

***Phyllocladus aspleniifolius* (Labill.) Hook. f.
and *Anodopetalum biglandulosum* (A. Cunn.) ex Endl.:
a comparative autecology of coexisting wet forest trees in
Tasmania.**

By

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Declaration

This thesis contains no material that has been accepted for the award of any other degree or diploma, nor any material previously published or written by another person except when due reference is made.

A handwritten signature in black ink, appearing to be 'EBL' or similar, written in a cursive style.

Abstract

This thesis describes and compares the autecology of two coexisting wet forest trees. It demonstrates temporal, spatial and biological differentiation of the reproduction, regeneration and growth characteristics which allow these taxa to coexist in superficially similar environments.

The distributions of the species and the environmental correlates of the communities in which they exist are compared and contrasted. The climatic range of *P. aspleniifolius* is greater than *A. biglandulosum* but this may be attributed to the greater vagility of *P. aspleniifolius* allowing it to occupy areas that are climatically susceptible to repeated disturbance by fire. It is determined that both are most important in poorly structured and diverse rainforest communities which are often associated with low fertility substrates. The physiological basis for this correlation was tested experimentally and by field measurements. *A. biglandulosum* performed best under acid conditions while *P. aspleniifolius* was relatively insensitive to fertility. These responses are manifest in the absence of both species from the most fertile sites which support floristically simple tall *Nothofagus cunninghamii* dominated forests. The preference of *A. biglandulosum* for acid sites and the insensitivity of *P. aspleniifolius* allow these species to take advantage of the decline in the performance of the important canopy dominant, *Nothofagus cunninghamii*, and hence increase their abundance on such sites. Other than possible exclusion from pure *Nothofagus cunninghamii* forest their geographic range and phytosociological associations are not limited by edaphic conditions. Field performance of both *A. biglandulosum* and *P. aspleniifolius* does, however, reflect the physiological growth response measured under experimental conditions.

The photosynthetic responses of *A. biglandulosum* and *P. aspleniifolius* were investigated in the contrasting micro-environments of the canopy, a gap and the understorey of a rainforest in Tasmania. Measurements were made using a portable infra-red gas analyser. Both species displayed the highest light saturation levels at the canopy but both produced the highest rates of photosynthesis in the gap environment. Diffuse light on cloudy days was important in the understorey environment. The rate of photosynthesis was affected considerably by low levels of stomatal conductance two days after rain. The results indicate that both species are "sun" plants and that their dependance upon high levels of light to maintain competitive growth rates would influence their regeneration opportunities and may induce competition for sites.

The phenological and demographic strategies of both species were compared. The timing of foliar and sexual development of *Phyllocladus aspleniifolius* and *Anodopetalum biglandulosum* were recorded at Mt Field in Tasmania. Seed production, seed predation, germination and survival were monitored in different regions of Tasmania. The wind dispersed *A. biglandulosum* suffered an extremely high level of fruit predation by a moth and by birds. The resultant low seed production is reflected in the poor seed regeneration in this species.

The timing of pollen release and female cone development in *P. aspleniifolius* indicates that outcrossing between populations is likely. Outcrossing may provide the species with a high degree of genetic fitness but may not necessarily explain its wide ecological amplitude as this situation contrasts with the poorly dispersed and possibly genetically limited *A. biglandulosum* which also has a broad ecological range. *P. aspleniifolius* produced spatially variable amounts of seed and is a mast seeder. The number of germinants two springs after seed fall reflected the variation in annual seed production and suggests that pulses in regeneration are likely although soil-stored seed and immigrant seed may offset this effect.

The consequences of the phenological differentiation on regeneration opportunities was explored. The contrasting strategies required different approaches, as *A. biglandulosum* depends largely upon vegetative regeneration and proliferation while *P. aspleniifolius* is an obligate seed regenerator.

A growth-form/disturbance typology of *A. biglandulosum* based on data from 48 sites was produced. A multivariate data set from each site summarizes a stands' growth-form as stem types, densities and diameters. A canonical correlation indicates a significant relationship between the growth-form data set and community floristics. The basic architecture associated with a particular forest is modified by proliferation in response to exogenic disturbances, such as fire and heavy snow-falls, or as a result of community processes such as crown senescence and tree-fall.

This study aimed to determine the range of the *P. aspleniifolius* regeneration niche in terms of differential microsite occupation, population structure and dispersion pattern at 52 forest sites. The distribution and sizes of stems were mapped on belt transects to within 0.5 m, and the microsites of seedlings and saplings were recorded. A variety of population structures exist and are related to community floristics and structure. Community variation provides different microsite opportunities. *P. aspleniifolius* showed a preference for elevated sites, including logs, buttresses and old stump mounds. Aggregation of seedlings is common and determined by microsite distribution and dispersal characteristics.

It is concluded that niche differentiation between *P. aspleniifolius* and *A. biglandulosum* is demonstrated in edaphic responses and reproductive biology, and niche overlap is evident in their use of the light environment. Although their coexistence is theoretically dependent upon niche differentiation, stochastic events producing opportunities for regeneration appear to be more important and therefore the results conform with the theory of non-equilibrium coexistence of species. The broad and common phytosociological associations may reflect Tertiary species extinctions which have produced an environment of low competition with few specialists. The extant species experience niche broadening via more opportunities for regeneration and hence greater levels of coexistence which are expressed as low beta diversity in Tasmanian wet forests.

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Chapter 1. Introduction

A basic aim in plant ecology is to explain the spatial and temporal patterns of species. To achieve this aim, interactions that occur between a taxon and its environment need to be explored. The first level of interaction is between the plant and its physiochemical environment. Plant species must acquire adequate amounts of water, carbon dioxide, mineral nutrition and light if they are to survive and reproduce. Thus, with freedom from competition for resources, the geographical range of plant species is delimited by their physiological tolerance of the availability of resources along gradients (Whittaker 1975, Austin 1985). This notion represents the basic premise of the fundamental niche (Hutchinson 1958). Biotic interactions provide further limits. Perhaps the most important of these interactions are competition and predation (Gause 1934, Grime 1977, Janzen 1971). The final result of physiochemical tolerances and biotic interaction is a limited range, defined as the realized niche (Hutchinson 1958, Connell 1978).

The realized niche is an expression of the fitness of a species to persist in the environment. It is measured in a relative sense by the abundance and vigour of the the species within a community. The extent of the realized niche, and hence, a species' distribution, is not constant but rather fluctuates in space and time as a result of endogenous and exogenous forces at many scales (Hutchinson 1961, Levins 1979, Whittaker and Goodman 1979).

The identification of factors governing species richness in plant communities has also been a major theme of plant ecology. This requires an understanding of the circumstances under which species coexist. If species are to coexist they must avoid competitive exclusion (Gause 1934). Classical ecological theories argue that coexistence requires differentiation of the trophic niche, i.e. differences in habitat and resource utilisation (Hardin 1960, Hutchinson 1958, Macarthur 1972, Whittaker 1975). While most work on this topic involves the consideration of competition between closely related species, it is also relevant to the coexistence of unrelated plants in communities (Grubb 1977a, Grime 1979)

The relationship between species coexistence and a heterogeneous environment has led some ecologists to develop the theory of non-equilibrium coexistence of plants (Hutchinson 1961, Levins 1979, Pickett 1980). This notion refers to disruption in the attainment of a competitive equilibrium, thus, preventing competitive exclusion of poorer competitors.

An important example of coexistence is the association between gymnosperms and the more recently evolved angiosperms. In Tasmania, *Phyllocladus aspleniifolius* (Labill.) Hook. f. (Podocarpaceae) and *Anodopetalum biglandulosum* A. Cunn. ex Endl. (Cunoniaceae) provide an ideal opportunity to compare and contrast the life strategies of coexisting members of these two groups. These species co-occur in many communities in Tasmanian wet forests but also occur separately in others (Kirkpatrick *et al.* 1988, Jarman *et al.* 1991). *P. aspleniifolius* and *A. biglandulosum* exhibit apparent dissimilarities in almost every facet of growth and reproduction. This dichotomy provides a focus for the comparison of growth characteristics and life history strategies and allows the consideration of the consequences of these differences on their spatial and temporal patterns of coexistence.

1.1 Coexistence in plant communities

1.1.1 Resource utilisation

Coexisting plants often differ enormously in their resource niches (Harper 1977, Tilman 1982). These differences are important in maintaining species richness. Differences in the ability to metabolise nutrients have provided the basis for the ecological theories of Grime (1979) and Tilman (1982). Both authors identify competitiveness as the key to site dominance and argue that it is the efficient use of resources that provides a species with a competitive advantage. Tilman (1982) argues that competitiveness reflects tolerance of low resource levels, and with the species with the lowest resource needs will displace others. Grime (1979), however, describes competitive species as those with the maximum capacity for resource capture, and argues that plants with the highest maximum relative growth rates will eventually express dominance by excluding inferior competitors from the site. Both authors, consider that the whole life cycle and hence interaction between populations is important to the outcome of competition. Hence, both concepts are relevant to community structure.

A high relative growth rate is the result of enhanced metabolic and physiological processes, such as the translocation of abundant nitrogen to the leaves which promotes higher photosynthetic productivity (Givnish 1988). Grime (1979) indicates a trade off exists between tolerance of low resource supplies and the ability to grow rapidly and to exploit resources. The trade off, and its attendant physiological constraints, results in a division between competitive "resource exploiters" and less competitive "stress tolerators".

Grime suggests that competitive exclusion would be very slow in extreme environments due to reduced growth rates and reproductive success impeding the expression of dominance. Effectively, the "slow dynamics of competitive exclusion" (Shmida and Ellner 1984) tends to influence the length of time that poor competitors can coexist in the presence of superior competitors. In essence, infertile substrates can be temporary refuges from competition. Factors which may promote coexistence by slow exclusion include vacant microsites, wide dispersion of microsites with low dispersal of competitors' seed and the longevity of adult plants.

The maintenance of some populations on low nutrient, or otherwise "stressful" sites, may depend upon mass effects, i.e. the input of seeds from neighbouring habitats, which can maintain otherwise non-viable populations (Shmida and Whittaker 1981). Slow enrichment of resources or removal of stresses is argued to result in community simplification (Shmida and Ellner 1984).

Grime (1977) expanded the r-K selection concept of life strategy to include evolutionary responses to extremes in resource availability ("stress"), competition and disturbance. Particular plant strategies are attributed to taxa dependent upon the relative importance of each factor in the environment and their ecological response. Grime (1977) attributed syndromes of morphology, growth form, reproductive characteristics and physiological tolerances to each strategy. He recognised the ruderal strategy in addition to the competitive and stress tolerant strategies.

Harper (1982) also recognised that differences in resource requirements are expressed not only as the rates of physiological processes, but also in the form and function of the plant parts that are responsible for resource capture. The relationship between the habitat and many physiological processes and attributes of growth underlines the ecological significance of efficient resource exploitation in the expression of competitiveness and site dominance *sensu* Grime (1979) and Tilman (1982).

1.1.2 Coexistence and the regeneration niche

In consideration of all factors thought likely to affect coexistence, a limitation of the competition theories, and competitor characteristics of Grime (1979) and Tilman (1982), is the failure to distinguish between adaptation to resource levels and adaptation to nonresource conditions. Grubb (1977) considers that differential use of resources is unlikely to be important for coexistence since all plants share the same basic needs of carbon dioxide, light, water and nutrients. Grubb (1977) summarizes a plant's niche as being made up of four components; the habitat niche, the life form

niche, the phenological niche, and the regeneration niche. By expanding the classical framework Grubb focused attention on the role of the regeneration niche. Important factors in the regeneration niche include the structure of surrounding vegetation (Watt 1947, Grubb 1977), host specific predation (Janzen 1971) and microhabitat requirements of seedlings (Grubb 1977, Harper 1977).

Differentiation in the regeneration niche allows poor competitors to establish episodically when the dominance of the competitive species is disrupted by disturbance (Pickett 1980). Disturbance at many scales has been recognised as producing a mosaic of patches at different successional stages (Whittaker and Levin 1977), and the subsequent development of ideas related to patch dynamics have become fundamental to habitat-niche differentiation and the "non-equilibrium" coexistence of plants with different competitive abilities (Levin 1979, Caswell 1982, Pickett 1980, Pickett and White 1985). The patches correspond to the patterns of past disturbances, colonisation, heterogeneity in the environment and interspecific interactions (Thompson 1985, Pickett 1982). For a species to persist, opportunities for regeneration must recur within its life span. Perhaps more importantly, viable propagules must be present at the time the opportunity arises.

Patterns of production and dispersal of propagules vary widely among woody plants (Canham and Marks 1985); they also vary widely in space and in time (Silvertown 1980, Givnish 1980, Norton 1988). Various attributes of seeds, including their size and abundance, dispersal mechanism and germination characteristics differentiate the responses of species to the environment (Canham and Marks 1985).

Although differences between the life history strategies of taxa are likely to promote coexistence by separating opportunities for regeneration, they may also pit alternative strategies against one another, resulting in different levels of success. Interplays between seasonality, pollination mechanisms, sex distribution, dispersal characteristics, fecundity, fruit predation and population structure have been correlated with one another, with the environment and with geographic distribution (Givnish 1980, Waller 1979). The success of different strategies has been discussed in relation to evolutionary fitness (Givnish 1980) and the adaptive significance for coexistence in communities (Darwin 1877, Schaffer 1974).

Two trophically similar species, one a disperser with high fecundity (space claimer) and the other a competitor with high survivorship (space holder), can coexist when a supply of refuge sites exist where the disperser can establish and grow for some time without competition from the other species (Levin 1976, Shmida and Ellner 1984).

Non-uniform seed dispersal is necessary for this condition to persist and this may lead to clumped distributions which reduce interspecific competition to levels where stable coexistence is possible.

How a regeneration strategy is manifest as the demographic and spatial arrangement of the population depends upon the suitability and distribution of microsites for germination and establishment (Whittaker 1975, Grubb 1977, Whittaker and Levin 1977, Harper 1977, Ogden 1985, Horn 1981, Pickett 1980, Christy and Mack 1984, Collins and Good 1987, Clayton Greene 1977, Harman and Franklin 1989) and the affect of the pattern of one species on the regeneration of another (Veblen 1982). The variability in early reproductive strategies is important to coexistence because it provides a probabilistic basis for different responses to stochastic events by providing differential access and abundance at all scales (Pickett 1980).

A population's dispersion and microsite association is important because, if ignored, it may mask controls on demographic distribution (Ogden 1985) including differences in size, availability and survival rate between one microsite and another. Demographic characteristics of long-lived species are not necessarily stable but rather may reflect the temporal patterns of past disturbance (Hett and Loucks 1976, Ogden 1985).

Demographic strategies have been recognized as adaptations to different environments as experienced by different species (MacArthur and Wilson 1967). Whittaker and Goodman (1979), however, argue that different species may experience the same environment, and fluctuations in it, differently. Hutchinson (1961) recognised this phenomenon and suggested that environmental fluctuations may constantly reverse the direction of competitive exclusion, allowing species to recover before being completely excluded. For this to occur, one species must have the advantage in some years, perhaps in seed production or suitable environment for seedling germination and survival. Whittaker and Goodman (1979) explain that demographic strategies are not confined to particular life forms, nor to particular environments. In fact, a community is a mixture of adaptive types that survive the same environment (Whittaker and Goodman 1979).

The demographic strategies of Whittaker and Goodman (1979) embody the concept of a fluctuating environment. Most important in a fluctuating environment is the need to buffer populations against periods unfavourable for regeneration. Whittaker and Goodman (1979) argue that each strategy will have associated specific biological characteristics. The strategies represent alternative means of dealing with the

pressure of competitive interactions and temporal and spatial variability in the environment. Ultimately, a wide range of demographies may evolve within a community as an expression of niche differentiation in what is superficially a common environment (Whittaker 1975).

1.2 The biology and ecology of *P. aspleniifolius* and *A. biglandulosum*.

Phyllocladus aspleniifolius is a gymnosperm. It is variable in height, ranging from only one or two metres on harsh subalpine sites to greater than 25 m on fertile, lowland sites. *P. aspleniifolius* is most prominent on poor soils and attains its best development in situations where the vigour of *Nothofagus cunninghamii* is reduced (Read and Hill 1988). It may live for more than 1 000 years (Ogden 1978) and can be a dominant or subdominant species.

The species is typically dioecious and rarely monoecious, it is wind pollinated and has irregular mast seeding years (Read 1989). *P. aspleniifolius* is sometimes animal dispersed (Calais and Kirkpatrick 1983, Tomlinson *et al.* 1989), it is sensitive to fire and regenerates from seed. Read (1989) indicated that soil storage of seed may be an important factor in regeneration after fire. Read and Hill (1988) found *P. aspleniifolius* regenerating only occasionally in gaps and suggested that regeneration after catastrophic disturbance was the norm:

Anodopetalum biglandulosum is an angiosperm with a relatively short lifespan, compared to *P. aspleniifolius*, although it can persist for greater than 200 years. It is often a component of the subcanopy but sometimes reaches the dominant canopy at a height of up to 20 m. It bears bisexual flowers, its seeds are wind dispersed, and regenerates predominantly by vegetative means, including resprouting after fire (Barker 1991), but also regenerates from seed.

Other than this scant biological data no research on *A. biglandulosum* has been published and there is a general lack of knowledge on any aspects of the life history of the the Cunoniaceae generally. In Australia there is little information on the relationships between members of the Cunoniaceae and the environment. Celman (1987), however, indicates that they are often restricted to poorer soils, and Boland *et al.* (1984) describes an association between the Cunoniaceae and riparian environments.

