics of A. selaginoides stands.

a tape measure and the transect was orientated parallel to the contour. The altitude of each stand was taken from a 1:100,000 topographic map, aspect was recorded, and the average slope was measured with an Abney level. The height of emergent A. selaginoides stems and the height of the closed canopy of associated trees was measured using an Abney level and tape measure. The pH of the top 10 cm of soil (bulked) was measured with a C.S.I.R.O. soil testing kit. Soil parent material was recorded and confirmed with the appropriate geological map. The diameter at breast height (d.b.h.) and the position along the transect were noted for all woody species with d.b.h. >1 cm. The projected cover of all major canopy and understorey species occurring along the transect was estimated using the following cover classes, 1=0-5%, 2=5-25%, 3=25-50%, 4=50-75%, 5=75-100% (Appendix 2). The cover information was ordinated using the program DECORANA (Hill 1979). To gain a measure of the relative biomass of each stand the basal areas for A. selaginoides, and for all other trees grouped together, was calculated.

The position and height of all established seedlings (ie. > 5 cm tall) of A. selaginoides were noted. Percent frequencies for seedlings and adults of A. selaginoides in 10cm size classes were determined at each stand. The size classes used were, 1= <1 cm d.b.h. (seedlings),

2=1-9.5cm, 3=10-19.5cm, and so on. Size class-frequency histograms were prepared. The proportion of seedlings occurring in canopy gaps is indicated on each histogram. These histograms were qualitatively assessed to decide whether each population was all-aged, even-aged, or comprised of a number of even-aged groups.

The relationship between age and diameter for A. selaginoides was investigated at stand B4. The ages of twelve trees were estimated by counting growth rings on increment cores taken 1 m above the ground. Annual ring formation was assumed (Ogden, 1978). A regression of diameter versus age showed a significant positive relation ($r=0.97$, $p<0.01$) indicating a good relationship between size and age. Ogden (1978) found similar results at two other widely separated sites. Considering the present concern for the conservation of A. selaginoides no further cores were collected. However as field work proceeded it became apparent that suppression of the species does occur and it is therefore necessary to treat the relationship between size and age with some caution.

RESULTS AND DISCUSSION

A wide range of forest types were encountered in the fifteen study sites. However, they fall into two broad groups: those forming closed forest with a large total

basal area, a high component of evergreen tree species, and a well developed but species-poor shrub understorey (thamnic rainforest, Jarman et al., 1984, see Appendix 1), and those which are relatively open with a low total basal area, a reduced evergreen component, an increase in the dominance of deciduous N. gunnii, and a dense tangled species-rich understorey (implicate rainforest and subalpine scrub, Jarman et al., 1984, see Appendix 1) (Table 2).

Basal area values for some stands dominated by A. selaginoides are larger than those obtained by Ogden and Powell (1979). They report basal areas between 54.2 and 208.5 m²/ha in wet sclerophyll (with Eucalyptus species dominant), mixed Eucalyptus/rainforest, and pure rainforests in Tasmania and support these figures with data derived from Gilbert (1959) which yield basal areas between 53.3 and 248.2 m²/ha. The larger values in these cases are derived from forests with scattered but extremely large Eucalyptus stems. A similar effect could be expected in stands dominated by large diameter A. selaginoides. Kirkpatrick and Harwood (1980) found a total basal area of 219 m²/ha for trees over 10 m tall in the forest where stand B1 was located. A value of 257.4 m²/ha for all trees greater than or equal to 1 cm d.b.h. was recorded in this study.

The ordination of the floristic data is presented in

TABLE 2*

Stand	Canopy height (m)		Basal area (m ² /ha)		
	<i>A. selaginoides</i>	Main canopy	<i>A. selaginoides</i>	Other species	Total
Group 1: thamnic rainforest					
B1	25-35	15-25	175.7	81.7	257.4
W3	25-35	15-25	187.3	85.1	272.4
B4	25-30	20	192.2	102.0	294.2
D1	18-20	12-15	175.9	97.4	273.3
A3	20-22	16	105.9	97.6	203.5
W2	15-18	8-10	102.3	63.1	165.4
A2	10	6	67.2	48.2	115.4
Group 2: implicate rainforest and subalpine scrub†					
BR2	8-10	5-6	74.1	‡	‡
B3	15	10-12	45.9	61.0	106.9
BR1	20-22	15-16	54.8	32.6	87.4
D2	7-8	5-6	67.1	55.3	122.4
A1‡	6-8	3-5	45.2	22.9	68.1
D3‡	4	2-3	42.6	63.7	106.3‡
B2‡	4-6	3-4	42.5	‡	‡
W1	8-10	5-7	27.0	‡	‡

*Stands arranged in order of the score on axis 1 of the D.C.A.

†Denotes subalpine scrub communities.

‡Not applicable due to lack of vertical stems.

Table 2. Canopy height and basal area of *A. selaginoides* stands

figure 2. Axes 1 and 2 display most of the variation in the stands studied with eigen values of 0.634 and 0.256 respectively. On axis 1 the thamnic rainforest communities (Group 1) have low scores and the implicate rainforest and subalpine scrub communities (Group 2) have high scores. With increasing score on axis 1 there is a general decline in tree height and basal area for each stand (Table 2). This reflects a shift towards the treeline. Stands W1 and B2 fall well to the right of the majority of stands in figure 2. Both stands are ecotonal and have high proportions of understorey species that are not common in the other stands (Appendix 2) but which are more likely to be found in more open subalpine and alpine communities (Kirkpatrick, 1983,1984). W1 is situated at the treeline and B2 lies close to the edge of an inverted tree line in an inter-montane basin.

Neither axis appears to correspond directly with any of the environmental factors recorded (Table 1).

Temperature, soil depth, drainage, and exposure are all likely to be important and these factors have been related to changes in rainforest communities on the West Coast Range by Kirkpatrick (1984).