Wardle (1966) and Stewart and Veblen (1982) studied New Zealand's *Weinmannia racemosa* (Cunoniaceae) which is an important component of forests over extensive

areas of New Zealand. Stewart and Veblen (1982) concluded that seed production is highly variable from year to year, although Wardle (1966) indicated that flowering is prolific every year, and that no particular trigger is required for germination which may occur immediately after seed fall in autumn. Vegetative regeneration is extensive after catastrophic disturbance, resulting in relatively even aged stands. In the absence of catastrophic disturbance regeneration appears to be continuous, with microsite preferences and gap-phase replacement evident.

The habitat in which *P. aspleniifolius* and *A. biglandulosum* both assume their greatest importance is similar. In some cases, the habitat supports a community in which *P. aspleniifolius* assumes single species dominance over a similarly depauperate understorey in which *A. biglandulosum* is dominant.

1.3 Thesis aims and structure

Although two plant species will differ in some aspects of their habitat niche, their life form niche, their phenological niche or their regeneration niche, the problem is to determine which of these differences enable coexistence. One way of studying this is to consider the combination of vital attributes *sensu* Noble and Slatyer (1979), demography, physiological processes, and probabilistic responses to the environment, which collectively make up what has often been referred to as a "strategy" (Ghiselin 1974, Grime 1977, Whittaker and Goodman 1979, see also Harper 1982). The "strategic" framework seems a useful way of comparing and contrasting species since it includes the whole life cycle and its relationship to environmental variability. The inclusion here of process, response and stochasm, will hopefully overcome the ambiguity often involved in ecological discussion by such often unexplained terms as adaptation and stress, which do not always elucidate causation.

This thesis addresses the following questions:

- 1) What are the geographical, phytosociological and environmental ranges of *P. aspleniifolius* and *A. biglandulosum*.
- 2) Do the phytosociological and edaphic correlates of *P. aspleniifolius* and *A. biglandulosum* reflect their physiological responses to soil nutrition? Do the responses infer trophic equivalence or divergence, and what are the implications for coexistence?

- 3) Do the photosynthetic performances of *P. aspleniifolius* and *A. biglandulosum* indicate stratification in the use of the light resource? What are the ramifications for regeneration opportunities?
- 4) What are the phenological characteristics of *P. aspleniifolius* and *A. biglandulosum* and how do these characteristics influence spatial and temporal interactions in the regeneration niche?
- 5) How are the demographic strategies of *P. aspleniifolius* and *A. biglandulosum* manifest in response to exogenous and endogenous disturbances in different communities, and do they promote coexistence or induce competition?

The next chapter will set the physical and historical biogeographic scene for Tasmania. The aim of the chapter is to provide insight into the effects of these broadly influential characteristics in the context of this study.

The third chapter will compare and contrast the distributions and phytosociological associations of *P. aspleniifolius* and *A. biglandulosum*. Environmental correlations between the species' distributions and the communities in which they occur together and alone will be explored.

In the fourth chapter the growth responses of each species to an applied nutrient regime will be compared to the ecological responses. This will be a comparison of their fundamental and their realized niches in an attempt to discern the influence of soil fertility on their coexistence. Several other attributes relevant to species substrate interactions will also be considered.

The fifth chapter of this thesis will consider the comparative photosynthetic responses of *P. aspleniifolius* and *A. biglandulosum* in the sun canopy, a gap and in the understorey. The comparisons are made throughout consecutive days in summer and in winter to elucidate the effect of diurnal and seasonal variation. The aim is to determine their relative responses to variation in light quality and diurnal conditions.

The second half of the thesis will consider the demographic strategies of *P. aspleniifolius* and *A. biglandulosum*. Chapter six deals with early phenological characteristics including pollination, seed production and predation, dispersal and germination in the field.

Following the phenological study the thesis will continue to investigate differentiation in the regeneration niche. In light of differences in the physiological and phenological niches the seventh and eighth chapters will deal with the demographic strategies of *A. biglandulosum* and *P. asplenifolius* separately.

The final chapter (chapter 9) is a general discussion. It draws together evidence from all of the research chapters and presents arguments that accommodate the spatial and temporal patterns of coexistence at all scales. Hence, it will consider broad influences on coexistence, such as on the distribution and environmental correlates of the species and communities in which they occur. Finally, it will discuss the community processes and autecological attributes that promote coexistence or induce competition between *P. asplenifolius* and *A. biglandulosum*.

Chapter 2. Physical and historical setting

2.1 Environment

Tasmania is an island of Gondwanic origin. It is situated on the Australian continental plate between 41°S and 43.5°S some 300 km off-shore and south of mainland Australia. It has a maritime cool to cold perhumid climate (Gentilli 1972). The range of mean annual temperatures across the island is 2.7°C to 13.6°C (Figures 2.1, 2.2). The coldest average minimum temperature recorded for the coldest month is -5°C and the highest average maximum temperature for the hottest month is 24.4°C.

Rainfall is predominantly delivered by the prevailing westerly wind system. Occasional heavy falls in the east are associated with low pressure systems located off the east coast. The mean annual rainfall declines along a gradient from west to east and from high to low altitudes (Figure 2.3). The wettest region in the west receives 3 600 mm of precipitation annually, and the driest, in an eastern rainshadow, receives 460 mm annually.

The topography of western Tasmania consists of rugged low ranges often separated by glacially cut valleys. A large plateau dominates the center of the island at about 1 000 m elevation. The drier east is characterised by broad valleys and low undulating hills. The north-east highlands are an exception and rise to 1 500 m. Snowfalls in winter are common in the west and center of the island and the north-east highlands with the higher peaks (1 300 - 1 600 m) holding snow for a few months.

The vegetation reflects the rainfall gradient and the distribution of geology. Rainforest and moorland is predominant in the west, giving way to a band of wet eucalypt forest before grading into dry sclerophyll vegetation in the east. The north-east highlands also support rainforest and wet eucalypt forests. Numerous mountain peaks support islands of alpine vegetation above 1 000 m (Kirkpatrick and Dickinson 1984).

A complex geology in the west supports a mosaic of vegetation. Highly siliceous parent materials are extensive and give rise to infertile organic soils which support sclerophyll heaths and moorlands but also relatively diverse rainforests. Soils derived from dolerite and basalt are also present in the west and support a range of rainforest and wet eucalypt forest types distributed in response to indirect topographic effects and their control on the distribution of fires (Jackson 1968).

Similar rainfall gradients, declining from west to east, occur in New Zealand and southern South-America. In the drier eastern landscapes, human set fires, have been implicated in the demise of some forests, including rainforests in all three areas (Ellis 1985, Molloy 1966, Thomasson 1959).

2.2 Historic biogeography

An important factor in the explanation of species coexistence is the biogeographic history of the biome in which they occur. The evolution of biogeographic and ecological relationships between angiosperms and gymnosperms provides a useful foundation for investigation and interpretation of theories of coexistence. In particular, the biogeographic history of Tasmanian wet forests will be important for any explanation of the broad range of communities and habitats in which *P. aspleniifolius* and *A. biglandulosum* coexist.

Throughout the world, the number of genera and species of gymnosperms is far less than that of angiosperms (Regal 1979). Gymnosperms are, however, commonly represented by the largest number of individuals in forests in many regions of the world. This is particularly evident in the forests of high latitudes in the northern hemisphere. There is evidence to suggest that gymnosperms were once more widespread (Florin 1963) and that they have contracted under pressure of competition with angiosperms (Regal 1979, Bond 1989).

Many Australian gymnosperms, including *Araucaria*, *Athrotaxis*, *Lagarostrobos*, *Phyllocladus* and *Podocarpus*, were more widespread in the early Tertiary and Pleistocene (Page and Clifford 1981, Singh *et al.* 1985) as was *Nothofagus* dominated forest. Hill and Read (1986) suggest that the fluctuating and drying climate of the later Tertiary period reduced the geographic range and diversity of the cool temperate wet forest species. Furthermore, it has been suggested that for conifers, genetic senescence has prevented speciation into new ecological niches (Scagel *et al.* 1968). Schmithusen (1960) argues that one consequence of the relictual status of conifers in the southern Andes is that they have been unable to compete successfully with the faster growing angiosperms on high quality sites and so are now confined to inferior sites, represented by low fertility or excessively cold, dry or wet conditions.

The situation in the northern hemisphere is different. Gymnosperms now dominate in the fire-prone forests, a situation attributed to their possession of serotinous cones which protect the seed during fire. Such cones evolved in the northern fire-prone environments before the competitively superior angiosperms evolved. The angiosperms were already present when the southern continents became drier and more fire-prone and rapidly evolved into this niche (Regal 1979). Many of the surviving gymnosperms of southern origin, particularly in wet forests, possess the alternative strategy of high vagility. The seeds survive fire on remote parents and disperse back to a suitable regeneration niche.

McGlone (1985) suggested that, in New Zealand, deforestation during the onset of the last stadial may have occurred over a period as short as 500 years. The reafforestation of these areas was dominated by the bird dispersed podocarps although a slow invasion of these forests by the wind dispersed and potentially dominant angiosperm flora is underway (Rogers 1989).

Macphail (1980) described the reafforestation of Tasmania after the last stadial. His evidence indicated that *P. asplenifolius* was common in forests dominated by *Eucalyptus* spp. across a large proportion of Tasmania. Its high vagility allowed it to lead rainforest species out of glacial refugia. Slowly, other rainforest species migrated across the landscape and *Nothofagus cunninghamii* began to dominate. Macphail (1980) argued that after thousands of years of wet conditions, soil leaching had depleted the fertility and resulted in the opening of the forest canopy. He recorded a coincident increase in diversity in these forests and recognised the arrival of *A. biglandulosum* at this point.

In New Zealand and Tasmania, the bird dispersed Podocarpaceae contribute significantly in terms of number of species to the gymnosperm flora. This may indicate the enhanced chance of survival, and reoccupation of sites, for bird dispersed gymnosperms in rapidly fluctuating environments.

Other than palynological data, evidence for the floristic composition of past communities in Tasmania is scant. However, the immense impact of extinctions since the mid Tertiary, but particularly during and since the Pleistocene, upon the wet forest flora of Tasmania has recently been demonstrated (Hill 1989, Jordan *et al.* 1991, Pole 1992). Past distributions are likely to have revealed greater habitat specificity or apparent specialisation of at least some of the extinct species. Numerous ecologists have alluded to the consequence of these extinctions: they allowed the remaining species to broaden their niches in environments of reduced competition. This is particularly so where

congenerics or other genera of the same family, with similar resource demands, have been removed. Perhaps greater than 12 Podocarpaceae, including two congenics of *P. aspleniifolius*, have become extinct in Tasmania (Pole 1992, Hill 1989) and a smaller number of extinct members of the family Cunoniaceae have also been detected (Pole 1992, Carpenter and Buchannan, in prep). No Tasmanian studies have demonstrated the consequences of niche broadening for the coexistence of the remaining species. Within this expanded realized niche a greater range of demographies and physiological performances may be expected as a result of the expression of a fuller range of ecological attributes which would otherwise be masked by competition.

Chapter 3. Phytosociology and environmental correlates of *Phyllocladus aspleniifolius* (Labill.) Hook. f. and *Anodopetalum biglandulosum* A. Cunn. ex Hook. f.

3.1 Introduction

Phyllocladus aspleniifolius and *Anodopetalum biglandulosum* are cool temperate wet forest species (Jarman *et al.* 1984, Kirkpatrick *et al.* 1988). They grow as trees in rainforest and wet eucalypt forest where they occupy various canopy positions from emergent to sub-dominant. They also occasionally grow as shrubs, particularly in non-forest communities, such as in alpine vegetation and moorland (Jarman *et al.* 1988).

Assemblages of species vary along environmental gradients (Whittaker 1975). Alternatively, habitats may be arranged in ecological sequences differing from one another by a different stage of intensity or else a discontinuum in a major environmental factor (Mueller-Dombois and Ellenberg 1974). Although the performance of a species along such environmental gradients does not necessarily indicate its physiological optimum for growth it does reflect the ecological optimum. An understanding of the phytosociological and environmental relationships of species helps in the refining of ecological hypotheses relevant to coexistence.

The association of gymnosperms and angiosperms has often been considered in the context of evolution and competition (Smithusen 1960, Regal 1979). While many conclusions emphasise the superiority of angiosperm breeding systems it is also noteworthy that gymnosperms often dominate harsher environments such as high altitude, infertile, poorly drained or cold sites. This, however, is not pangeographic, as is evident from the radiation of gymnosperms in the northern hemisphere and the contrasting restriction of species in the southern hemisphere.

The distribution and composition of communities in which *P. aspleniifolius* and *A. biglandulosum* occur have altered considerably during and since the Pleistocene (Macphail 1980). Many taxa that are no longer extant in Tasmania were components of wet forest communities before this time (Hill 1989, Pole 1991, Carpenter and Buchannan in prep.). In an environment of reduced competition many species, including *P. aspleniifolius* and *A. biglandulosum*, may cover greater environmental ranges than previously, due to niche broadening (Hill 1990). This is reflected in the limited numbers of tree species that dominate the wide diversity of rainforest communities. The variation is often structural and influenced by the relative abundance of species (Jarman *et al.* 1991, Kirkpatrick *et al.* 1988).

The aim of this chapter is to describe the communities containing *Phyllocladus aspleniifolius* and/or *Anodopetalum biglandulosum*, and to determine their environmental relationships.

Definition and Classification of Forests containing *P. aspleniifolius* and *A. biglandulosum*

3.2.1 Rainforest.

Australian rainforests have been widely accepted as "closed forests" *sensu* Specht (1970). In recognition of the difficulties the closure criterion placed on the classification of some Tasmanian open canopy vegetation, Jarman and Brown (1983) redefined rainforest using the criteria of floristic composition and regeneration processes. Thus, they defined Tasmanian rainforests as those forest communities which are dominated by trees (> 8m tall) that are able to regenerate in response to small scale community processes such as in the gap phase or else continuously, being shade tolerant. The dominant genera include *Nothofagus*, *Atherosperma*, *Eucryphia*, *Athrotaxis*, *Lagarostrobos*, *Phyllocladus* or *Diselma*, and, in some cases, *Anodopetalum* and *Richea* (Jarman and Brown 1983).

The Tasmanian rainforest has been classified according to floristics by Jarman *et al.* (1984, 1991) into 48 types including 8 intermediate groups. The communities in this classification range from forests of simple floristics and structure dominated by *Nothofagus cunninghamii* and/or *Atherosperma moschatum* (callidendrous) to forests of greater diversity and structural complexity dominated by, for example *P. aspleniifolius* and *A. biglandulosum*, but also *Nothofagus cunninghamii*, *Athrotaxis selaginoides*, *Eucryphia lucida*, *E. milliganii*, *Leptospermum* spp. *Agastachys odorata* and *Richea pandanifolia* (implicate). Between these extremes are forests of intermediate diversity with a characteristic layered structure produced by the presence of shrub species (thamnic). *Phyllocladus* and *Anodopetalum* are most abundant in the thamnic/implicate range of the continuum (Appendix 1).

The three major divisions described above represent sub-alliances of the *Nothofagus cunninghamii* alliance which comprises the bulk of rainforests in Tasmania. A second, far less extensive alliance is the *Athrotaxis cupressoides* alliance which tends to be limited to subalpine environments (Jarman *et al.* 1991).

P. aspleniifolius is characteristic of and predominant in seven of the 19 thamnic communities and five of the nine implicate communities. *A. biglandulosum* is characteristic of, and predominant in 5 thamnic and 3 implicate communities. *P. aspleniifolius* dominates two communities intermediate between thamnic and callidendrous and *A. biglandulosum* is subdominant in one other. Both species are often present in many of the communities for which they are not listed as characteristic.

3.2.1 Wet eucalypt forests

Some of the vegetation types included in the present study are not covered by the rainforest definition, for example, where *P. aspleniifolius* and/or *A. biglandulosum* are in association with dominant sclerophyll species described by Jarman and Brown (1983) as doubtful rainforest species. Many of these communities are defined as wet eucalypt forests (Kirkpatrick *et al.* 1988). This definition includes forests in which at least one of the subordinate strata is dominated by rainforest species, *sensu* Jarman and Brown (1983) and known as mixed forest (Gilbert 1959), or broad-leaved shrubs, or ferns (Kirkpatrick *et al.* 1988).

The wet eucalypt forests have been classified by Kirkpatrick *et al.* (1988). Sixty four communities were described, each being dominated by one of 14 *Eucalyptus* spp.. Twenty three communities contain *P. aspleniifolius* and five of those support *A. biglandulosum*. Only one wet eucalypt forest type supports *A. biglandulosum* without *P. aspleniifolius* (Appendix 1).

The distributions of rainforest and wet eucalypt forest in Tasmania are illustrated in Figure 3.1. The distributions of *Anodopetalum* and *Phyllocladus* are illustrated in Figure 3.2.

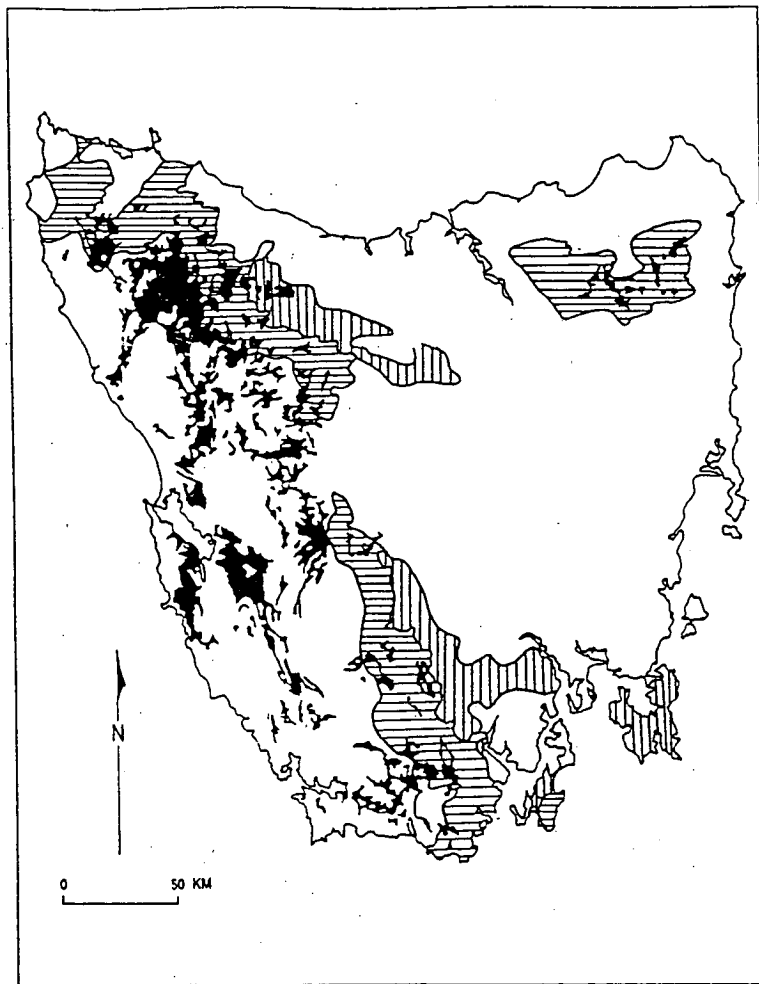


Figure 3.1. The distribution of rainforest and wet eucalypt forest in Tasmania. (After Kirkpatrick and Dickinson 1984 and Kirkpatrick *et al.* 1988). Key: Rainforest ■, Tall eucalypt forest (30-70% cover) over medium trees —; Tall eucalypt forest (30-70% cover) over low trees |.

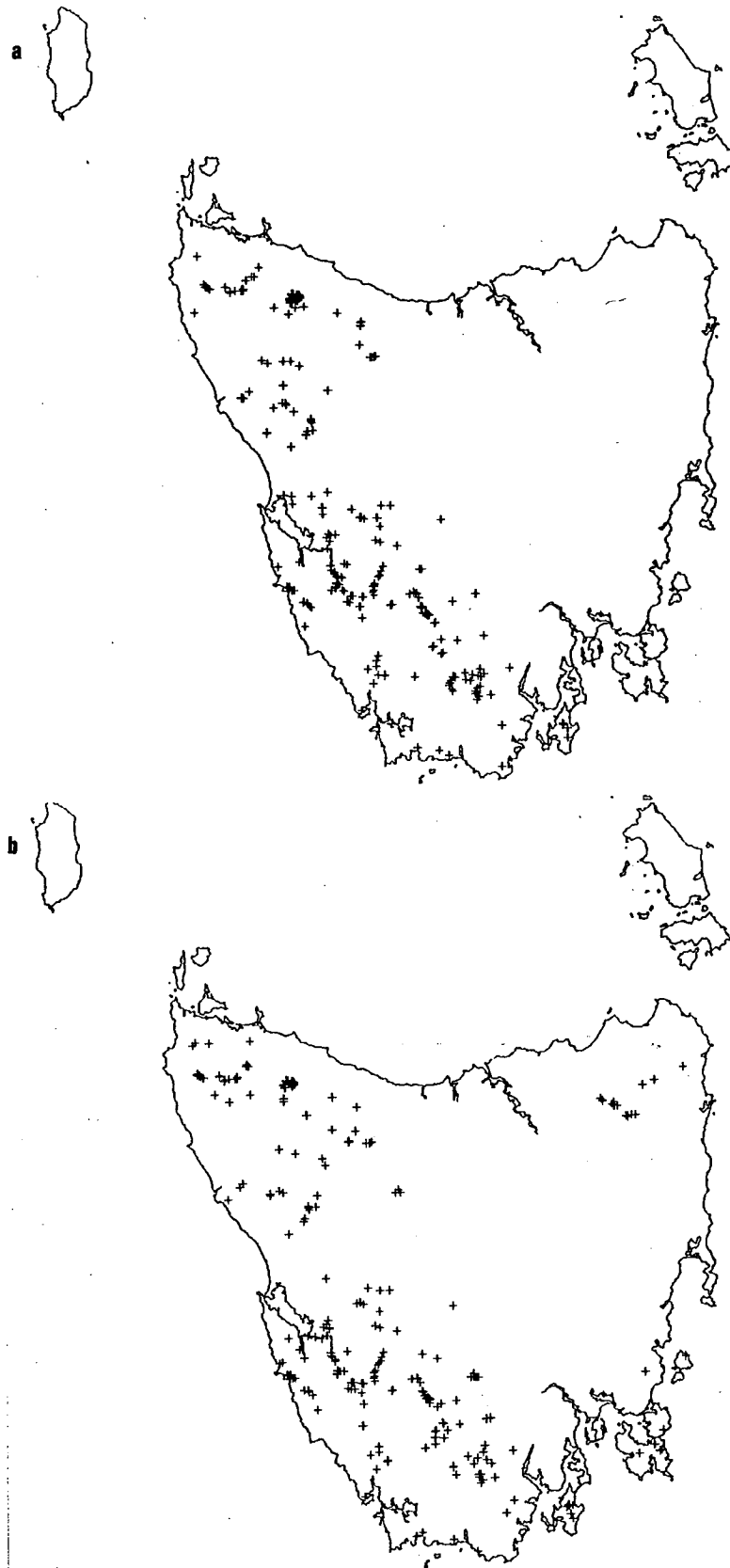


Figure 3.2. The distributions of *Anodopetalum biglandulosum* (a) and *Phyllocladus aspleniifolius* (b). Sites extracted from the TASFORHAB data base.

3.3.1 Methods

3.3.1 Climatic correlation for *P. aspleniifolius* and *A. biglandulosum*

The computer program BIOCLIM models the distribution of mean monthly temperatures and precipitation using a set of mathematical surfaces which interpolate values between climate stations. The calculation of 16 climatic variables is possible using BIOCLIM and these summarise monthly, quarterly and annual variation in temperature and precipitation. The indices are derived from mean monthly estimates of mean daily maximum and minimum temperatures and total precipitation. Estimates made by the program are based on cells which cover the state of Tasmania on a 200 m grid.

The climatic profile of a taxon can be estimated by entering the set of records from which a taxon has been found, defined by latitude, longitude and altitude. The program returns a summary of the 16 climatic variables for the target locations which includes minimum, maximum and mean values for each variable.

The BIOCLIM program can also be used to predict habitat climatically suitable for a species based on the extracted profile. The BIOCLIM profile can be compared to the distribution of all climates in the grid and maps can be produced showing which cells in the grid have climatic means which are within limits set in a subroutine called PRDICT.

The climate profiles of *P. aspleniifolius*, *A. biglandulosum*, *Nothofagus cunninghamii* and *Nothofagus gunnii* were determined with the use of the BIOCLIM computer program. The site records for each of these species were extracted from the TASFORHAB data base (Peters 1983). This data base contains distribution records of species from a wide range of communities throughout Tasmania. The data were collected by many biologists and forest assessors. Doubtful distributional data were checked for accuracy and removed if necessary.

Using the PRDICT subroutine and the climatic data generated in BIOCLIM, predictions of climatically suitable habitats were made for *P. aspleniifolius* and *A. biglandulosum*. This was done to determine the potential range according to their realised climatic niche.

The 16 climatic variables for *Nothofagus cunninghamii* and *N. gunnii* were analysed using principal components analysis (PCA). The two strongest components of the variation, mean annual precipitation and mean annual temperature (Figure 3.3), were selected to produce two dimensional plots to represent the climatic envelope for rainforest

generally. Two dimensional plots were produced in the same way for *P. aspleniifolius* and *A. biglandulosum* and overlain on the "rainforest" climatic envelope.

3.3.2 Phytosociology

Floristic data from 98 sites were collected from 100 m² quadrats throughout the range of the distributions of *P. aspleniifolius* and *A. biglandulosum*. Cover was also estimated for each species in modified Braun-Blanquet classes. The cover classes were: rare, <1%, 1-5%, 5-25%, 25-50%, 50-75%, >75%. The data were entered in the ecological data management package DECODA (Minchin 1990). The floristic and abundance data were classified in a two-way table using the polythetic divisive classification program TWINSpan (Hill 1979).

3.3.3 Environmental Correlates

The community data were ordinated using the multidimensional scaling (MDS) procedure. This procedure is superior to other ordination methods in its ability to recover the relationships in the floristic data (Minchin 1987). Vectors of best fit were determined for environmental variables. The relationship of the floristics to the environmental gradient, represented by the vector, is tested for significance using 100 Monte-Carlo simulations which allow a probability statement to be made. The environmental gradients that were considered were drainage, slope, aspect, altitude, mean annual precipitation, and geological type and age.

Those gradients that were found to have a significant relationship with the floristic continuum were selected for further analysis. The vector scores of each classification group were compared in a pair-wise Kruskal-Wallis rank analysis.

The rock types were ranked by professional geologists according to their mineral composition and age, with the intent of producing an index of site fertility. The ranking procedure was repeated independently by 3 geologists from the University of Tasmania and the average of the expert opinions became the final rank. As such the data were multi-state non-continuous and were therefore not suitable for analysis of variance.

It should be noted that the geological substrate's were determined from 1:50 000 geological maps and as such some "noise" in the data may be expected due to the level of accuracy of both the maps and site location. Geological substrate is often difficult to determine in the field due to the absence of exposures.

Due to the confounding influence of fire across the fertility gradient the TWINSpan groups were stratified into sclerophyll or other communities. Due to the confounding influence of altitude on the correlation of floristic composition of the remaining sites with fertility, these sites were stratified into 100 m altitude intervals. The continuous altitudinal intervals, along which all other environmental gradients were insignificant, were tested for their relationship with fertility. Consequently, only the sites in TWINSpan groups 2, 3, 5 and less than 400 m elevation were compared in this analysis. Group 7 and the sclerophyll groups 1 and 6 were described separately.

A concentration index was calculated to describe the relative frequency of co-occurrence of common species with *P. aspleniifolius* and/or *A. biglandulosum*. The calculation was based on 98 sites in which *P. aspleniifolius* or *A. biglandulosum* were recorded.

The calculation was;

$$\text{highest \% frequency / lowest \% frequency} * 100.$$

The highest and lowest % frequency in the calculation represented the frequency of occurrence of each selected species in quadrats containing one or the other of *P. aspleniifolius* and *A. biglandulosum*.

The total cover of each species in association with either *P. aspleniifolius* or *A. biglandulosum* was standardized to account for differences in the frequency of association. The total cover associated with *P. aspleniifolius* was used as the standard and the total cover associated with *A. biglandulosum* was adjusted using the calculation;

$$\text{Mean cover in association with } A. \text{ biglandulosum} * \text{difference in frequency of association between } A. \text{ biglandulosum and } P. \text{ aspleniifolius} + \text{total cover in association with } A. \text{ biglandulosum} * -1$$

3.4 Results

3.4.1 Climatic correlates.

The BIOCLIM climatic data are summarized in Appendix 2. The climatic space for rainforest generally (defined by the *Nothofagus cunninghamii* and *N. gunnii*) is illustrated by the envelope in Figure 3.4. The climatic profile of the association between *P. aspleniifolius* and *A. biglandulosum* is variable, ranging from mean annual precipitation rates of 1 020 mm pa to greater than 3 000 mm pa. The mean maximum temperature in the hottest month is 20° C and mean minimum temperatures in the coldest month are 1 to 1.5° C. The altitudinal range of the association recorded in this study is from sea level to about 970 m a.s.l. but is predominantly between 100 and 600 m a.s.l.

The climatic envelope of *P. aspleniifolius* is similar to that of the rainforest generally, and is entirely enclosed by it. The climatic space of *A. biglandulosum* is also completely contained within the general rainforest envelope but does not occur in the driest part of the rainforest range. The warmest of these drier sites are located in the south-east and east of the state while the coolest are high altitude sites along the eastern limits (rainshadow) of extensive rainforest areas and in the north-east.

The confinement of *P. aspleniifolius* within the envelope is an unexpected result considering the distribution of the species throughout many wet eucalypt forests that do not contain *Nothofagus cunninghamii*. This result indicates that *Nothofagus cunninghamii* has the same climatic range as *P. aspleniifolius* but differences in communities indicate other influences such as disturbance regimes.

The predicted distributions of *P. aspleniifolius* and *A. biglandulosum* (Figure 3.5) indicate that the north-east of Tasmania has a suitable climate for *A. biglandulosum* although it does not currently occur there. This prediction is based on the same two principal components of the 16 BIOCLIM variables used to produce the climatic envelope. It should be noted that the prediction is based on the strength of the positive relationship between actual distribution and the climate of all other areas. Some areas of known distribution for *P. aspleniifolius* have not been predicted. All of the omitted sites are on the east coast of Tasmania which experiences lower rainfall than the west in the driest months. The eastern distribution may experience cloud trapping during summer easterly winds, consequently increasing the effective rainfall (Neyland 1992).

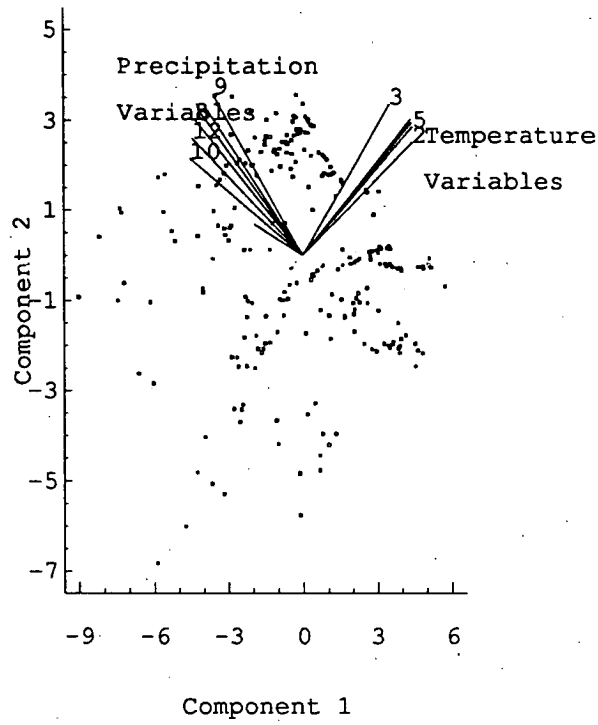
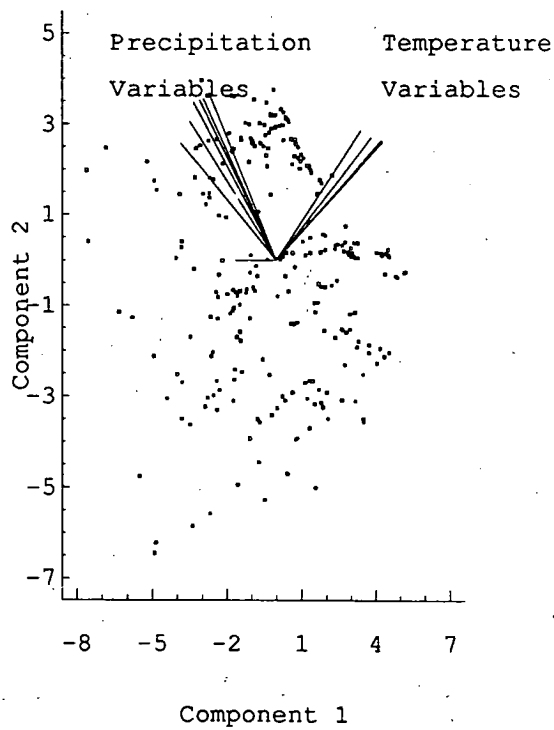
*Phyllocladus aspleniifolius*

Figure 3.3. Scatterplots of the principal components of the variation in the 16 climatic variables produced by BIOCLIM. The length of the vectors represent the relative contributions of each variable.