All Group 1 stands, except A2 and W3, show seedling and adult distribution patterns suggestive of gap-phase regeneration whilst Group 2 stands appear to be continuously regenerating. Stand B3 appears to be

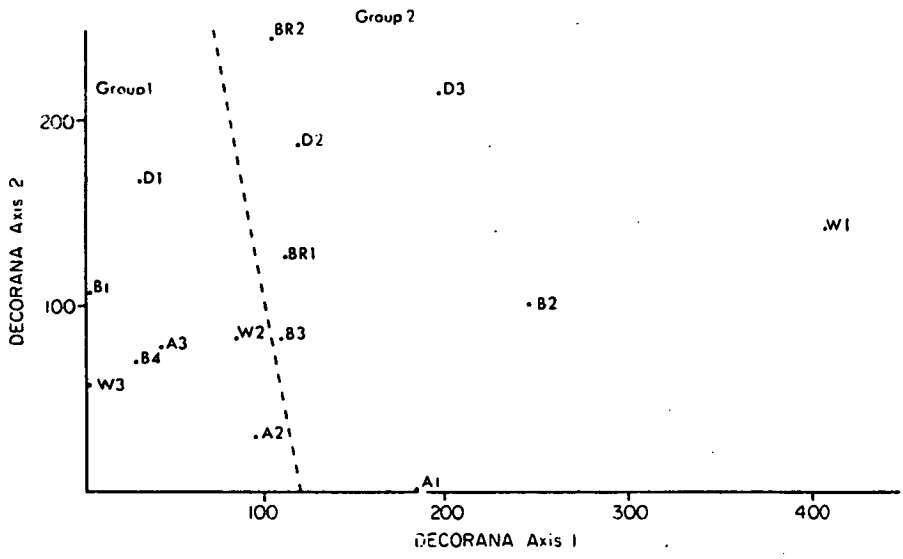


FIG. 2. Axis 1 versus Axis 2 for the ordination of sample stands using DECORANA.

regenerating continuously but regeneration is concentrated in a canopy gap. Floristically it is an implicate rainforest.

Most of the A. selaginoides seedlings in group 1 stands occur in distinct canopy gaps (Fig 3a) which have been formed by the wind throw of one or more trees. Two such gaps have been formed by the fall of groups of A. selaginoides individuals at stand B1. These trees appear to be the victims of self-thinning. A number of standing A. selaginoides stems in the mid size class range (20=50 cm dbh) are dead or severely suppressed. Their fall will no doubt create new canopy gaps. Self-thinning in A. selaginoides has been reported by Ogden (1978) and Kirkpatrick and Harwood (1980).

In Group 1 stands, A. selaginoides seedlings are found growing on fallen tree trunks and at least a few of the standing adults are supported aurally by their roots, with a considerable cavity below the base of the bole. There is no evidence of erosion from around the trees. This suggests that these adults may also have germinated on top of logs which have long since rotted away. In some cases adult trees are clumped in small groups of 3 to 9 individuals, further suggesting that they have regenerated in gaps. Such clumps were evident in stands A3, B1, B4, D1, and W2. At B4 the transect crossed a dense patch of young A. selaginoides stems with

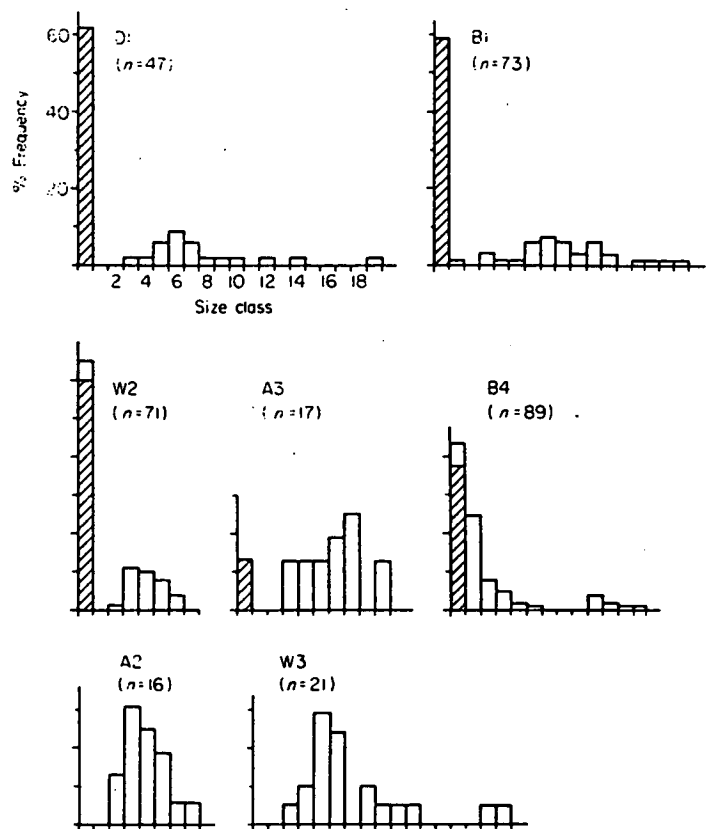


FIG. 3(a). Per cent frequency versus size class histograms for *A. selaginoides* populations. Size classes are 1=<1 cm d.b.h. (seedlings), 2=1-9.5 cm, 3=10-19.9 cm, and so on. Hatched areas represent the proportion of seedlings located in canopy gaps.

dbhs from 2-34 cm, the smallest stems being severely suppressed. This patch measures approximately 10x15 m and contains 19 stems. These individuals may have regenerated following gap formation, with the range of stem sizes reflecting differences in vigour and an extended recruitment period before canopy closure.

At stands A2 and W3 no seedlings or saplings were found. A2 appears to be undisturbed, with mature A. selaginoides stems emerging through a low dense canopy of N. cunninghamii and Eucryphia milliganii. At W2 a few of the largest A. selaginoides stems have been removed in a light selective logging. In this case, the gaps created by the removal of single trees were apparently too small to allow the establishment of a new generation of A. selaginoides. However, there is considerable regeneration of N. cunninghamii and Atherosperma moschatum in this stand. Across the valley, on the lower slopes of Mt Kate, a similar forest at similar altitude and aspect and on the same soil parent material, has been logged more intensively. Many A. selaginoides trees have been removed and the resulting large gaps and the extensive network of snig tracks have been heavily colonized by A. selaginoides seedlings.

The size class histograms for A. selaginoides support the view that Group 1 stands are not regenerating continuously. The stands appear to have either

discontinuities in their size (age) structures or no individuals in the smallest size classes (Fig 3a).