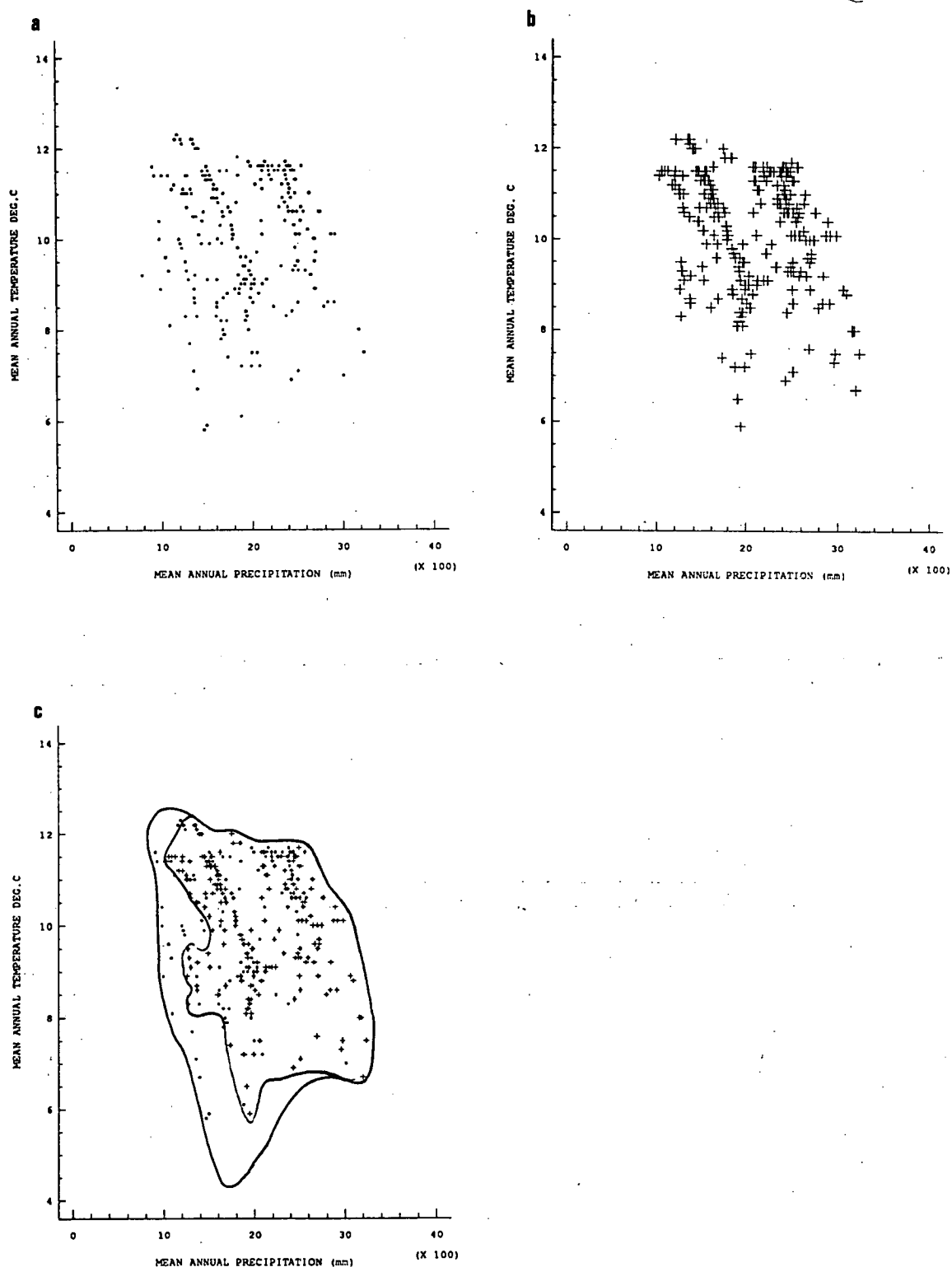
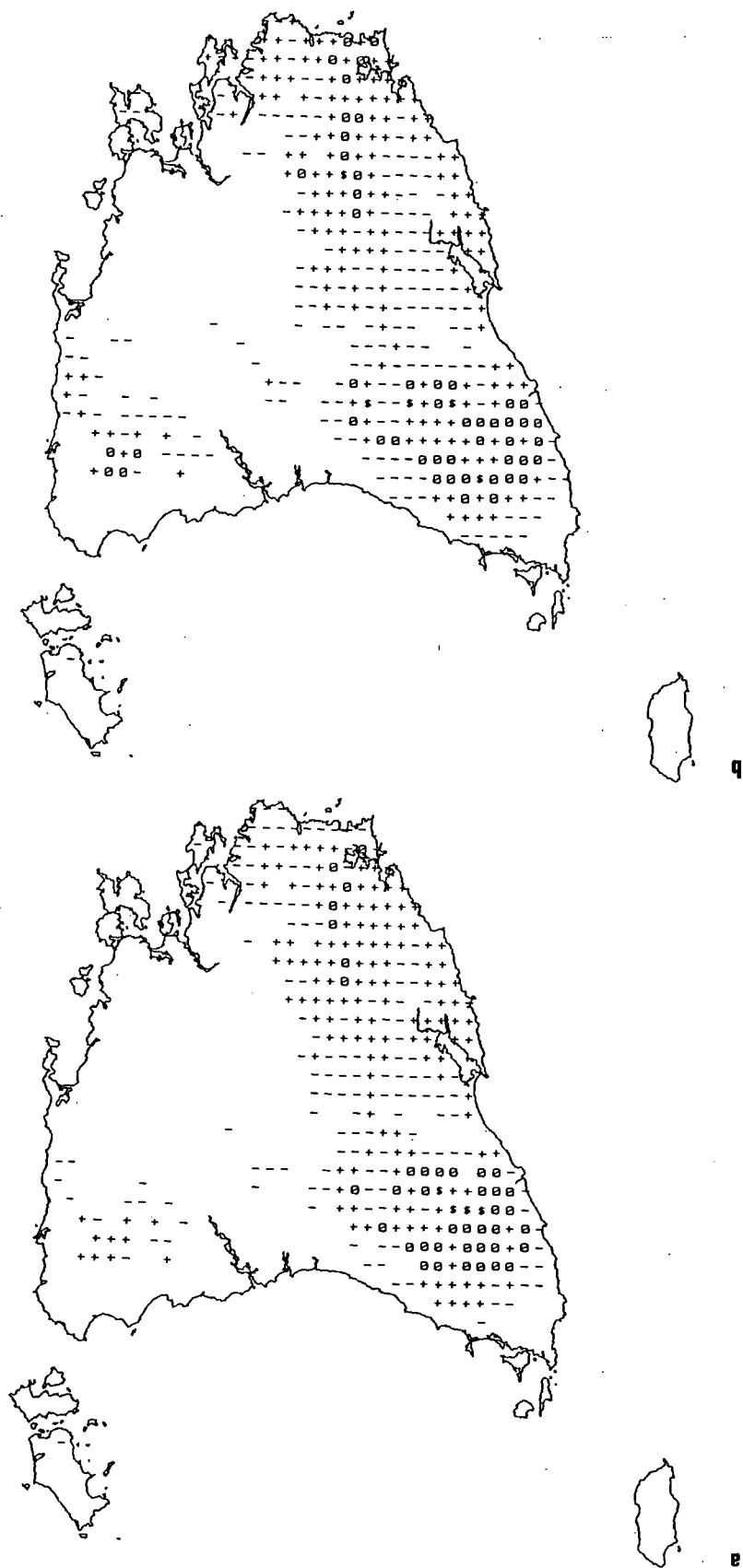


Figure 3.4. Scatter plots of mean annual temperature versus mean annual precipitation representing the climatic space for sites recorded in the TASFORHAB data base for (a) *P. aspleniifolius* and (b) *A. biglandulosum*. The climatic envelope (c) of *Nothofagus* spp. (outer) with the distribution of *P. aspleniifolius* and *A. biglandulosum* (inner) overlaid.

Figure 3.5. The predicted distributions of a. *P. asplenifolius* and b. *A. biglandulosum* based on the PRDICT subroutine in the program BIOCLIM. All 16 climatic parameters fall inside the range of known distribution (-), all 16 fall in the 90 percentile 5-95% (+), 13-15 parameters fall in the interquartile 25-75% (0), all 16 fall in the interquartile 25-75% (\$).



3.4.2 Floristic Association and Environmental Correlates.

The TWINSpan classification (Figure 3.6, Table 3.1) indicates a range from sites with relatively depauperate vegetation to those of much greater diversity. It is important to note a bias in the data, that is, no sites were sampled which contain neither *P. aspleniifolius* nor *A. biglandulosum*. Never the less it is clear that both species span a large range of forest types within the data set.

The vector-fitting procedure indicates significant relationships between aspect, rainfall, altitude and geological type and age and the floristic continuum (Figures 3.7 and 3.8). The super-imposed TWINSpan communities illustrate various degrees of separation along those gradients. Kruskal-Wallis comparisons by ranks confirm that significant differences exist between the TWINSpan groups along the selected gradients, $P < 0.05$ (Table 3.2, Figure 3.8).

The first division made by the TWINSpan programme is one based largely on the diversity of epiphytic ferns. The division separates callidendrous from non callidendrous types, but also separates wet sclerophyll forest at higher altitudes from other sclerophyll or heathy vegetation.

A. biglandulosum features as an indicator species in the second level of the TWINSpan classification hierarchy being absent from all sites in group 1 and from five of the eleven in group 7 (Figure 3.6). *P. aspleniifolius* is present at all sites. These divisions are, therefore, of considerable interest for indicating species that are associated strongly with *P. aspleniifolius* but not *A. biglandulosum*.

Group 1 contains some of the sclerophyll associates of *P. aspleniifolius*, including *Pittosporum bicolor*, *Olearia viscosa*, *O. argophylla*, *Notelaea ligustrina*, *Eucalyptus delegatensis*, *Pomaderris apetala*, *Acacia dealbata*. This group of communities was typically located on south-east to south-west aspects at altitudes above 600 m in areas of significantly lower rainfall than all but group 5 (Table 3.2, Figure 3.8).

Group 7 reflects the greater range of communities at high altitudes that support *P. aspleniifolius*. In particular *P. aspleniifolius* is more common with *Athrotaxis cupressoides*, *A. laxifolia*, *Astelia alpina*, *Eucalyptus coccifera*, *Podocarpus lawrencei* and *Persoonia gunnii*. The sites in group 7 occupy the south-western quadrant at a mean altitude greater than 775 m. The altitude is also reflected in the high rainfall class (Figure 3.8).

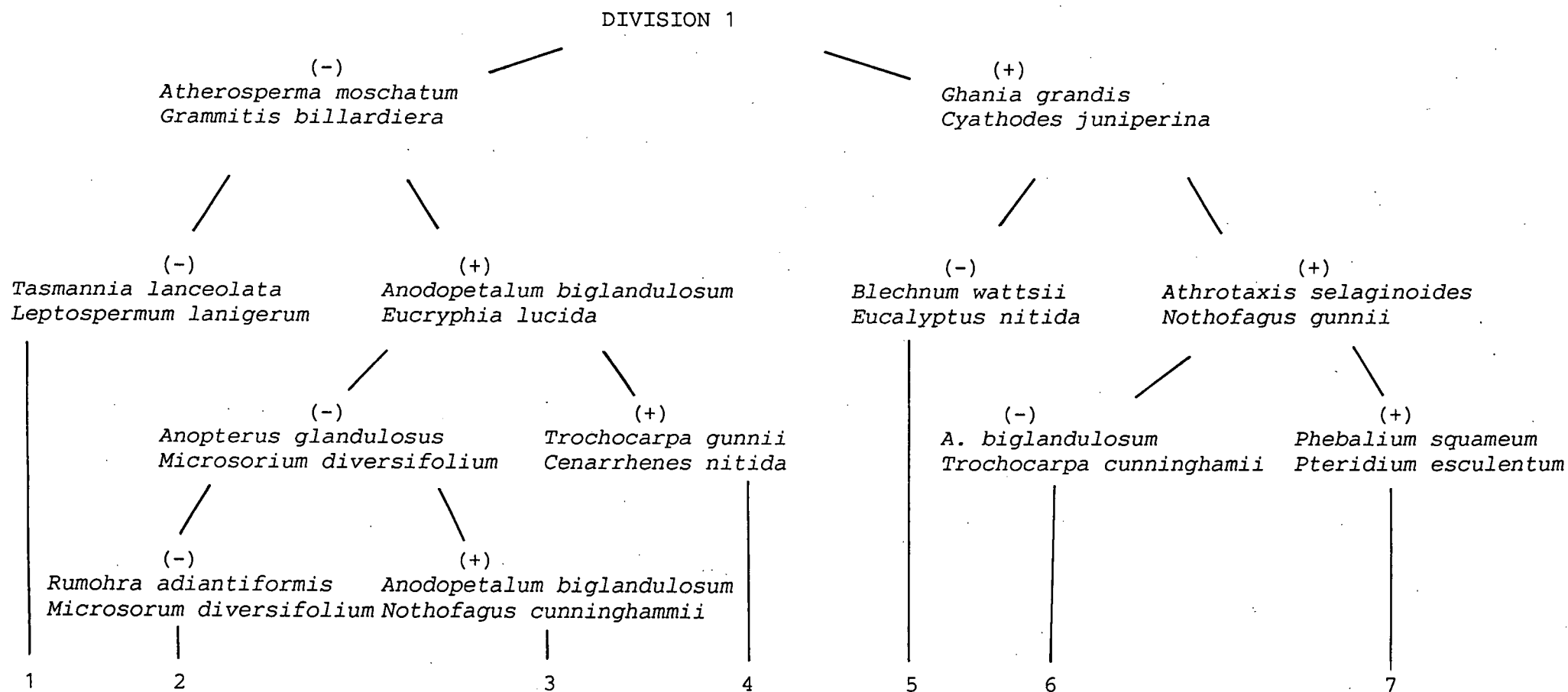


Figure 3.6. The Twinspan division tree showing the positive and negative indicator species for each division. See Table 3.5. for characteristic species of each group.

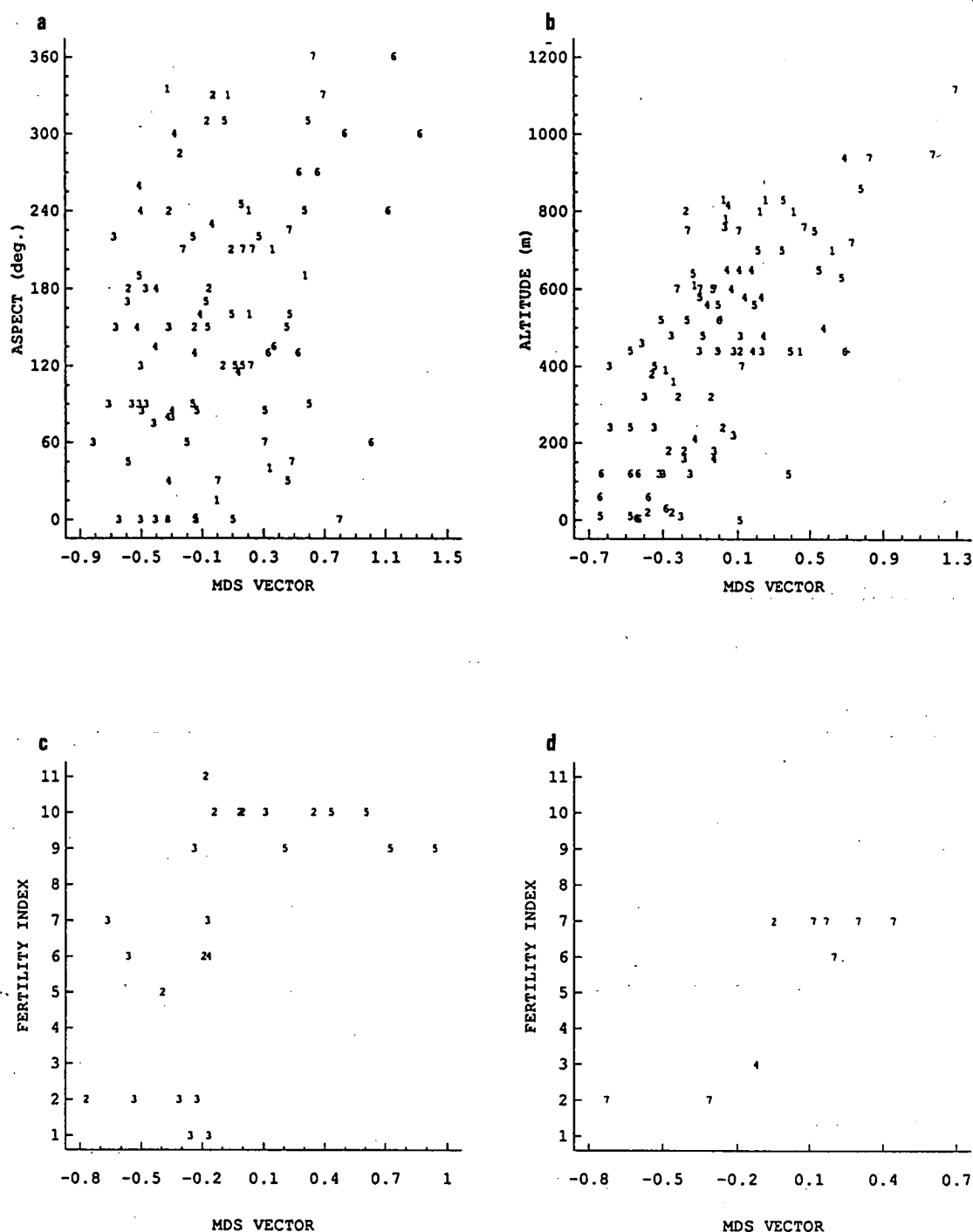


Figure 3.7. The values of three environmental gradients (a) Aspect, (b) Altitude and (c) Fertility in rainforest < 400 m asl. and (d) Fertility in rainforest > 750 m asl. plotted against the appropriate vector derived from the Multi-dimensional Scaling vector-fitting procedure in the program DECODA. $P < 0.05$ for all gradients (Monte-Carlo simulations). The communities determined by the TWINSpan program (Figure 3.6) are indicated.