In group 2 stands, regeneration does not appear to rely on canopy gap formation. With the exception of stand B3, the seedling regeneration is evenly distributed along the transects. At B3, seedlings were present throughout the transect but there was a definite clustering in a gap created by the fall, but not the death, of a large N. gunnii. Its root mat is still intact. Although the number of individuals measured in these stands is low, their size (age) structures can be interpreted as being reverse J-shaped (Fig 3b). A reverse J-shaped form in a size or age class distribution is considered to be indicative of a continuously regenerating tree population (Hett and Loukes, 1976; Veblen et al., 1980).

As well as the gap-phase regeneration documented above, A. selaginoides is capable of recolonizing catastrophically disturbed areas provided a seed source remains in the immediate vicinity. Trials conducted by the Forestry Commission (Internal Report 1982), indicate that effective seed dispersal is restricted to areas no further away than twice the height of the parent tree. Forests disturbed by logging on Mt Kate (see page 6) and on the West Coast Range near stands BR1 and BR2 show good levels of A. selaginoides regeneration. Many seed trees

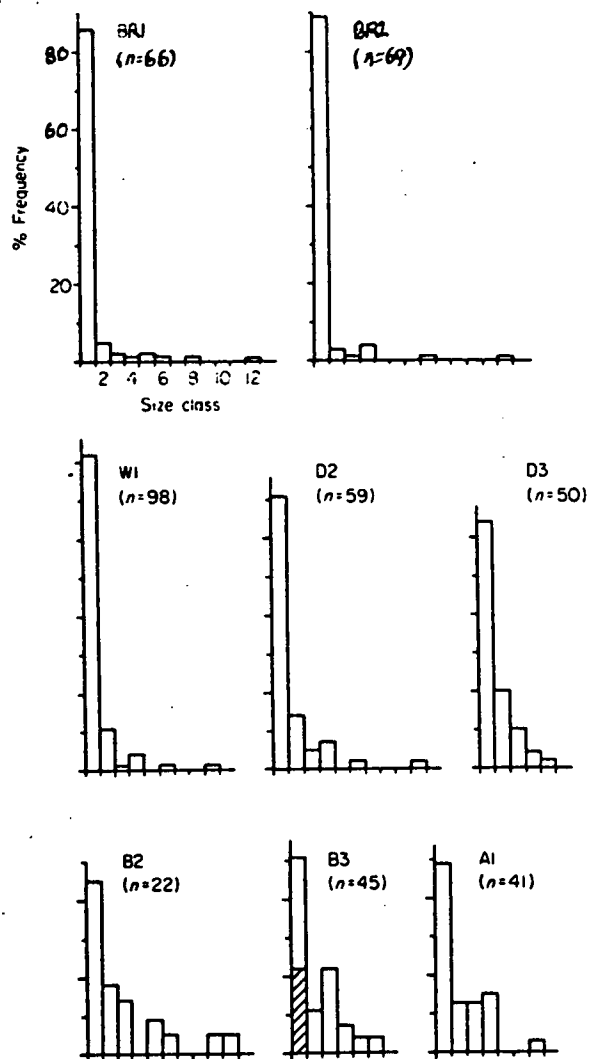


FIG. 3(b). Per cent frequency versus size class histograms for *A. selaginoides* populations. Size classes are 1=<1 cm d.b.h. (seedlings), 2=1-9.5 cm, 3=10-19.9 cm, and so on. Hatched areas represent the proportion of seedlings located in canopy gaps.

remain and seedlings and saplings are very common in heavily disturbed areas. Calais and Kirkpatrick (1983) found that A. selaginoides had a low but continuous rate of replacement where top soil was not removed by logging activities.

By far the most frequent cause of natural catastrophic disturbance in Tasmania is wildfire. Although A. selaginoides has been observed recolonizing burnt areas, instances of regeneration following fire are relatively rare. Good examples of healthy seedling, sapling, and pole stands have been observed on previously burnt sites near stands B1, BR1, and D3. In all cases seed trees are within 50 m of the regeneration. Ogden (1978) considered that the 3 distinct generations of A. selaginoides at Swifts Creek are the results of past fires.

Even though A. selaginoides can regenerate after burning, fire is more likely to eliminate the species than to promote its regeneration. Extensive areas of A. selaginoides have been completely destroyed by fire since European settlement (Kirkpatrick 1977b) and it appears that the species is killed by all but the lightest fires (Calais and Kirkpatrick 1983).

Physiological characteristics suggest further that the species is not well adapted to fire. Seeds are retained in the cones for only a short period (Ogden

1978), they are viable for only 3 to 4 months, and heavy seed crops occur only once every 5 to 6 years (Calais and Kirkpatrick 1983). Growth rates of A. selaginoides are generally slow and Ogden (1978) found that they varied from site to site. At high altitudes diameter increases were as little as 0.4 mm per annum. In the present study, diameter increases in excess of 5 mm per annum have been observed on good sites, and cones have not been found on individuals less than about 2m high. Ogden (1978) also reports a prolonged seedling phase, with the average age of a 1m tall seedling being 42 years. These factors, combined with poor seed dispersal, ensure that the recolonization of large burnt areas proceeds at a very slow rate.

Where thamnic rainforest containing A. selaginoides is burnt, it is probable that ground beyond the seed dispersal range of any surviving A. selaginoides stems will be closed to further A. selaginoides regeneration by other species which can regenerate vegetatively or have better seed dispersal (see Kirkpatrick 1984). In such an event, gap formation or catastrophic disturbance would be required to allow further recolonization of A. selaginoides. Aging of a few individuals on a previously burnt area near stand B1 revealed that the site was open to regeneration for a period of sixty to seventy years. Here the A. selaginoides individuals emerge from a dense

closed scrub dominated by Richea scoparia. The stand now appears to be closed to further pine regeneration.

Fires are now common in Tasmania, even in the wettest areas but just how common they were before the arrival of Europeans is not known. The loss of fire sensitive plant communities in recent times (Kirkpatrick 1977b, Kirkpatrick and Dickinson 1984) suggests that before European interference fires were less frequent, or of a different nature than those of today. Therefore a fire regime similar to that of the present cannot have been responsible for the maintainance and spread of A. selaginoides in the past. If the intervals between fires were much longer, or if fires were of a less intense (ie. more patchy) nature then fires may have been instrumental in the establishment of new generations of A. selaginoides.