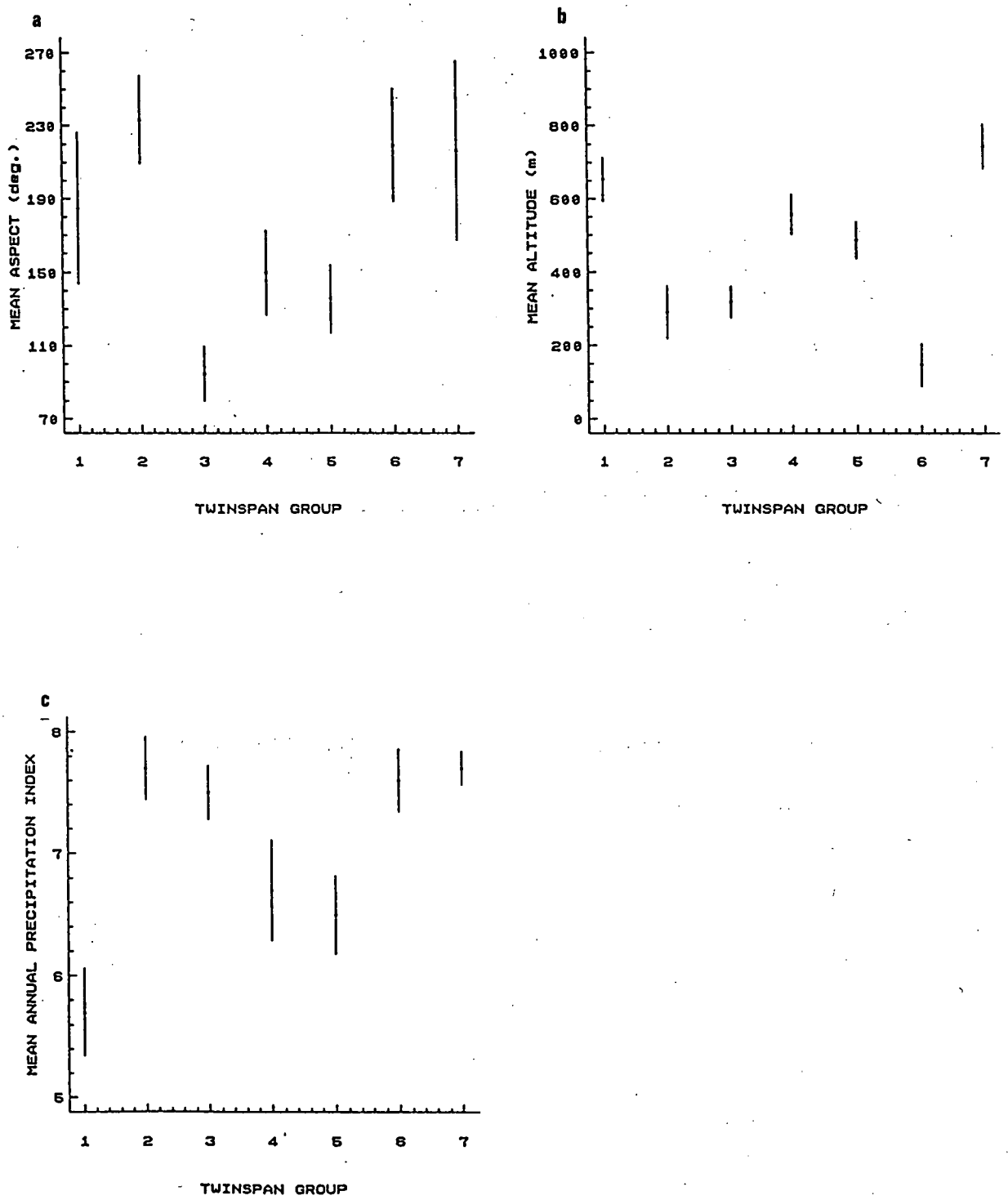


Figure 3.8. The means and standard errors of 7 TWINSPAN groups along three environmental gradients (a) Altitude, (b) Annual precipitation and (c) Aspect.

Table 3.1. Summary description of the seven TWINSpan groups used in the analysis of variance. Descriptions: sclerophyll (SCLE), rainforest (RF), callidendrous (C), thamnic (T), implicate (I); montane rainforest (MONT). The fertility is the average of the fertility scale in table 3.3; 1-5 (high), 5-8 (med), 8-11 (low). Aspect refers to quadrant of the compass that the average aspect occurs in. Characteristic species are those that occur in 20% or more of the quadrats in a TWINSpan group. The species cover-class represents the average cover in the group at sites supporting the characteristic species in each TWINSpan group: 1 (<5%), 2 (5-25%), 3 (>25%).

	TWINSpan Group Number						
	1	2	3	4	5	6	7
Description	SCLE	RF	RF/C	RF/T	RF/I	SCLE	MONT
Fertility	med	med	high	med	low	low	high
Altitude	high	low	mid	mid	mid	low	high
Rainfall	low	high	med	low	low	med	high
Aspect	sw	sw	se	se	se	sw	se
<hr/>							
	Cover Class						
	1	2	3	4	5	6	7
Characteristic Species							
<i>Phyllocladus aspleniifolius</i>	2	2	2	2	2	2	3
<i>Anodopetalum biglandulosum</i>		2	3	3	2		2
<i>Microsorium diversifolium</i>	2	2	2				
<i>Polystichum proliferum</i>	2						
<i>Hymenophyllum peltatum</i>	2			2			
<i>Pimelea drupacea</i>	2	2					
<i>Pittosporum bicolor</i>	2						
<i>Rumohra adiantiformis</i>	2	2					
<i>Atherosperma moschatum</i>	2	2	2	2	2	2	
<i>Grammitis billardieri</i>	2	2	2	2	1	2	
<i>Hymenophyllum australe</i>	2	2	2		2		
<i>Hymenophyllum rarum</i>		2	2	2			
<i>Eucryphia lucida</i>		2	3	2	2		
<i>Blechnum wattsii</i>	2	3	2	2	2	2	
<i>Nothofagus cunninghamii</i>	2	2	3	3	2	2	2
<i>Trochocarpa cunninghamii</i>	2	2		2	2		2
<i>Anopterus glandulosus</i>		2	2	2	2	2	2

<i>Cenarrhenes nitida</i>	2	3	3	2	2	2
<i>Eucalyptus delegatensis</i>	2					
<i>Trochocarpa gunnii</i>			2	2	2	2
<i>Monotoca glauca</i>	2	2			2	
<i>Drymophila cyanocarpa</i>	2	2		2	2	
<i>Leptospermum lanigerum</i>	2				2	
<i>Tasmannia lanceolata</i>	2	2	2	2	2	2
<i>Orites diversifolia</i>			2			
<i>Prionotes cerinthoides</i>		2		2	2	2
<i>Gleichenia microphylla</i>					2	
<i>Aristotelia peduncularis</i>				2		
<i>Gahnia grandis</i>	2	2	1	3	2	2
<i>Acacia verticillata</i>					2	
<i>Eucalyptus nitida</i>					2	
<i>Melaleuca squarrosa</i>					2	
<i>Pteridium esculentum</i>					2	
<i>Eucalyptus subcrenulata</i>				2		
<i>Agastachys odorata</i>		2		2	2	2
<i>Leptospermum glaucescens</i>					2	2
<i>Olearia persoonioides</i>				2		2
<i>Athrotaxis selaginoides</i>				2		2
<i>Eucryphia milliganii</i>		2		2		3
<i>Richea pandanifolia</i>		2		2		3
<i>Cyathodes juniperina</i>	1		1	2	2	2
<i>Astelia alpina</i>						2
<i>Athrotaxis cupressoides</i>						2
<i>Bauera rubioides</i>						2
<i>Monotoca submutica</i>						2
<i>Nothofagus gunnii</i>						3
<i>Sprengelia incarnata</i>						2
<i>Persoonia gunnii</i>					1	2

Table 3.2. The summary statistics and results of a Kruskal-Wallis one-way analysis of variance for a. altitude; b. rainfall; c. aspect and d. geological fertility for rainforest < 400 m a.s.l.. Under the heading Homogeneous Groups different columns indicate statistically different ranks.

ALTITUDE

TWINSpan Group	(n)	Average	Average Rank	Homogeneous Groups
6	13	228.3	25.5	X
2	10	290.0	31.4	XX
3	19	319.4	34.4	XX
5	18	436.6	48.1	XX
4	12	531.3	58.8	XX
1	14	655.0	71.0	XX
7	12	777.3	81.8	X

Test statistic = 43.5789 Significance level = 0.001

RAINFALL

TWINSpan Group	(n)	Average	Average Rank	Homogeneous Groups
1	14	6.0	26.8	X
5	18	6.5	40.9	XX
4	12	6.5	39.8	XX
6	13	7.3	55.5	XX
3	19	7.5	60.0	X
2	10	7.7	61.6	X
7	12	7.8	65.0	X

Test statistic = 24.6508 Significance level = 0.003

Table 3.2 continued.

ASPECT

TWINSPAN Group	(n)	Average	Average Rank	Homogeneous Groups
3	19	94.7	32.1	X
5	18	133.3	43.3	XX
4	12	139.5	44.5	XX
7	12	170.0	52.7	XX
1	14	182.8	57.7	XX
6	13	193.5	59.3	XX
2	10	233.5	71.1	X

Test statistic = 16.9941 Significance level = 0.009

Groups 4, 5 and 6 were differentiated in the third level of the hierarchy. Group 4 contains thanmic rainforest and group 5 contains implicate rainforest types with some sclerophyll components. The sites occur on similar aspects, within similar altitudinal and rainfall ranges.

Group 6 has an even stronger sclerophyll element than group 5 with *Eucalyptus* spp. dominating most sites. *A. biglandulosum* is poorly represented while *P. aspleniifolius* occurs at all sites. This group is significantly different from group 4 in its rainfall range

but similar to group 5. It is found on southern to western aspects and is significantly lower in altitude than all but group 2 (Table 3.2, Figure 3.8).

Groups 2 and 3 are divided at the fourth level of the classification. Group 2 represents the least diverse rainforest in which *P. aspleniifolius* and *A. biglandulosum* are predominant. These forests are able to occupy western aspects but only in high rainfall areas at low to mid altitudes.

Group 3 includes sites in which *A. biglandulosum* is present but *P. aspleniifolius* is absent or poorly represented. These are the least diverse sites and are dominated by *Nothofagus cunninghamii*. Such sites tend to be along creek-flats in callidendrous forest. The sites were generally located between 200 and 400 m altitude in high rainfall areas.

3.4.3 Geological fertility

Only communities in groups 2, 3, 4, 5 and 7 were significantly correlated with geological fertility (Figure 3.7). In the lowland rainforest all but one community from group 4, which is predominantly confined to mid altitudes, were excluded by the stratification process (described in the methods) and the single site was not included for further analysis.

In the lowland rainforest, groups 2 and 5 support *P. aspleniifolius* and *A. biglandulosum* in association. The fertility of sites carrying groups 2 and 5 is similar (Table 3.3) but sites in group 2 cover a greater range of fertility with some sites at both extremes of the gradient (Table 3.3). Group 5 is most commonly found in the less fertile section of the gradient on Precambrian and Triassic unmetamorphosed sandstones and siltstones but also on Holocene sand and gravels and Pleistocene glacial tills.

Group 3 occurs on significantly more fertile sites than groups 2 and 5 (Table 3.3.). *P. aspleniifolius* is commonly absent from the most fertile sites in group 3 which support forest closely related to the callidendrous types and occur on either Tertiary basalt or Jurassic dolerite. The remainder of sites in group 3 occur on sites of lower fertility and support *P. aspleniifolius*. All of the sites in this group support *A. biglandulosum*.

High altitude rainforest (> 750 m a.s.l.) was also found to differ along a fertility gradient but has been classified predominantly in TWINSPAN group 7. One site each from groups 2 and 4 were located at this elevation. All of the sites in this group are dominated by gymnosperms. The differences include sclerophyll species on the medium fertility

sites such as glacial tills, pebbly mudstone and sandstone which are dominated by *Athrotaxis selaginoides*, and the dominance of *Athrotaxis cupressoides* on the relatively fertile dolerite (Figure 3.8, Table 3.3). However, the separation of the *Athrotaxis* spp. is more likely to reflect the altitudinal distribution of rock type rather than the control of fertility. *P. aspleniifolius* is commonly found as a shrub in association with *Athrotaxis cupressoides*. *A. biglandulosum* is rare among these records and is also a small shrub where it does occur.

Group 1 sites occurring on different substrate's are also differentiated floristically. This dichotomy separates sclerophyll sites in the south-east of the state on Jurassic dolerite from sites in the north-east of the state on Permian glacio-marine sequences of pebbly mudstone and sandstone and on Devonian granodiorite. All sites support *P. aspleniifolius*. The south-eastern sites are dominated by *Eucalyptus delegatensis*, with other wet sclerophyll species and *Anopterus glandulosus* and *Cenarrhenes nitida* present, while *A. biglandulosum* is absent. At the north-eastern sites, the stands are free of *A. biglandulosum*, *Anopterus glandulosus* and *Cenarrhenes nitida* which are also all absent from the north-east region. While the regional biogeographic history (Kirkpatrick and Brown 1984, Hill and Read 1987) may explain the absence of these species from the north-eastern group the similarity of the remaining species is at odds with the different substrate's.

The remaining sclerophyll group, group 6, occurs on a variety of substrate's but is most common on low fertility Precambrian and Triassic unmetamorphosed sandstones and siltstones.

The concentration index (Table 3.4) indicates that some of the smaller shrub species in groups 2, 3 and 4 (callidendrous to thamnic types), such as *Trochocarpa cunninghamii*, *Cyathodes glauca* and *Tasmannia lanceolata* tend to be more common associates of *P. aspleniifolius* than of *A. biglandulosum*. Larger shrubs and small trees such as *Anopterus glandulosus*, *Agastachys odorata* and *Eucryphia* spp. tend to associate with *A. biglandulosum* more often than with *P. aspleniifolius*. Four shrub species, *Cyathodes juniperina*, *Monotoca glauca*, *Pimelea drupacea* and *Tasmannia lanceolata* which tend to concentrate with *P. aspleniifolius* also occur at greater cover levels in that association. Two species, *Agastachys odorata* and the ground fern *Blechnum wattsi* which occur more often with *A. biglandulosum* also occur more abundantly with it than with *P. aspleniifolius*. Two tree species, *Eucryphia lucida* which tends to occur more often with *A. biglandulosum* and *Athrotaxis selaginoides* which is neutral, both occur more abundantly with *P. aspleniifolius*. Table 3.4 also reiterates the sclerophyll associates of *P. aspleniifolius*.

Table 3.4. A concentration index CI (highest % freq/lowest % freq *100) based on 98 quadrats containing either or both of *P. aspleniifolius* and *A. biglandulosum* indicates the relative frequency of co-occurrence of common species (present in > 15 % of quadrats) . Total cover is a standardized coefficient of total cover for each species when in association with either *P. aspleniifolius* or *A. biglandulosum*. *P. aspleniifolius* occurs in 83% of quadrats containing *A. biglandulosum* and *A. biglandulosum* occurs in 62% of quadrats containing *P. aspleniifolius*.

Species	CI	Total Cover	
More common with		P.asp	A.big
<i>Phyllocladus aspleniifolius</i>		313	282
<i>Cyathodes juniperina</i>	137	74	35
<i>Drymophila cyanocarpa</i>	164	41	41
<i>Eucalyptus nitida</i>	120	50	43
<i>Gahnia grandis</i>	123	135	137
<i>Hymenophyllum peltatum</i>	187	24	26
<i>Hymenophyllum rarum</i>	106	26	26
<i>Leptospermum lanigerum</i>	212	38	42
<i>Monotoca glauca</i>	250	30	22
<i>Phebalium squameum</i>	212	42	39
<i>Pimelea drupacea</i>	114	27	16
<i>Pittosporum bicolor</i>	175	28	26
<i>Tasmannia lanceolata</i>	157	81	72
<i>Trochocarpa cunninghamii</i>	152	73	70
More common with			
<i>A. biglandulosum</i>		179	274
<i>Anopterus glandulosus</i>	120	118	117
<i>Agastachys odorata</i>	117	60	84
<i>Blechnum wattsii</i>	110	172	202
<i>Eucryphia lucida</i>	139	74	35
<i>Eucryphia milliganii</i>	118	120	125
<i>Hymenophyllum australe</i>	121	53	58
<i>Microsorium diversifolium</i>	113	24	22
<i>Prionotes cerinthoides</i>	121	70	65

Neutral concentration

<i>Grammitis billardieri</i>	103	80	83
<i>Rumohra adiantiformis</i>	104	25	18
<i>Atherosperma moschatum</i>	102	132	137
<i>Athrotaxis selaginoides</i>	103	46	33
<i>Cenarrhenes nitida</i>	102	135	135
<i>Nothofagus cunninghamii</i>	105	291	288
<i>Olearia persoonioides</i>	100	46	49
<i>Orites diversifolia</i>	100	23	18
<i>Richea pandanifolia</i>	100	62	60

Unique to *P. aspleniifolius**Eucalyptus delegatensis**Acacia dealbata**Aceana novae-zelandiae**Archeria hirtella**Athrotaxis cupressoides**Athrotaxis laxifolia**Baeckea gunniana**Bedfordia salicina**Billardiera longifolia**Blandfordia punicea**Blechnum nudum**Boronia citriodora**Callistemon paludosus**Cyathodes parvifolia**Donatia novae-zealandiae**Dianella revoluta**Dianella tasmanica**Epacris heteronema**Eucalyptus coccifera**Exocarpos humifusus**Grammitis magellanica**Helichrysum antenarium**Hymenophyllum marginatum**Leptospermum scoparium**Lycopodium fastigiatum**Lycopodium varium**Olearia viscosa**Olearia argophylla**Olearia stellulata**Orites revoluta**Podocarpus lawrencei**Pomaderris apetala**Restio tetraphyllus**Richea sprengelioides**Stylidium graminifolium*

3.5 Discussion

Community differentiation has often been demonstrated along environmental gradients similar to those considered in this study (e.g. Whittaker 1975, Noy-Meir 1971, Austin and Cunningham 1981). The differentiation of communities along gradients includes species replacement series (Meuller-Dombois and Ellenberg 1974) as the intensity of the environmental factor and consequently the habitat changes along the gradient (Austin 1985). In the present study the TWINSpan groups are significantly correlated with particular intervals along altitudinal, rainfall, aspect and fertility gradients (Figures 3.6 and 3.7). However, neither the presence or absence of *P. aspleniifolius* and *A. biglandulosum* nor their co-existence is correlated with any particular gradient.

In Tasmania, Ogden (1978) and Kirkpatrick (1977) both noted the increasing importance of gymnosperms with increasing altitudes, a phenomenon evident in the present study (Table 3.1) (Appendix 1). In New Zealand Druitt *et al.* (1990) demonstrated that the Podocarpaceae dominate the zone from 750 m to tree-line (1 160 m) but that species replacement occurs along this interval with no lowland or montane species persisting beyond 1 050 m. This is not the case in the present study although *P. aspleniifolius* and *A. biglandulosum* are relatively scarce in the montane *Athrotaxis cupressoides* alliance (Appendix 1) which is clearly delimited from the bulk of other rainforest types by altitude (Figure 8a) (Jarman *et al.* 1991). Both species also occur at sea-level (Appendix 2) but the absence of *A. biglandulosum* from some sclerophyll communities between sea-level and the tree-line indicates that although altitude distinguishes some communities (Figure 3.8) it does not differentiate the distributions of *P. aspleniifolius* and *A. biglandulosum*.

Cullen and Kirkpatrick (1988) illustrated that the separation of *Athrotaxis selaginoides* and *A. cupressoides* at high altitude is associated with relative frost risk. Read (1985a) indicated that *P. aspleniifolius* was relatively frost sensitive among the canopy dominants in Tasmania and the restriction of *A. biglandulosum* to similar altitudinal limits may also indicate its relative susceptibility to frost.

The rainfall gradient also separates sclerophyll groups of communities that are free of *A. biglandulosum* (Figure 3.8). In this case the wetter of the sclerophyll groups (6) receives similar rainfall to all of the rainforest groups while the drier sclerophyll group (1) reinforces the well known juxtaposition of sclerophyll and rainforest communities in Australia. Again, the relevance to the co-existence of *P. aspleniifolius* and *A. biglandulosum* lies in: the absence of *A. biglandulosum* from a group of sclerophyll communities which

experience rainfall similar to that in rainforest; the presence of *P. aspleniifolius* in sclerophyll communities with significantly different rainfalls (Figure 3.8).

Rainforest is found on many geological types in Tasmania ranging from rich basalts to quartzite (Jarman *et al.* 1991). Little is known of the correlation between particular rainforest communities and fertility except that a floristic and structural gradient from tall forests of simple floristics and structure (callidendrous) to low forests of greater diversity and structural complexity (Implicate) is "often" associated with substrate fertility (Jackson 1968, Read and Hill 1988, Brown *et al.* 1990). Within the lowland rainforests in the present study, geological fertility is important as an ecological gradient.

In New Zealand's lowland forests, marked changes in dominant species are correlated with different soils and their interaction with slope (drainage) (Norton and Leathwick 1990, Duncan *et al.* 1990). Both conifers and broad-leaf taxa dominate the better quality sites with a shift to conifer dominance on poorer soils or sites of high fertility that are repeatedly disturbed (Norton and Leathwick 1990). Separation of *P. aspleniifolius* and *A. biglandulosum* occurs on the highly fertile basalts and dolerites in callidendrous forests where *P. aspleniifolius* appears to have been excluded. Read and Hill (1988) suggest that the absence of *P. aspleniifolius* from such forests is due to competitive exclusion by the faster growing *Nothofagus cunninghamii*, which is often the only canopy species. *P. aspleniifolius* does, however, occur without *A. biglandulosum* on fertile deep basalts where fire appears to have been important in moulding the community. Consequently, this condition also results in a sclerophyll association. *P. aspleniifolius* and *A. biglandulosum* co-exist in all of the other rainforests along the fertility gradient.

P. aspleniifolius and *A. biglandulosum* are particularly common in implicate rainforests which are the most diverse and occur on the lower fertility substrate's. Grime (1977) indicates that the diversity of plant communities generally is higher on infertile sites. He argues that nutrient limitations produce small plants allowing more space for a greater diversity of smaller plants beneath a sparse dominant canopy. Hence, the diversity of species, but particularly the strong association between *P. aspleniifolius* and *A. biglandulosum*, does not necessarily indicate a site preference but rather reduced competition for space. While such sites may not be optimum both species demonstrate the ability to tolerate infertile substrate's.

Few differences are apparent in the index of concentration of rainforest species with either *P. aspleniifolius* or *A. biglandulosum* (Table 3.4). *P. aspleniifolius* and *A. biglandulosum* associate with most other rainforest species and occur in many of the rainforest

communities described by Jarman *et al.* (1984 and 1991) (Appendix 1). This broad range of association is typical of many other rainforest species in Tasmania with relatively few being clearly habitat specific, for example the congeners *Athrotaxis* spp. and *Eucryphia* spp. Historically, many Tasmanian rainforest species have been shown to be plastic in their community association in response to environmental change (Macphail 1980, Macphail and Hill 1984). Particular attributes of species, such as vagility, in concert with historic influences and active processes, such as pedogenesis, play an important role in the formation of communities over long periods (Macphail 1980). The influence of fire is important in the modern distribution of rainforest (Jackson 1968), particularly fire used by Aboriginal people (Jones 1969, Ellis 1985). Influences such as these may be important in the separation of *P. aspleniifolius* and *A. biglandulosum* in Tasmanian wet forests.

Macphail's pollen analysis (1982) indicates that communities similar to those of today which are dominated by *Eucalyptus* spp. but in which *P. aspleniifolius* is also important were wide spread across Tasmania in the early post glacial Holocene period. It is argued by Macphail that this association reflects the high vagility of the bird dispersed *P. aspleniifolius*, allowing it to quickly re-occupy climatically suitable rainforest habitats ahead of other species. Poorly dispersed rainforest species, such as *Nothofagus cunninghamii* and *A. biglandulosum*, would take considerably longer to re-occupy climatically suitable habitat. Hence, some of Macphail's *P. aspleniifolius*/sclerophyll forests may still exist in climatic disequilibrium. A similar phenomenon is apparent in New Zealand where an extensive area of Podocarp dominated forest exists along the mid-west coast of the south island. It is suggested that this region was freed from forest during the Pleistocene glacial maxima and that re-establishment of forest has been led by the highly vagile members of the Podocarpaceae (McGlone 1985). *Nothofagus* species are slowly moving back into this climatically suitable area, and in northern areas can actually be observed as slowly migrating fronts or as isolated but expanding remnants (Rogers 1989).

Today, *Anodopetalum* and *Phyllocladus* are present in wet eucalypt communities but *Phyllocladus* is present in a greater range (Appendix 1). (Kirkpatrick *et al.* 1988). These forests generally occur on margins of, or adjacent to, rainforest communities though they may cover extensive areas. In the absence of fire the sclerophyll dominants may fail to regenerate and the community will become pure rainforest (Gilbert 1959). Under present climatic conditions, however, mixed forests may be perpetuated under a fire regime which includes a fire return period less than the life span of the *Eucalyptus* spp. The association of *P. aspleniifolius* with a greater range of sclerophyll elements in mixed forests concurs with the BIOCLIM profiles in which *A. biglandulosum* does not occupy the

drier parts of the general rainforest envelope which supports these forest types. However, mixed forest sites that support *P. aspleniifolius* but not *Nothofagus cunninghamii* are apparently climatically suitable for the *Nothofagus* alliance of rainforest as all sites in the recorded distribution of *P. aspleniifolius* fall within the general rainforest envelope (Figure 3.4). The absence of rainforest from these sites must be attributable to factors such as migration history or the stability of the well dispersed *P. aspleniifolius* in the face of repeated fires. Similarly, the disparate wet forest distributions of *P. aspleniifolius* and *A. biglandulosum* may be an artifact of these factors.

The absence of *A. biglandulosum* from the climatically suitable areas of rainforest in the north-east of Tasmania may be attributable to regional extinction. Its low vagility preventing it from re-establishing in the area. This taxon has not been recorded as pollen in the north-east in the past 5 000 years (I. Thomas pers. comm.) and if it were ever present there its regional extinction is likely to have occurred during the Pleistocene, a time when other rainforest species, recorded in fossils, became extinct in western Tasmania (Jordan 1991). A single stochastic dispersal event may extend its distribution into this climatically suitable region, although modern habitat fragmentation makes this difficult.

3.5.1 Conclusion

Climatic, physical, pyrric and historic factors have influenced the past and modern distributions of *P. aspleniifolius* and *A. biglandulosum*, and in doing so explain some of the variation in floristic association between the two species. However, many complex environmental factors present as gradients are important in determining the relative abundance and the remaining variation in the floristic associations (Jarman *et al.* 1983, 1991). However, these factors are inter-related and some are indirect environmental gradients, *sensu* Austin and Cunningham (1981).

P. aspleniifolius displays a wider range of sclerophyll associates than *A. biglandulosum*. An efficient means of dispersal, permitting rapid re-establishment on sites after fire and a greater range in dispersal are attributes of *P. aspleniifolius* which may explain these gross differences. There is some evidence to suggest that the distribution of *A. biglandulosum* in relation to climatically suitable rainforest habitat is in disequilibrium.

In rainforest communities, *P. aspleniifolius* and *A. biglandulosum* display their strongest association and dominance on the older and relatively infertile substrate's. It is not clear, however, if this is due to physiological adaptation to low nutrients or an autogenic

process similar to that described by Grime (1979). It would therefore be useful to measure the physiological responses of both species to a nutrient gradient and to compare these results with the ecological response in the field.

Chapter 4. *Phyllocladus aspleniifolius* and *Anodopetalum biglandulosum*: A comparison of physiological and ecological growth response to substrate fertility and pH.

4.1 Introduction

The previous chapter illustrated that the phytosociology of communities associated with *P. aspleniifolius* and *A. biglandulosum* varies in a consistent manner along environmental gradients such as altitude, rainfall, aspect and fertility. The phytosociological response is complicated by the interaction of these factors and the effects of other untested and indirect environmental gradients. However, fertility was shown to exert an influence upon the community composition and structure illustrated by the gradient from callidendrous to implicate and sclerophyll forest types. The ability to metabolise nutrients is important in determining the status of a species in the community. Indeed, the physiological responses of species affect their competitive ability (Grime 1979) and thus largely determine community composition along environmental gradients (Whittaker 1975).

The co-existence of two species will be affected by the ecological response of each to soil conditions, and the foundation for this expression is their physiological response to soil conditions. In Tasmania there has been very little work completed on the edaphically controlled growth responses of wet forest species. It is, however, clearly evident from field observation, that the growth rates and abundance of dominant species varies along a soil fertility gradient (Jackson 1968, Read 1985a, Brown *et al.* 1991). Jackson, in particular, also suggests that the pH of the soil is important in delimiting communities.

In a pot trial in which the growth responses to soils of high and of low fertility were measured, Read (1985a) showed that there were ecologically meaningful differences in growth between the dominant species of the rainforest. Brown *et al.* (1991) described the relationship between the floristics, diversity, and structure of rainforests and the environment in Tasmania. They concentrated particularly on the geochemistry and soil chemistry, and concluded that the three broad categories of rainforest (callidendrous, thamnic and implicate) are strongly correlated with these attributes; the callidendrous types being found on the best quality sites, such as basalt soils; and the implicate types being characteristic of sites of low nutrient status, for example, conglomerate glacial tills; while thamnic rainforests are typical of sites with intermediate fertility, such as soils derived from dolerite.

P. aspleniifolius and *A. biglandulosum* can be found in association on soils derived from a range of parent materials, including basalt, dolerite, quartzite, carbonate and sedimentary rocks, at various altitudes and on various slopes and aspects. It would be useful, therefore, to understand how the growth responses to different nutrient regimes are reflected in co-existence in the field.

Species that co-exist on soils of a particular fertility status are expressing a similar realized niche but this may be a limited overlap between quite different fundamental niches. Thus, the ability of *P. aspleniifolius* and *A. biglandulosum* to attain their greatest importance on the relatively low nutrient acid sites provided the impetus for the following nutrient experiments.

Phyllocladus and *Anodopetalum* also represent an opportunity to consider the status of species that may actively affect the soil environment, *sensu* Crocker's (1952) pedogenically affective biotypes. *P. aspleniifolius* possesses root nodules similar to those described by Baylis *et al.* (1963) as having a mycorrhizal association. The association was determined to increase phosphorus uptake which facilitates growth rates up to seven times higher than uninfected plants (Baylis *et al.* 1963). It is likely that this symbiotic relationship enables growth rates on low nutrient soils to be maintained at higher rates than may otherwise be expected (Read 1985a), and hence, allows *P. aspleniifolius* to dominate forests on such sites. Other nodulated Podocarpaceae are claimed to fix atmospheric nitrogen (Bergerson and Costin 1964, Robbins 1962)

Anodopetalum, on the other hand, has been determined by Webb (1953) to be an aluminium accumulator. Aluminium accumulators may influence the uptake of P, K and Ca in other plants by depositing litter containing > 1 000 ppm Al which is subsequently mineralised and incorporated into the surface soil horizons. The aluminium content of plants generally varies with the pH of the soil (Webb 1953). Plants with an acid cell sap which grow in soil containing aluminium phosphates have a means of utilizing soluble phosphate. Aluminium tolerance would therefore be an advantage on acid sites. No members of the Coniferae that have been tested are aluminium accumulators but they often occur on acid soils and have acid cell saps (Roberts and Doyle 1938).

The aim of this chapter is to determine the relationship between the physiological growth responses (fundamental niche) to the nutrient and pH status of the substrate and to compare them with the ecological responses (realized niche).

4.2 Methods

4.2.1 Experiment 1

This experiment considered the effect of nutrient level and pH on growth rates of *P. aspleniifolius*, *A. biglandulosum*. The wide-spread rainforest dominant, *Nothofagus cunninghamii*, was also included as a basis for comparison to the potentially largest, and fastest growing, rainforest tree. The experiment included samples from two populations of *P. aspleniifolius* and *Nothofagus cunninghamii* and one of *A. biglandulosum* (due to the rarity of seedlings). All seedlings were collected from the field as young as possible. *N. cunninghamii* was cotyledonous, *P. aspleniifolius* had juvenile leaves, and *A. biglandulosum* had only two sets of leaves. Samples of populations were taken from relatively high and low fertility substrates. Sample one of *Phyllocladus* (P1) was taken from a basalt soil and sample two (P2) from peat over a quartzite substrate. Sample one of *Nothofagus* (N1) was taken from a shale soil and sample two (N2) was taken from peat over sandstone. The *Anodopetalum* sample (A1) was taken from peat over quartzite.

All wildlings were grown in slimline pots in sand and vermiculite for at least three months before beginning the treatments to ensure that they were well established, and to exhaust nutrient reserves from the collection sites.

The experiment was designed in randomised blocks containing the four treatments and three replicates. Each replicate contained seven individuals of each of the five sample populations, i.e. 21 specimens of each species-sample per treatment. The plants were chosen for each replication of each treatment using a stratified random subsample based on three classes of seedlings: large, medium and small. The height of each specimen was measured at day one of the experiment. A Kruskal-Wallis ANOVA indicated no significant difference in heights at day one within species between treatments. An additional subsample of 12 plants for each sample was measured and weighed to provide an estimate of the starting biomass of each plant.

The treatments included a full strength and a 1/10th of full strength Hoaglands nutrient solution, plus aluminium, at pH 4.0 and pH 6.5. The nutrient recipe is in Appendix 3. The treatments were:

1. full strength solution, pH 6.5 (full pH 6.5)
2. full strength solution, pH 4.0 (full pH 4)

3. 1/10th of full strength solution, pH 6.5 (1/10 pH 6.5)
4. 1/10th of full strength solution, pH 4.0 (1/10 pH 4)

Each plant was placed in the nutrient solution. The nutrient solution was drained and its pH adjusted daily, it was re-applied using a plastic watering can, dowsing the plants to ensure the solution leached through the substrate. This allowed the pH of the leachate to be measured ensuring correct levels. The pH of the standing solution remained within 0.3 pH of its application level for the duration of the experiment.

At the end of the experiment, the final heights, biomass, and root:shoot ratios were measured. The results for each of these attributes were analysed using a pair-wise Kruskal-Wallis one way analysis of variance.

4.2.2 Field Measurement

The ecological response of *P. aspleniifolius* and *A. biglandulosum* to a fertility and pH gradient was considered in the field using a selection of sites of different geological substrates and ages. This measurement aimed to determine the relationship between the growth responses obtained in experiment 1 and the expression of those responses in the field. The field sites were all located in a relatively small area of complex geological variation centred on the Mt Read volcanics in the west of the state. This was intended to minimise regional climatic variation. Eight sites were selected over a range of elevation from 120 to 760 m a.s.l.

The sites were selected to represent a gradient in the comparative status of *P. aspleniifolius* and *A. biglandulosum*; four sites supported *P. aspleniifolius* and *A. biglandulosum* in various abundance, one site *A. biglandulosum* only, one site *P. aspleniifolius* only and two sites neither. At each site floristic and structural data were collected from a quadrat measuring 20x20 m. The species present were recorded from seven strata between 0 and 41 m; <1, 1-2.5, 2.5-5, 5-8, 8-15, 15-27, 17-41. The percentage cover of each strata was also recorded. The basal area of *P. aspleniifolius* and *A. biglandulosum* was estimated from stem diameters.

The geology and geological age of the substrate was noted at each site. A soil pit was dug to the depth of the B horizon to determine the depth of the O and A horizons and depth to the B horizon. A sample of soil from the A1 horizon was removed for analysis. The colour of each sample was determined using a Munsell soil colour chart. The pH of

the soil sample in deionised water (1:1) was measured using a portable pH meter (Hannah HI 8424).

The A horizon total phosphorus (ppm) was determined using a method described in detail in Jackson (1958). In brief, duplicate dry and finely ground 5 mg soil samples were digested in HNO_3 and HClO_4 . When digestion was complete, the vanadomolybdophosphoric yellow colour method in nitric acid was used to produce colour for measurement of light absorbents in a Hach DR 2000 spectrophotometer. Absorbents was measured at 470 nm and Beer's law was applied to determine the total amount of P present in ppm.

Total nitrogen (%) in the A horizon was measured using the Kjeldahl method, also described in Jackson (1958). Duplicate finely ground and dried 5 mg soil samples were digested in concentrated H_2SO_4 . The digestion was distilled into boric acid containing a mixed colour indicator. N/14 HCl was used for back titration.