Other catastrophic disturbances in Tasmania which may contribute to regeneration of A. selaginoides include heavy snow falls, severe wind storms and landslides. The extent of these disturbances is not yet known but they are not as widespread or common as in other mountain regions of the cool temperate Southern Hemisphere. Tasmania lacks the volcanic and seismic activity common in southern South America and the north island of New Zealand, and has done so for approximately the last 15 million years (Sutherland 1980). By world standards,

seismic activity in Tasmania is low (Shirely 1980) and although weak to moderate earth tremors are common, they do not appear to be responsible for widespread destruction of forests as is common in southern South America.

It seems probable that the stimulation of A. selaginoides regeneration in thamnic rainforest is due to the increased light availability in canopy gaps. In an undisturbed state these forests have a high biomass concentrated in the canopy, usually only a light shrub layer, and relatively dark conditions on the forest floor. By contrast implicate rainforests with deciduous N. gunnii dominating the canopy and subalpine scrub communities have a lower biomass which is concentrated much closer to the ground and the transmission of light to the forest floor is much higher. Thus regeneration can occur without canopy disturbance. This view is supported by the work of Read (1985) which indicates that A. selaginoides is a shade-intolerent species.

A regeneration strategy similar to that of A. selaginoides is displayed by Araucaria hunsteinii K. Schumm., a forest emergent endemic to New Guinea. In stands studied by Enright (1982a) the spatial pattern of A. hunsteinii individuals suggests that this species relies on disturbance for regeneration opportunities except where it grows beneath a canopy of the

semi-deciduous species, Pouteria luzonensis (Merr.)
Bachni. Enright (1982b) also demonstrated that A.
hunsteinii seedlings have a poor tolerance to low light
levels.

Other factors which may stimulate the regeneration
of A. selaginoides in thamnic rainforest include reduced
moisture or nutrient competition and changes in the
temperature regime when canopy gaps form.

The size of the gap required to create suitable
regeneration conditions for A. selaginoides or the rate
at which these gaps occur has not been investigated.
However, it appears likely that the minimum gap size
would vary depending on canopy height and closure. For
example, at D1 and B4, A. selaginoides is regenerating in
small gaps formed by the fall of solitary trees but at
W3, one of the tallest stands studied, there was no
regeneration despite removal of several trees. In mesic
hardwood forests in the eastern U.S.A., Runkle (1982) has
shown that small gaps (formed by the fall of one or a few
trees) arise in about 1% of the forest area in any year.
A lower rate would be expected in Tasmanian rainforests
due to the greater longevity of the species involved, in
excess of 300 years (Calais and Kirkpatrick 1982). A low
rate of gap formation and a minimal gap size limitation
may in part explain the discontinuous distribution of A.
selaginoides in thamnic rainforests.

CONCLUSION

The results of this study indicate that A. selaginoides is capable of successful regeneration under the natural conditions prevailing in Tasmanian cool temperate rainforests. However, it uses different regeneration strategies depending on forest type and this is reflected by differences in demographic structure across its geographic range. In implicate rainforest containing high proportions of N. gunnii and in subalpine scrub, A. selaginoides demonstrates a capacity to regenerate continuously without canopy disturbance. Increased transmission of light to the forest floor, as a result of the low, open and deciduous nature of the canopy appears to be a likely explanation. In the taller, darker thamnic rainforests suitable conditions for regeneration are not present below the closed canopy of evergreen trees. As a consequence, A. selaginoides relies on gap formation or catastrophic disturbance for regeneration opportunities. The extreme longevity of A. selaginoides means that once established it can remain dominant for many centuries and canopy disturbances need only occur very infrequently for its presence to be maintained. By regenerating in canopy gaps A. selaginoides will maintain its presence in the forest as

isolated trees or scattered groups.

In the event of catastrophic disturbance A. selaginoides is capable of massive regeneration provided a seed source remains nearby. However such regeneration is rarely seen because the main source of catastrophic disturbance in Tasmania is fire. A. selaginoides is poorly adapted to this form of disturbance and is at a selective disadvantage under frequent or widespread fire regimes because of its long seedling phase and poor seed dispersal.

The ability to use large or small scale disturbance events for regeneration may prove to be a common feature of the long lived conifers of the cool temperate southern hemisphere. It has been reported previously for some conifer species in southern South America, New Zealand, and New Guinea and is now demonstrated in A. selaginoides in Tasmania.

ACKNOWLEDGEMENTS

I thank J.B. Kirkpatrick and S.J. Jarman for their helpful criticism of the manuscript and C. Charlseworth for her drafting of the figures. The work was made possible through a grant from The Australian Heritage Commission to The Tasmanian Conservation Trust.

REFERENCES

- Beveridge, J.L. (1973) Regeneration of podocarps in central North Island podocarp forests. Proc. N.Z. Ecol. Soc. 11,48-55.
- Bowman, D.M.J.S. & Kirkpatrick, J.B. (1984) Geographic variation in the demographic structure of stands of Eucalyptus delegatensis R.T. Baker on dolerite in Tasmania. J. Biogeogr. 11,427-437.
- Burke, W.D. (1974) Regeneration of podocarps on Mt Tarawera, Rotorua. N.Z. J. Bot. 12,219-226.
- Calias, S.S. & Kirkpatrick, J.B. (1983) Tree species regeneration after logging in temperate rainforest, Tasmania. Pap. Proc. Roy. Soc. Tasmania. 117,77-83.
- Cameron, R.J. (1960) Natural regeneration of podocarps in the forests of the Whirinaki River Valley. N.Z. J. For. 8,337-364.
- 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.
- Curtis, W.M. (1963) The student's flora of Tasmania, Part II. Government Printer, Tasmania.
- Curtis, W.M. (1967) The student's flora of Tasmania, Part III. Government Printer, Tasmania.
- Curtis, W.M. & Morris, D.I. (1975) The student's flora of Tasmania, Part I. Government Printer, Tasmania.