The following equation was applied to calculate total N (%) in each soil sample;

$$\text{Nitrogen \%} = (T-B) * N * 1.4/W$$

T= titration of sample, ml N/14 HCl

B= standardized titration, ml N/14 HCl for blank

N= normality of acid

W= weight of soil

Analysis of Strata

The structural data collected during the field measurement were reconstructed diagrammatically to illustrate the structural differences between callidendrous, thamnisc and implicate forest types. For this analysis, data from each forest was collected from a seven height ranges. All species with heights in each range were included together. For each particular forest the height ranges (when present) were assigned to one of six strata 1. emergent, 2. dominant, 3. sub-dominant, 4. shrubs, 5. ground layer including ferns, lilies and other low plants and 6. epiphytic ferns. This was considered useful under the assumption that species in structural groups are in competition for resources (Mueller-Dombois and Ellenberg 1974), and presumably this occurs irrespective of their life-form or age. Each strata was thus characterised by its floristic composition, the growth forms present and its diversity.

4.2.3 Experiment 2

This trial was designed to determine the effect of interspecific competition on the growth of *P. aspleniifolius* and *A. biglandulosum*.

The treatments were; (1) two *P. aspleniifolius* per separate pot and two *A. biglandulosum* per separate pot, and (2) one of each per pot. A control treatment in which single individuals were grown in each pot was included to determine the growth rates free from any competition. Two soil types were used, one derived from quartz and the other from dolerite. The plants were grown in slimline pots containing 2/3 field soil and 1/3 sand to improve the drainage and reduce expansion and contraction of the field soils with the wetting and drying cycle.

The experiment was completely randomised within each of two blocks. Each block contained five replicates of each combination of species in each soil type. The starting height and number of leaves of each plant was measured. The pots were placed in a glass house and watered regularly using tap water for one year. Due to the expectation of very slow growth rates the environment was manipulated in an attempt to increase the length of the growing season. The temperature was not allowed to drop below 8° C during winter and the photoperiod was maintained at a minimum of 12 hours during winter. The position of each pot within each block was altered occasionally to reduce the effect of location in the glasshouse. The results were analysed using a one-way ANOVA.

4.2.4 Spatial Relationships

The spatial relationship between the two species in the field was tested to detect association or disassociation in space that was greater than that attributable to chance. A selected group of quadrats was chosen based on at least 30 separate subplots within the quadrats being occupied by either species. The subplots measured 3X3 m and the presence of one or both species was tabulated in a 2X2 contingency table before testing for a Chi-square distribution by applying the following formula:

$$X^2 = (ad - bc)^2 * n / (a+b)(c+d)(a+c)(b+d)$$

Where n = the total number of subplots

a = the total number of subplots containing both species

b= the total number of subplots containing species b but not species a

c= the total number of subplots containing species a but not species b

d= the total number of subplots containing neither species.

4.2.5 Nitrogen fixation

P. asplenifolius was tested for its ability to fix atmospheric nitrogen using the methods detailed by Hardy *et al.* (1973). Samples of roots from each of the above populations were cleaned of soil and other foreign organic particles before being placed in 40 ml test tubes and sealed with a gastight Subseal. Four ml of acetylene was injected into test tubes using a syringe. Gas samples of 0.5 ml were extracted after one hour. The samples were analysed using a Pye Unicam Series 104 gas chromatograph. The chromatograph was equipped with a 1.5 m Porapak R column which was run at 50° C. The carrier gas was nitrogen at a flow rate of 35 ml/min. The column was calibrated.

This method works on the principle that acetylene reduction produces a ratio of ammonium to nitrogen of 3:1. Any increase in the amount of nitrogen may be as a result of fixation by the plant roots or a symbiotic organism. A positive result requires confirmation by a more sensitive method but a negative response can be interpreted absolutely.

4.2.6 Aluminium accumulation

A. biglandulosum was assessed for indications of Al accumulation. This was achieved by using an electron probe. Thin sections of *A. biglandulosum*, one from a quartzite soil and the other from a basalt soil, were scanned using an electron probe. The probe assesses the elemental composition of the specimen by identifying emitted X-ray signatures which are indicative of the identity and abundance of elements.

The electron beam was focused on areas of accumulation of what was suspected to be Al succinate. These accumulations were clearly visible under a low power stereo microscope. The beam was also focused on other areas of the thin sections at random and at other anatomical features.

4.3 Results

4.3.1 Experiment 1

Significant differences within samples and between treatments are indicated in Table 4.1. The average responses of samples within species are compared in Figure 4.1. The nutrient level appears to be the predominant influence over plant productivity.

Biomass (Table 4.1) For P1 (*Phyllocladus* from fertile soil) and P2 (*Phyllocladus* from infertile soil) there is no significant differences between treatments. For N1 (*Nothofagus* from fertile soil), biomass is significantly higher in treatments full pH 6.5 and full pH 4 than in treatment 1/10 pH 6.5. Treatment 1/10 pH 4 is intermediate and is not significantly different from the highest or the lowest results. For N2 (*Nothofagus* from infertile soil), the biomass after treatments full pH 6.5 and full pH 4 is significantly higher than after treatments 1/10 pH 6.5 and 1/10 pH 4. For A1 (*Anodopetalum* from infertile soil) treatments full pH 4, 1/10 pH 6.5 and 1/10 pH 4 are not significantly different and are all significantly higher than treatment full pH 6.5.

Height change (Table 4.1) The response of height did not reflect biomass relationships in all cases. For P1, treatments full pH 6.5, full pH 4, and 1/10 pH 4 are similar and are greater than treatment 1/10 pH 6.5. For P2, treatments full pH 6.5 and full pH 4 are significantly higher than treatments 1/10 pH 6.5 and 1/10 pH 4. For N1 treatments full pH 6.5 and full pH 4 produced the greatest change in height and are significantly higher than both other treatments, of which 1/10 pH 4 is higher than 1/10 pH 6.5. For N2, the pattern of response is similar to N1. For A1, treatments full pH 4 and 1/10 pH 4 are statistically similar and significantly different to treatments 1/10 pH 6.5 and full pH 6.5.

Root length (Table 4.1) For P1, full pH 6.5 and full pH 4 roots were significantly longer than after treatment 1/10 pH 4. Treatment 1/10 pH 6.5 produced an intermediate response. For P2, treatment full pH 4 produced a significantly longer root than treatment 1/10 pH 6.5; all other treatments were similar. For both N1 and N2 there were no significant differences between treatments. For A1, treatment full pH 6.5 was significantly different to full pH 4 and 1/10 pH 4 while 1/10 pH 6.5 was not significantly differently different to any other treatment.

The root:shoot ratios (Table 4.2) indicate increased investments in roots than shoots for P2, N1 and N2 under the low nutrient treatments (1/10 pH 6.5 and 1/10 pH 4). For P1 no differences are clear. Treatment full pH 4 produced a high root to shoot ratio in A1; otherwise there are no clear differences.

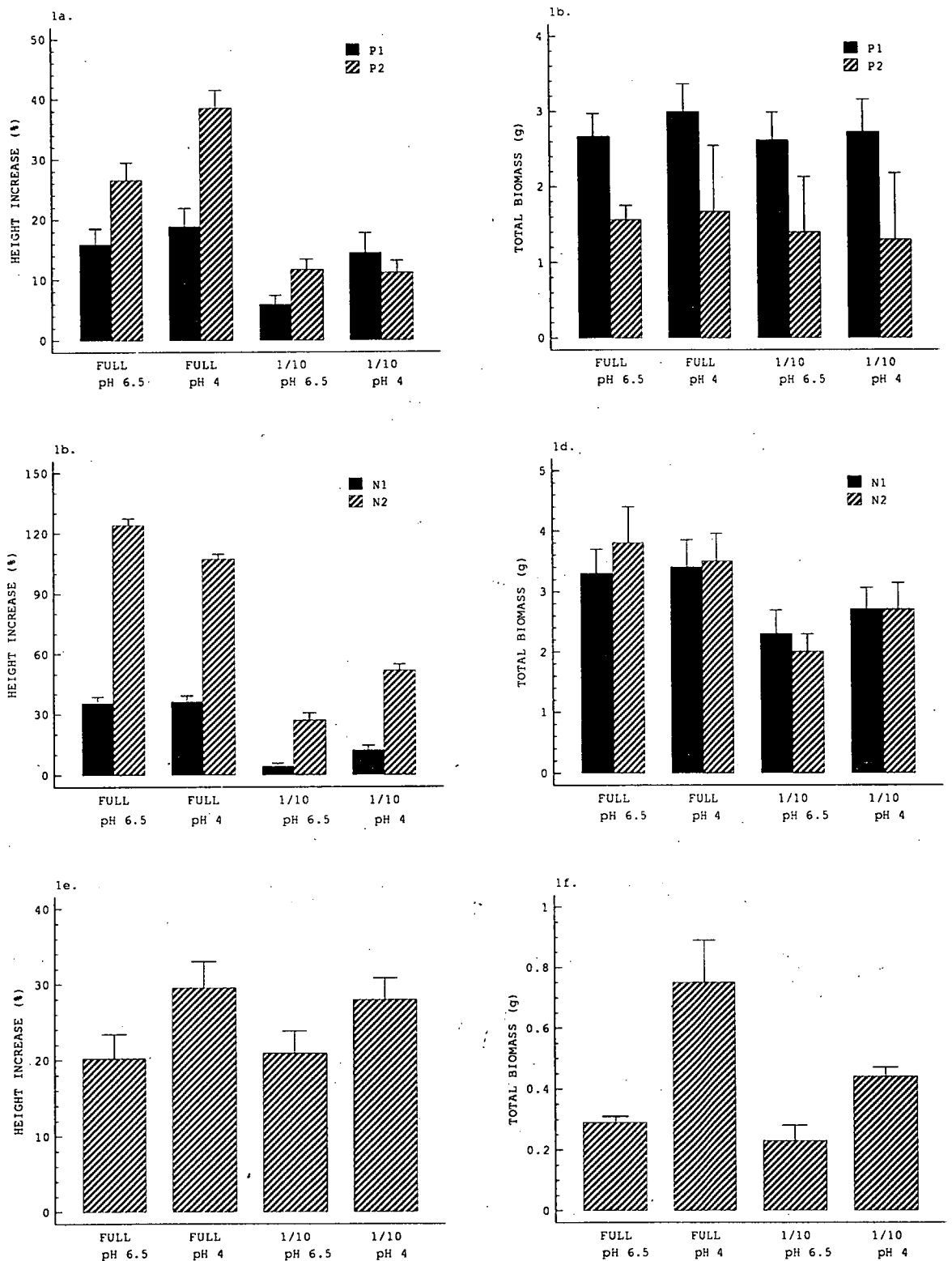


Figure 4.1. Bar graphs of the means and standard errors of the growth (change in height (%)) and total biomass (g) after four treatments on two provenances of 1a and b. *P. aspleniifolius*, 1c and d. *N. cunninghamii*, 1e and f. one provenance of *A. biglandulosum*.

Table 4.1. Growth responses for total biomass, change in height and root length. P1- *Phyllocladus* sample 1; P2- *Phyllocladus* sample 2; N1- *Nothofagus* sample 1; N2- *Nothofagus* sample 2; A1- *Anodopetalum* sample 1. Different superscripts (a, b and c) indicate significant differences (* $P < .1$, $P < .05$, ** $P < .01$) between the average rank from a Kruskal-Wallis one-way ANOVA within populations (rows).

Sample	Full pH 6.5	Full pH 4	1/10 pH 6.5	1/10 pH 4
Biomass				
P1	41.90	46.64	40.38	40.88
P2	42.9	48.85	38.47	39.57
N1	46.28 ^a	48.47 ^a	33.78 ^b	41.45 ^{ab}
N2	49.14 ^a	49.57 ^a	31.64 ^b	39.64 ^b
A1	23.79 ^{b**}	49.90 ^{a**}	39.80 ^a	40.95 ^a
Height				
P1	47.26 ^{a**}	47.76 ^{a**}	30.78 ^{b**}	48.50 ^{a**}
P2	51.78 ^{a**}	58.38 ^{a**}	28.66 ^{b**}	31.16 ^{b**}
N1	57.95 ^{a**}	60.00 ^{a**}	19.50 ^c	32.54 ^{b**}
N2	58.54 ^{a**}	56.66 ^{a**}	20.16 ^{c**}	34.61 ^{b**}
A1	34.33 ^b	49.28 ^a	37.88 ^b	48.50 ^a
Root Length				
P1	57.42 ^a	51.21 ^a	40.05 ^{ab}	24.84 ^{b**}
P2	39.85 ^{ab}	53.57 ^a	33.00 ^{b*}	47.55 ^{ab}
N1	33.00	56.35	46.71	37.92
N2	51.29	36.21	42.61	45.84
A1	60.50 ^a	32.57 ^{b*}	35.35 ^{ab}	34.71 ^b

Table 4.2. Root to shoot ratios and standard errors of the mean for 21 specimens and 4 treatments. P (*P. asplenifolius*); N (*N. cunninghamii*); A (*A. biglandulosum*). 1 and 2 refer to populations.

	Root:Shoot	(se)
P1		
Full pH 6.5	0.841	(.14)
Full pH 4	0.734	(.07)
1/10 pH 6.5	0.760	(.04)
1/10 pH 4	0.797	(.06)
P2		
Full pH 6.5	0.671	(.06)
Full pH 4	0.725	(.05)
1/10 pH 6.5	1.299	(.22)
1/10 pH 4	1.040	(.09)
N1		
Full pH 6.5	1.15	(.11)
Full pH 4	1.09	(.09)
1/10 pH 6.5	1.63	(.06)
1/10 pH 4	1.57	(.11)
N2		
Full pH 6.5	0.542	(.04)
Full pH 4	0.609	(.05)
1/10 pH 6.5	0.908	(.04)
1/10 pH 4	0.799	(.05)
A1		
Full pH 6.5	0.876	(.12)
Full pH 4	2.430	(.77)
1/10 pH 6.5	0.968	(.08)
1/10 pH 4	0.852	(.07)

Table 4.3. A summary of the variables measured at eight rainforest sites. A- *A. biglandulosum* present; P- *P. aspleniifolius* present; Cal- callidendrous, Th- thamnisc, Imp- implicate rainforest.

Site	pH	P ppm	N%	Geology	Altitude	Type
1	4.6	975	0.65	Dolerite	680 m	Cal
2	5.1	560	0.27	Fe rich mudstone	180 m	Cal
3	4.4	69	0.13	Alluvium	120 m	Cal/Th A
4	4.2	229	0.40	Andesite	760 m	Th, P
5	4.5	105	0.14	Black shale	640 m	Th/Imp A, P
6	4.3	133	0.15	Clay till on siltstone	240 m	Tall Imp A, P
7	4.5	37	0.20	Conglomerate till	640 m	Imp A, P
8	4.5	46	0.20	Felsic volcanic	620 m	Imp A, P

4.3.2 Field measurement

The soil data (three variables) from the eight sites were analysed using principal components analysis (Figure 4.2, Table 4.3). The plot of the first two principal components illustrates the distribution of the sites in relation to the variables measured. The eight sites show a considerable degree of spread along the vectors representing variation in each of pH, %P and %N. A canonical correlation between all soil variables and the first two MDS axes indicate a strong linear relationship between soil pH, P(ppm) and %N on the one hand, and the floristic indices on the other (Figure 4.3). The callidendrous types are clearly different from the thamnisc and implicate types which tend to be more closely associated.

Although the callidendrous forest occurred on the sites with the highest pH some thamnisc and implicate forests occurred on sites with pH only marginally lower. However, *P. aspleniifolius* and *A. biglandulosum* were relatively more important in the forests on the sites with the lowest and intermediate pH (Table 4.3).

A dichotomy in the distribution of P (ppm) is evident in the data with callidendrous forest occurring on sites with high P and thamnisc and implicate on sites with intermediate and low soil P. The diagram in Figure 4.4 illustrates the structural differences along this gradient and indicates increasing complexity under lower P and lower pH. The number of and diversity in each strata also increase along the same gradient (Table 4.4). The abundance of *P. aspleniifolius* and *A. biglandulosum* at the eight sites is variable. Generally, the basal area is highest for both species in the thamnisc forest types (4, 5 and 6) but declines in the less productive implicate types. Both species are absent from the two callidendrous forests.

On the most fertile sites at which *P. aspleniifolius* is present it occupies only the dominant stratum. This suggests that it is not regenerating at these sites, whereas at the less productive sites with a more complex structure it is present in all possible strata. *A. biglandulosum* is only a member of the dominant stratum at sites 7 and 8 where the canopy is less than eight metres high. At sites 3, 5 and 6 *A. biglandulosum* increases in height but is not present in the dominant stratum, being confined to the subdominant, shrub and ground fern strata.

The basal area, soil P and pH results broadly concur with the results from experiment 1. This may indicate that total P and a critical pH value may be delimiting nutrient availability on these sites. This level of pH would also be critical with regard to the status of Al in the soil, Al being soluble at pH 5 and less.

Biplot for First Two Principal Components

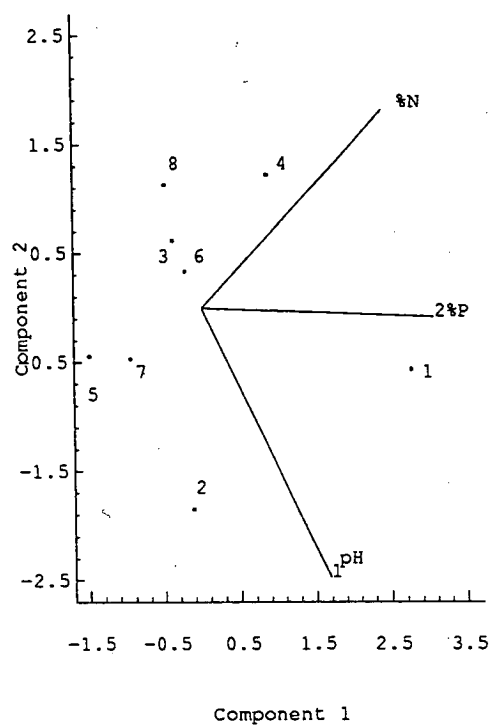


Figure 4.2. A scatter plot of the first two principal components. The length of the vectors indicates the relative strength of each variable in relation to the spread of the data points.