- Davies, J. (1983) Huon Pine Survey. Tasmania National Parks and Wildlife Service, Wildlife Division Technical Report No 83/2.
- Elder, N.L. (1963) Evidence of climatic change from the vegetation of the North Island. Proc. N.Z. Ecol. Soc. 2,143-171.
- Enright, N.J. (1982a) The ecology of Araucaria species in New Guinea. 111. Population dynamics of sample stands. Aust. J. Ecol. 7,227-237.
- Enright, N.J. (1982b) The ecology of Araucaria species in New Guinea. 11. Pattern in the distribution of young and mature individuals and light requirements of seedlings. Aust. J. Ecol. 7,39-48.
- Florin, R. (1963) The distribution of conifer and taxad genera in time and space. Acta Hort. Bergiani Band 20, No 4.
- Gilbert, J.M. (1959) Forest succession in the Florentine Valley, Tasmania. Pap. Proc. R. Soc. Tasm. 93,129-151.
- Grant, P.J. (1963) Forests and recent climatic historey of the Huiarau Range, Urewera region, North Island. Trans. Roy. Soc. N.Z. 82,329-410.
- Hett, J.M. & Loucks, O.L. (1976) Age structure models of balsam fir and eastern hemlock. J. Ecol. 64,1029-1044.

- Hill, M.O. (1979) DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and systematics, Cornell University, Ithaca, New York.
- Holloway, J.T. (1954) Forests and climates of the South Island of New Zealand. Trans. Roy. Soc. N.Z. 82,329-410.
- Jarman, S.J. & Brown, M.J. (1983) A definition of cool temperate rainforest in Tasmania. Search. 14,81-87.
- Jarman, S.J., Brown, M.J., & Kantvilas, G. (1984) Rainforest in Tasmania. National Parks and Wildlife Service Tasmania.
- Kirkpatrick, J.B. (1977a) Native vegetation of the West Coast region of Tasmania. In Banks. M.R. and Kirkpatrick. J.B. (Eds): Landscape and Man. Royal Society of Tasmania, Hobart. 55-80.
- Kirkpatrick, J.B. (1977b) The impact of man on the vegetation of the West Coast region, Tasmania. In Banks. M.R. and Kirkpatrick. J.B. (Eds): Landscape and Man. Royal Society of Tasmania, Hobart. 151-156.
- Kirkpatrick, J.B. (1983) Treeless plant communities of the Tasmanian high country. Proc. Ecol. Soc. Aust. 12,61-77.
- Kirkpatrick, J.B. (1984) Altitudinal and successional variation in the vegetation of the northern part of the West Coast Range, Tasmania. Aust. J. Ecol. 9,81-91.

- Kirkpatrick, J.B. & Dickinson, K.J.M. (1984) The impact of fire on Tasmanian alpine vegetation and soils. Aust. J. Bot. 32,613-629.
- Kirkpatrick, J.B. & Harwood, C.E. (1980) Vegetation of an infrequently burned Tasmanian mountain region. Proc. Roy. Soc. Victoria. 91,79-107.
- Lloyd, R.C. (1960) Growth study of regenerated Kauri and podocarps in Russell Forest. N.Z. J. For. 8,341-355.
- McKelvey, P.J. (1953) Forest colonization after recent volcanicity at West Taupo. N.Z. J. For. 6,435-448.
- Millington, R.J., Jones, R., Brown, D., & Vernon, B. (1979) Houn Pine - Endangered? Environmental Studies Occasional Paper 9. Board of Environmental Studies, University of Tasmania, Hobart.
- Nicholls, J.L. (1956) The historical ecology of the indigenous forest of the Taranaki upland. N.Z. J. For. 7,17-34.
- Norton, D.A. (1983) The population dynamics of subalpine Libocedrus bidwillii forests in the Cropp River valley, Westland, New Zealand. N.Z. J. Bot. 21,127-134.
- Ogden, J. (1978) Investigations of the dendrochronology of the genus Athrotaxis D. Don. (Taxodiaceae) in Tasmania. Tree-Ring Bulletin. 38,1-13.

- Ogden, J & Powell, J.A. A quantitative description of the forest vegetation on an altitudinal gradient in the Mount Field National Park, Tasmania, and a discussion of its history and dynamics. Aust. J. Ecol. 4,293-325.
- Read, J. (1985) Photosynthetic and growth responses to different light regimes of the major canopy species of Tasmanian cool temperate rainforest. Aust. J. Ecol. 10,327-334.
- Runkle, J.R. (1982) Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology. 63,1533-1546.
- Schmithusen, J. (1960) Die nadelholzer in den waldgesellschaften der sudlichen Anden. Vegetatio. 9,313-327.
- Shirely, J.E. (1980) Tasmanian seismic activity-natural and reservoir-induced. Bull. Seismol. Soc. Am. 70,2203-2220.
- Sutherland, L. (1980) A tale of two continents. Aust Nat. Hist. 20,49-56.
- Veblen, T.T. (1982) Regeneration patterns in *Araucaria araucana* forests in Chile. J. Biogeogr. 9,11-28.
- Veblen, T.T., Schlegel, F.M. & Escobar, R.B. (1980) Structure and dynamics of old-growth Nothofagus forests in the Valdivian Andes, Chile. J. Ecol. 68,1-31.

- Veblen, T.T., Schlegel, F.M. & Oltremari, J.V. (1983) Temperate broad-leaved evergreen forests of South America. In Ovington, J.D. (Ed.) Temperate broad-leaved evergreen forests. Elsevier Scientific Publishers, Amsterdam.
- 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, P. (1963a) The regeneration gap of the New Zealand gymnosperms. N.Z. J. Bot. 1,301-315.
- Wardle, P. (1963b) Vegetation studies on Sactretary Island, Fiordland. Part 5. Population structure and growth of rimu, (Dacrydium cupressinum). N.Z. J. Bot. 1,208-214.
- 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.

APPENDIX 1

Jarman et al. (1984) propose 4 major groups for Tasmania's cool temperate rainforests. These groups are based on structure and floristic composition. A short summary of their work is presented below. They suggest a minimum height of 8 m for rainforest. Some of the stands investigated in this study are less than 8 m tall and therefore are subalpine scrub communities.

1. Callidendrous rainforest.

Tall forests with closed canopies. Nothofagus cunninghamii is dominant and sometimes over 30m tall. Atherosperma moschatum is usually subdominant. The understorey is open with only scattered shrubs. Conifer species are uncommon and if present are usually represented by Phyllocladus aspleniifolius. The term 'callidendrous' is derived from two Greek words, kalos (beautiful) and dendron (tree).

2. Thamnic rainforest.

Intermediate in structure between 1 and 3. Trees obtain moderate heights, up to 30 m in some cases. There is a mixtrure of tree species including N. cunninghamii, Lagarostrobos franklinii, Athrotaxis selaginoides, P. aspleniifolius, and Eucryphia lucida. A. moschatum is

also common but it is usually a subordinate species. There is a well developed understorey intermediate between 1 and 3 in both density and species richness. The term 'thamnic' is derived from the Greek word, thamnos (shrub).

3. Implicate rainforest.

Low in structure (often less than 20 m) with mostly broken, uneven canopies. Dominants include Nothofagus gunnii, N. cunninghamii, L. franklinii, P. aspleniifolius, A. selaginoides, Diselma archeri, Eucryphia milliganii, and E. lucida. Single dominance of any one species is rare. The species rich understorey is continuous with the canopy and is tangled with a network of low branches and twisted stems. The term 'implicate' is derived from the latin word, implicatus, meaning tangled or interwoven.

4. Open montane rainforest.

Usually less than 15 m tall and dominated by Athrotaxis cupressoides. The canopy is open and uneven. The understorey can be grassy, or comprised of low heath or dense shrubbery usually less than half the height of the forest.

REFERENCE

Jarman, S.J., Brown, M.J., & Kantvilas, G. (1984)

Rainforest in Tasmania. National Parks and Wildlife
Service Tasmania.

APPENDIX 2

DISTRIBUTION AND COVER OF UNDERSTOREY SPECIES.

Stand number	B				B				B				B			
	W	B	D	A	W	A	R	B	R	D	A	D	B	W		
	1	3	4	1	3	2	2	2	3	1	2	1	3	2	1	
<i>Lomatia polymorpha</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pittosporum bicolor</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Polystichum proliferum</i>	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Atherosperma moschatum</i>	2	2	1	2	1	-	-	1	-	1	-	-	-	-	-	-
<i>Prionotes cerinthoides</i>	1	-	1	1	1	-	1	1	1	1	1	-	-	-	-	-
<i>Olearia persoonioides</i>	1	-	-	1	-	-	1	-	1	-	1	-	-	-	-	-
<i>Coprosma nitida</i>	1	-	-	-	-	1	1	-	1	1	1	-	-	-	-	-
<i>Drimys lanceolata</i>	1	-	1	1	1	-	1	1	-	-	1	1	-	-	-	-
<i>Blechnum wattsi</i>	-	-	2	-	1	-	1	1	2	1	-	-	-	-	-	-
<i>Gahnia grandis</i>	-	-	1	-	-	-	-	-	1	1	-	-	-	-	-	-
<i>Cyathodes juniperina</i>	-	-	-	-	1	-	-	-	1	1	1	-	-	-	-	-
<i>Uncinia tenella</i>	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-
<i>Phyllocladus aspleniifolius</i>	1	1	1	1	1	2	-	-	1	1	-	-	-	2	-	-
<i>Nothofagus cunninghamii</i>	3	3	3	2	3	2	3	1	1	1	1	2	-	2	-	-
<i>Athrotaxis selaginoides</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>Richea pandanifolia</i>	1	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Archeria eriocarpa</i>	3	-	2	1	-	3	-	-	1	-	2	-	1	-	-	-
<i>Trochocarpa cunninghamii</i>	-	3	-	1	1	3	1	-	1	1	1	2	-	-	-	-
<i>Trochocarpa gunnii</i>	-	-	-	1	1	3	-	-	1	1	2	-	1	-	-	-
<i>Eucryphia milliganii</i>	-	-	2	-	-	-	3	-	2	3	-	-	-	2	-	-
<i>Anopterus glandulosus</i>	-	-	2	2	-	-	-	1	1	1	2	-	1	-	-	-
<i>Anodopetalum biglandulosum</i>	-	-	-	2	-	-	-	4	-	1	2	-	-	-	-	-
<i>Orites diversifolia</i>	-	-	1	-	1	-	1	-	1	-	-	1	-	1	-	-
<i>Tetracarpaea tasmanica</i>	-	-	1	-	-	-	-	1	1	-	-	1	1	1	-	-
<i>Lycopodium spp</i>	-	-	1	-	-	-	-	1	1	-	-	1	1	1	-	-
<i>Archeria hirtella</i>	-	-	-	1	-	-	-	1	1	-	2	-	2	2	-	-
<i>Astelia alpina</i>	-	-	-	-	1	-	1	-	1	-	2	2	3	2	1	-
<i>Nothofagus gunnii</i>	-	-	-	-	-	3	-	3	3	3	2	-	3	1	3	-
<i>Richea scoparia</i>	-	-	-	-	-	-	1	-	-	-	2	2	2	2	1	-
<i>Richea milliganii</i>	-	-	-	-	-	-	1	-	1	-	-	-	-	2	-	-
<i>Olearia alpina</i>	-	-	-	-	-	-	-	1	-	2	-	-	1	1	-	-
<i>Agastachys odorata</i>	-	-	-	-	-	-	-	1	-	2	1	-	-	1	-	-
<i>Cenarrhenes nitida</i>	-	-	-	-	-	-	-	1	-	1	2	-	-	1	-	-
<i>Monotoca submutica</i>	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
<i>Aristotelia peduncularis</i>	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
<i>Telopea truncata</i>	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
<i>Eucryphia lucida</i>	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Persoonia gunnii</i>	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-
<i>Diselma archeri</i>	-	-	-	-	-	-	-	-	-	-	2	-	2	-	-	-
<i>Uncinia compacta</i>	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-
<i>Milligania densifolia</i>	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
<i>Orites revoluta</i>	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
<i>Olearia pinifolia</i>	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-

APPENDIX B.

TWINSPAN CLASSIFICATION OF THE 57 SAMPLE STANDS x 114
SPECIES.

Species list.

No Species

- 1 *Richea scoparia*
- 2 *Richea gunnii*
- 3 *Richea sprengelioides*
- 4 *Orites acicularis*
- 5 *Orites revoluta*
- 6 *Olearia ledifolia*
- 7 *Olearia phlogopappa*
- 8 *Cyathodes pavifolia*
- 9 *Cyathodes straminea*
- 10 *Leptospermum rupestre*
- 11 *Coprosma nitida*
- 12 *Boronia citriodora*
- 13 *Helichrysum backhousii*
- 14 *Drimys lanceolata*
- 15 *Phyllocladus aspleniifolius*
- 16 *Trochocarpa thymifolia*
- 17 *Epilobium* spp
- 18 *Poa* spp
- 19 *Lycopodium* spp
- 20 *Nothofagus cunninghamii*
- 21 *Bellendenia montana*
- 22 *Epacris serpyllifolia*
- 23 *Baeckia gunniana*
- 24 *Sphagnum* spp
- 25 *Astelia alpina*
- 26 *Gleichenia dicarpa*
- 27 *Asperula pusilla*
- 28 *Hierochloa redolens*

- 29 *Restio australis*
- 30 *Empodisma minus*
- 31 *Acaena novae-zelandiae*
- 32 *Polystichum proliferum*
- 33 *Diselma archeri*
- 34 *Microcachrys tetragona*
- 35 *Podocarpus lawrencii*
- 36 *Blechnum pennamarina*
- 37 *Luzula* spp
- 38 *Lissanthe montana*
- 39 *Pentachondra pumila*
- 40 *Richea acerosa*
- 41 *Helichrysum hookeri*
- 42 *Oreobolus pumilo*
- 43 *Senecio gunnii*
- 44 *Olearia pinifolia*
- 45 *Eucalyptus coccifera*
- 46 *Exocarpos humifusus*
- 47 *Atherosperma moschatum*
- 48 *Bauera rubioides*
- 49 *Richea pandanifolia*
- 50 *Leptospermum lanigerum*
- 51 *Pultenaea subumbellata*
- 52 *Acaena montana*
- 53 *Monotoca submutica*
- 54 *Abrotanella fosterioides*
- 55 *Richea dracophylla*
- 56 *Cenarrhenes nitida*
- 57 *Nothofagus gunnii*
- 58 *Eucalyptus subcrenulata*
- 59 *Telopea truncata*
- 60 *Trochocarpa cunninghamii*
- 61 *Tetracarpaea tasmanica*
- 62 *Microstrobos niphophilus*

- 63 *Cyathodes petiolaris*
- 64 *Oreobolus acutifolius*
- 65 *Actinotus suffocata*
- 66 *Ewartia meridithiae*
- 67 *Juncus* spp
- 68 *Blechnum wattsii*
- 69 *Uncinia compacta*
- 70 *Orites diversifolia*
- 71 *Microlaena tasmanica* var. *subalpina*
- 72 *Carex* spp
- 73 *Euphrasia* spp
- 74 *Celmisia saxifraga*
- 75 *Boronia rhomboidea*
- 76 *Geranium potentilloides*
- 77 *Cyathodes juniperina*
- 78 *Anopterus glandulosus*
- 79 *Isophysis tasmanica*
- 80 *Eucryphia milliganii*
- 81 *Cyathodes dealbata*
- 82 *Trochocarpa gunnii*
- 83 *Archeria eriocarpa*
- 84 *Archeria hirtella*
- 85 *Prionotes cerinthoides*
- 86 *Olearia persoonioides*
- 87 *Olearia alpina*
- 88 *Gleichenia alpina*
- 89 *Richea milliganii*
- 90 *Agastachys odorata*
- 91 *Stylidium graminifolium*
- 92 *Persoonia gunnii*
- 93 *Gahnia grandis*
- 94 *Pittosporum bicolor*
- 95 *Lomatia polymorpha*
- 96 *Anodopetalum biglandulosum*

- 97 *Uncinia tenella*
- 98 *Leptospermum nitidum*
- 99 *Milligania densifolia*
- 100 *Carpha alpina*
- 101 *Forstera lelidifolia*
- 102 *Gentiana diemensis*
- 103 *Senecio leptocarpus*
- 104 *Eucryphia lucida*
- 105 *Aristotelia peduncularis*
- 106 *Hypolepis rugosula*
- 107 *Helichrysum ledifolium*
- 108 *Gnaphalium umbricola*
- 109 *Lagenophora stipitata*
- 110 *Cardamine* spp
- 111 *Gaultheria hispida*
- 112 *Athrotaxis cupressoides*
- 113 *Athrotaxis selaginoides*
- 114 *Athrotaxis laxifolia*

Stand list

No	Stand	Stand designation
1	Pine Lake 1	(PL1)
2	2	(PL2)
3	Ironstone Mnt 1	(IM1)
4	2	(IM2)
5	Lake Field 1	(LF1)
6	2	(LF2)
7	Dunning Rivulet 1	(DR1)
8	Pine Lake 3	(PL3)
9	4	(PL4)
10	Wild Dog Tier 1	(WDT1)
11	Forgotten Lake	(FL)
12	Cheyne Range 1	(CR1)
13	2	(CR2)

14	3	(CR3)
15 Labyrinth	1	(L1)
16	2	(L2)
17 Tarn Shelf	3	(TS3)
18 Walls of Jeruselem	5	(WJ5)
19 Upper Fish River	1	(UF1)
20	2	(UF2)
21	3	(UF3)
22	4	(UF4)
23	5	(UF5)
24 Wild Dog Tier	2	(WDT2)
25 Walls of Jeruselem	4	(WJ4)
26 Tarn Shelf	1	(TS1)
27	2	(TS2)
28 Mickeys Creek	1	(MC1)
29	2	(MC2)
30 Lake Dobson		(LD)
31 Walls of Jeruselem	1	(WJ1)
32	2	(WJ2)
33	3	(WJ3)
34 Pine Valley	1	(PV1)
35	2	(PV2)
36 Mt Kate	1	(MtK1)
37	2	(MtK2)
38	3	(MtK3)
39 Weindorfs Forest	1	(W1)
40	2	(W2)
41	3	(W3)
42 Mt Bobs	1	(B1)
43	2	(B2)
44	3	(B3)
45	4	(B4)
46 Mt Dundas	1	(D1)
47	2	(D2)

48	3	(D3)
49 Mt Anne 1		(A1)
50	2	(A2)
51	3	(A3)
52 Bradshaws Road 1		(BR1)
53	2	(BR2)
54 Mt Read 1		(MtR1)
55 Mt Anne 4		(A4)
56 Dunning Rivulet 2		(DR2)
57 Mt Read 2		(MtR2)

[illegible]

APPENDIX C.

PRELIMINARY INVESTIGATIONS OF THE RELATIVE DROUGHT
RESISTANCE AND TOLERANCE TO WATERLOGGING OF A.
CUPRESSOIDES AND A. SELAGINOIDES SEEDLINGS.

Drought resistance.

Two trials were performed to investigate the relative resistance of A. cupressoides and A. selaginoides seedlings to drought stress. Seedlings were collected and raised in the same manner as for the frost resistance trials (see Chapter 4).

Trial 1.

Batches of 20 A. cupressoides and 20 A. selaginoides potted seedlings were subjected to drought periods (no watering) of 4, 6, and 7 weeks.

A further 20 seedlings of each species were reserved as controls and watered regularly. All 160 seedlings were randomised in 1 large block in a glasshouse.

At the end of each drought period the respective batches of seedlings were rewatered and monitored for recovery.

The results of the treatments are recorded in Table 1. There is no significant difference in the survival rates of A. cupressoides and A. selaginoides seedlings for any of the drought periods (Chi² test for 2x4 contingency table)).

Seedling survival				
Drought duration	4 weeks	6 weeks	7 weeks	Control
<u>A. cupressoides</u>	20	14	8	20
<u>A. selaginoides</u>	20	16	8	20

Table 1.

The survival of A. cupressoides and A. selaginoides seedlings following periods of drought.

Trial 2.

Twenty one A. cupressoides and twenty two A. selaginoides potted seedlings were watered to field capacity at 8.00 am and left for 3 hours. They were then removed from the pots, all of the soil was carefully washed from their roots, and the seedlings were then placed in a tub of water. After being patted dry with absorbent paper, each seedling was weighed and placed on the bench in the laboratory at c 20°C. To determine moisture loss, the seedlings were reweighed at 2 hourly intervals for the next 10 hours and once again after 23 hours. The seedlings were then placed in an oven at 105°C and dried for 24 hours. The roots and shoots were separated and the root/shoot ratio for each seedling was calculated.

The results of this trial suggest that there is no difference in the rate of water loss of either species. Although there is a significant difference in the percentage weight loss at 10 and 23 hours (Fig. 1), the seedlings had suffered over 60 % weight loss at this stage and were probably well beyond a point of recovery. There is no significant difference in the root/shoot ratios of the two species (Students 't' test, Tab. 2), suggesting that neither species has a superior capacity to survive drought by exploiting larger volumes of soil.

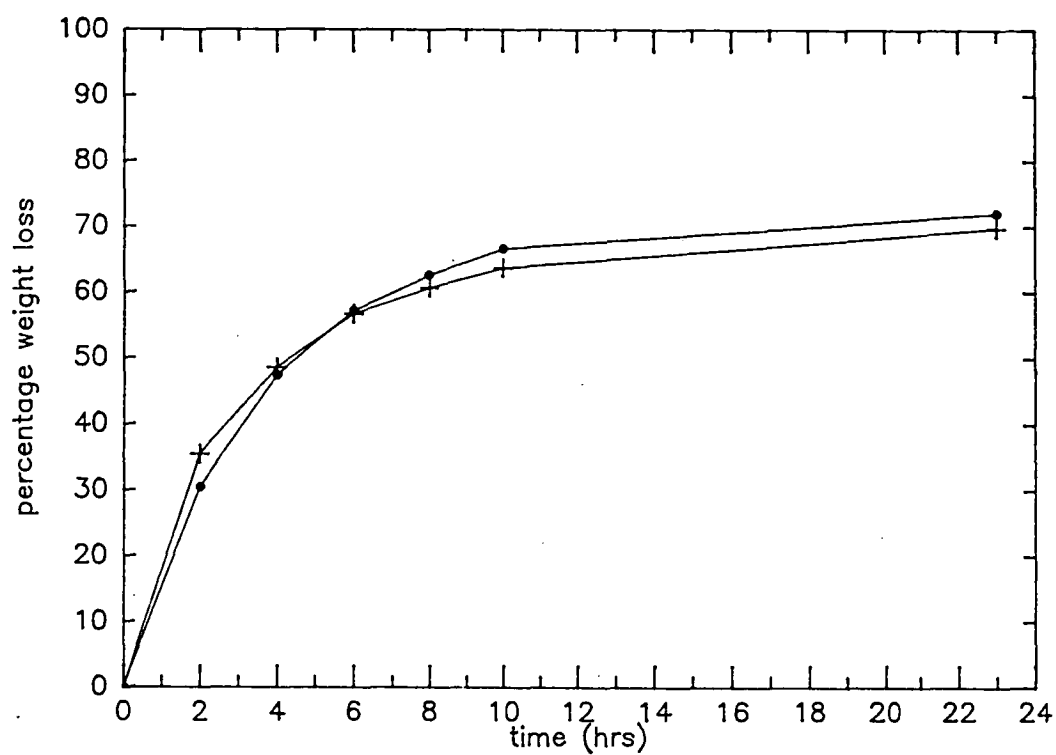


Figure 1.

Rate of moisture loss of A. cupressoides and A. selaginoides seedlings.

Root/Shoot ratios	
<u>A. cupressoides</u>	<u>A. selaginoides</u>
N=21	N=22
Mean = 0.5144	Mean = 0.4976
SD = 0.0902	SD = 0.1364

No significant difference (Student's t test)

Table 2.

Root/Shoot ratios for 21 A. cupressoides and 22 A. selaginoides seedlings.

Waterlogging resistance.

Twenty seedlings of A. cupressoides and A. selaginoides were placed in tubs which were filled with water so as to create waterlogging to the surface of the soil. A further 20 seedlings of each species were used as controls. All of the seedlings were randomized on a bench in the glasshouse. The condition of the seedlings was observed during the next 8 weeks. At this stage all of the waterlogged seedlings were severely discoloured. They were then removed from the tubs and allowed to drain. Rewatering of the water logged seedlings proceeded at the same rate as the controls. After 3 weeks all of the seedlings had recovered to a normal healthy state. There was no difference in the response of the two species.