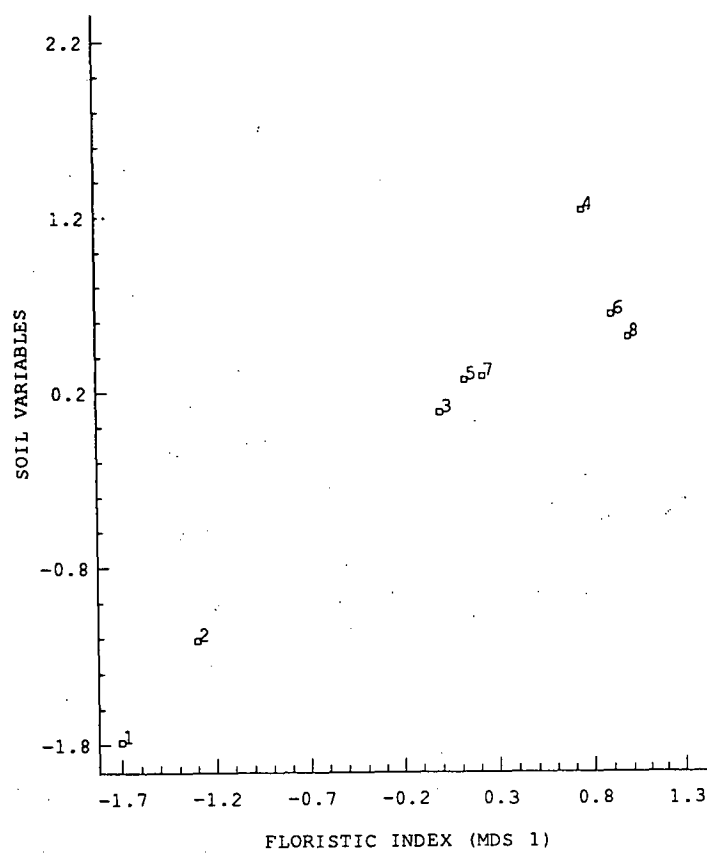


Figure 4.3. Canonical correlation analysis of eight sites using soil variables % P, % N and pH (Y axis) and floristic scores from the first two Multidimensional scaling axes (X axis).

Table 4.4. The strata and number of member species for eight sites in the Mt Read region of Tasmania. The subscripts indicate the presence of # *P. aspleniiifolius* and * *A. biglandulosum* in a particular strata; 1. emergent, 2. dominant, 3. sub-dominant, 4. shrubs, 5. ground layer including ferns, lilies and other low plants and 6. epiphytic ferns.

Strata						
Site	1	2	3	4	5	6
1		1	1	1	3	
2		1	1		3	4
3		4	4*	4*	2	2
4		2#	1	4	2	
5		3#	2*	4*	3	
6	1#	4#	4*	6*	3	1
7	2	5#*	8#*	8*	1	
8		5#*	7#*	10#*	3	

The results of the first experiment generally concur with the observations and measurements made in the field. *Nothofagus cunninghamii* dominates the most fertile substrates in the absence of *P. aspleniiifolius* and *A. biglandulosum*. *P. aspleniiifolius* and *A. biglandulosum* increase basal area with increasing soil fertility but only share canopy dominance with *Nothofagus cunninghamii* on the relatively infertile sites (Figures 4.3 and 4.4, Table 4.3).

Table 4.5. The summary data from eight quadrats containing n subplots measuring 3x3 m. The data record the number and condition of all subplots at each site as follows:

A= *P. aspleniifolius* and *A. biglandulosum* present

B= *A. biglandulosum* only

C= *P. aspleniifolius* only

D= *P. aspleniifolius* and *A. biglandulosum* absent

n= A+B+C+D

All χ^2 values are insignificant at the 0.05 level indicating that *P. aspleniifolius* and *A. biglandulosum* tend to be distributed randomly throughout the forest.

Site	1	2	3	4	5	6	7	8
A	1	1	2	3	2	1	1	3
B	10	6	7	8	24	15	22	22
C	11	11	22	5	17	9	8	17
D	106	14	65	16	85	71	97	86
n	128	32	96	32	128	96	128	128
χ^2	0.001	2.06	0.01	0.01	0.71	0.39	0.56	0.31

P < 0.05

Table 4.6. One-way analysis of variance and a multiple range test for the growth responses of *P. aspleniifolius* and *A. biglandulosum* free from competition (1,4); in interspecific competition (2,5); and in intraspecific competition (3,6) on dolerite (a) and quartzite (b) soils. Non-significant differences ($P < 0.05$) are indicated by X's in the same columns, and between treatment totals irrespective of species and soil type.

P. aspleniifolius

Source of variation	SS	d.f.	MSS	F	Sig.
Between treatments	46.48	5	9.29	2.08	0.075
Within treatments	330.83	74	4.47		
Total (corrected)	377.32	79			

Treatment	Count	Average	Homogeneous Groups
3a	20	3.15	X
2a	10	3.72	XX
1a	10	4.43	XX
5b	10	4.89	X
6b	20	4.89	X
4b	10	5.09	X

A. biglandulosum

Source of variation	SS	d.f.	MSS	F	Sig.
Between treatments	87.31	5	17.46	2.54	0.035
Within treatments	507.91	74	6.86		
Total (corrected)	595.23	79			

Table 4.6. continued.

Treatment	Count	Average	Homogeneous Groups
5b	10	1.23	X
4b	10	1.83	X
6b	20	2.75	XX
3a	20	3.01	XX
2a	10	4.35	X
1a	10	4.52	X

Source of variation	SS	d.f.	MSS	F	Sig.
Between treatments	378614	2	189306.79	1.495	.2271
Within treatments	21141086	167	126593.33		
Total (corrected)	21519699	169			

0 missing value(s) have been excluded.

4.3.3 Experiment 2

A summary of the results of a competition trial appear in Table 4.6. Before the trial commenced a one-way ANOVA indicated that there was no significant difference amongst the initial intraspecific heights. At the end of the trial there was no block effect detectable for all treatments and both species.

The analysis of variance of the transformed data (log normalised) does not indicate significant differences between plants grown singularly and those in competition. This result is consistent for inter and intraspecific competition (Table 4.6, Figure 4.5). Nor are there significant differences between the growth rates in inter versus intraspecific competition. However, there is a consistent trend in which the highest growth rate is recorded in single plant treatments, followed by those in interspecific competition and finally those in intraspecific competition. The consistency in this trend, both between the species and between the treatments, suggests that significant results may have been obtained if the experiment ran for a second year.

The data trend indicates that both *P. aspleniifolius* and *A. biglandulosum* have performed better in competition with each other than in competition with a con-specific (i.e. growth where the niche may be partitioned versus growth with a trophic equivalent). There is no evidence to suggest that either species benefits from growing with the other.

A pair-wise comparison of the growth response of *P. aspleniifolius* for all treatments indicates that intraspecific competition on dolerite produces a significantly lower growth rate than any quartz treatment. There are no significant differences between any other treatments involving *P. aspleniifolius*.

A similar analysis of *A. biglandulosum* growth response indicates that the growth rates of single plants and those in interspecific competition are higher in dolerite than in quartz. Intraspecific growth rates are similar in both soils.

The higher growth rate of *P. aspleniifolius* in quartz as compared to dolerite was not expected due to the inherently lower fertility of quartz. However, the consistency across all treatments suggests that the result is not erroneous. The reversal in the expected response results in a reversal in the competitive relationship between *P. aspleniifolius* and *A. biglandulosum* on different soils. *P. aspleniifolius* performs better than *A. biglandulosum* in competition on quartz, whereas *A. biglandulosum* performs better than *P. aspleniifolius* in competition on dolerite.

4.3.4 Nitrogen Fixation

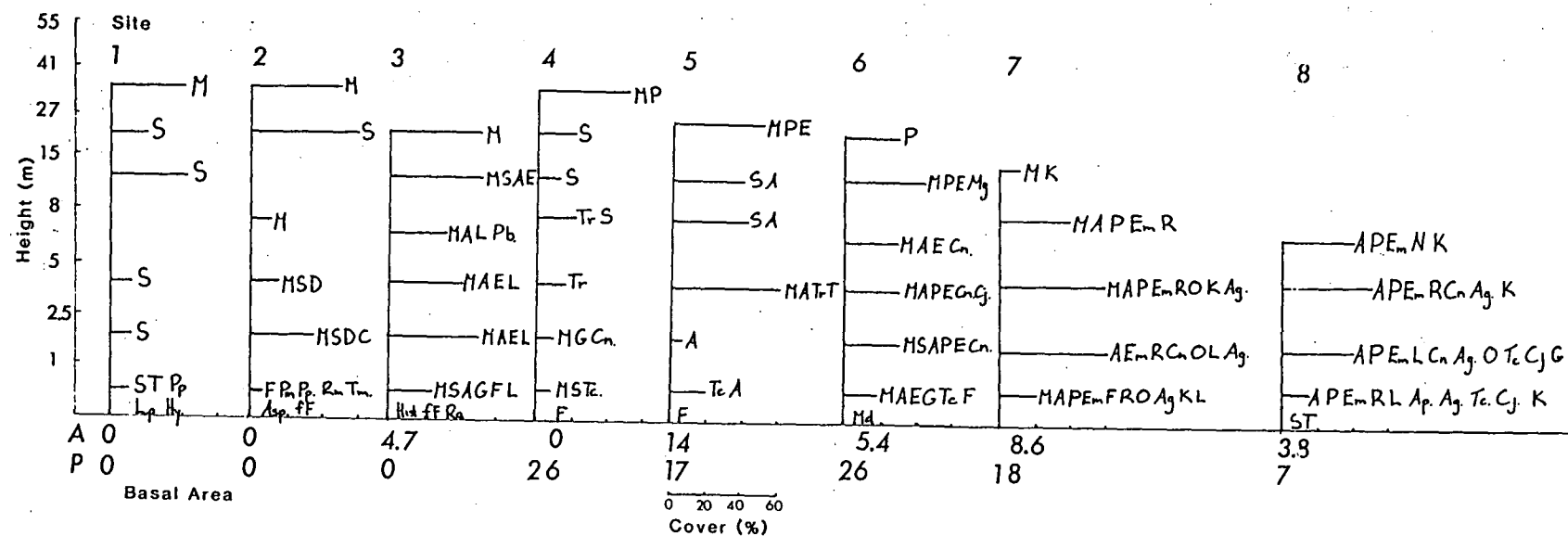
The roots of *P. aspleniifolius* did not produce any nitrogen that was able to be measured using the methods outlined by Hardy *et al.* (1973). No further analysis was considered necessary in the light of this result.

4.3.5 Aluminium Accumulation

The accumulations of suspected Al succinate assessed using the electron probe were organic; they did not contain any accumulation of Al. No other areas on the thin sections showed Al accumulation greater than background quantities.

Figure 4.4. A diagram indicating the height, % cover and floristic composition of strata at eight sites along a soil fertility and pH gradient in western Tasmania.

A. <i>A. biglandulosum</i>	Pp. <i>Polystichum proliferum</i>
P. <i>P. aspleniifolius</i>	Lp. <i>Libbertia pulchella</i>
M. <i>Nothofagus cunninghamii</i>	Tm. <i>Tmesipteris billardieri</i>
S. <i>Atherosperma moschatum</i>	Rm. <i>Rumorha adiantiformis</i>
D. <i>Dicksonia antarctica</i>	Asp. <i>Asplenium</i> spp.
C. <i>Coprosma quadrifida</i>	fF. <i>Hymenophyllum</i> spp.
E. <i>Eucryphia lucida</i>	Pb. <i>Pittosporum bicolor</i>
L. <i>Anopterus glandulosus</i>	Cn. <i>Cenarrhenes nitida</i>
G. <i>Gahnia grandis</i>	Tc. <i>Trochocarpa cunninghamii</i>
F. <i>Blechnum wattsii</i>	Tr. <i>Trochocarpa gunnii</i>
T. <i>Tasmania lanceolata</i>	Mg. <i>Monotoca glauca</i>
K. <i>Athrotaxis selaginoides</i>	Cj. <i>Cyathodes juniperina</i>
R. <i>Richea pandanifolia</i>	Md. <i>Microsorium diversifolium</i>
O. <i>Olearia persoonioides</i>	Ag. <i>Agastachys odorata</i>
N. <i>Nothofagus gunnii</i>	Ap. <i>Aristotelia peduncularis</i>
	Em. <i>Eucryphia milliganii</i>
	Hist. <i>Histiopteris incisa</i>



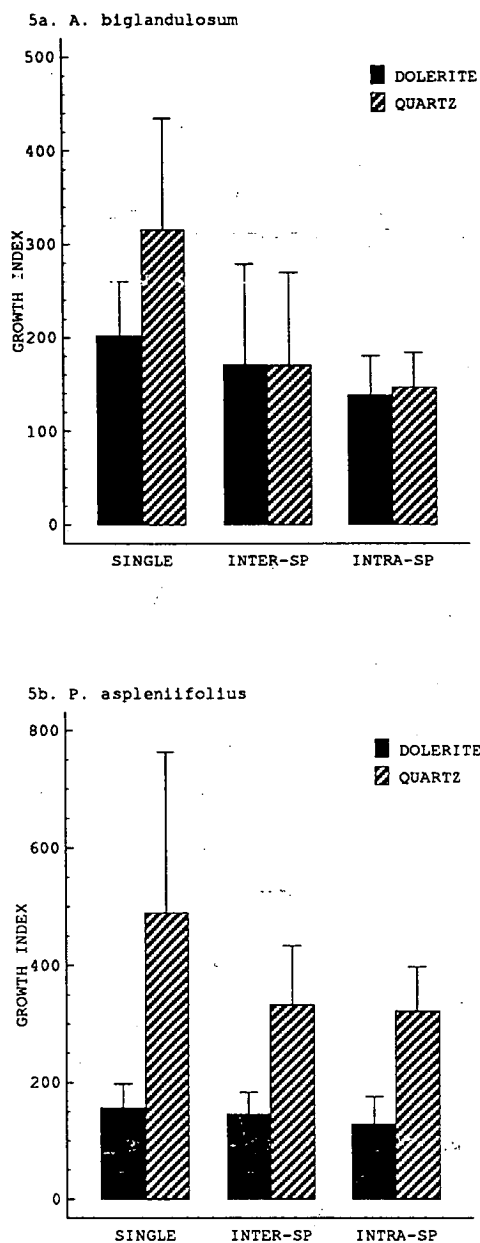


Figure 4.5. Means and standard errors of growth index (change in height % * change in number of leaves) in pot trials in two soils for a. *P. aspleniifolius* and b. *A. biglandulosum* after three treatments: a single plant; in inter-specific competition; in intra-specific competition.

4.4 Discussion

In the first experiment, the three species differed in the growth responses that were measured, and this reflects the differential success in competition on different substrates in the field. Differences between the provenances, of *P. aspleniifolius* and *N. cunninghamii* are also evident, particularly in the change in height (Figure 4.1). The height of a species is important as it determines the relative position of the canopy in the forest structure at which it must compete for light and space (Figure 4.4) (Horn 1971, Givnish 1982). For *P. aspleniifolius* (P2) and *Nothofagus cunninghamii*, the greatest height response is to full strength nutrient treatments regardless of pH. The greater height in the acid low nutrient treatment compared to the 1/10 pH 6.5 treatment is not apparent as total biomass nor are there differences in root length. The difference in height may reflect more efficient translocation of nutrients, particularly phosphorus, from the roots to the stem, inducing increased meristem cell division or cell elongation (Russell 1973).

The height of *A. biglandulosum* indicates a preference for acid sites which are often infertile and support vegetation characterised by an emergent open canopy (Figure 4.4). The openness of the forest canopy may be important in allowing a small tree to gain enough light. However, on fertile acid sites, such as on basalt soils in north-western Tasmania, *A. biglandulosum* is also sometimes well represented in the understorey, but normally in communities in which the understorey is not diverse.

Except for *A. biglandulosum* in the high nutrient acid solution all plants produced their highest root:shoot ratios in the low nutrient treatments regardless of provenance. This is a common response to infertility which reflects the extra investment in roots that plants require to extract nutrients from infertile substrates (Grime 1979). In the high nutrient acid treatment, *A. biglandulosum* produced short dense roots and a very high root:shoot ratio but increased height significantly more than at pH 6.5 regardless of nutrient level. The strong growth response at pH 4 and high mortality in pH 6.5 suggests that the soil pH may be more important than nutrient level for the growth of *A. biglandulosum*.

The quantity of biomass produced by *P. aspleniifolius* was insensitive both to nutrient level and to pH, however, the basalt provenance (P1) produced more biomass under all conditions though it was not reflected in height growth. The reversal in the comparative performance between the provenances, when expressing the height increment as biomass, suggests that genetic differences exist between the provenances that are reflected in both growth rate (biomass) and growth form (height) and that the

provenance from the fertile basalt is more efficient at the uptake and metabolism of nutrients.

In a study of north-west Pacific pines, Ryan *et al.* (1986) concluded that the five species they studied were tolerant of acid solutions and high aluminium levels compared to agronomic plants. In fact, two of the three species studied displayed better growth at pH 3 and 175 ppm aluminium (a relatively high level). The present results do not support a beneficial effect of either low pH nor the presence of aluminium, instead they lend support to the contention that *P. aspleniifolius* is relatively insensitive to pH.

For *A. biglandulosum* and *Nothofagus cunninghamii*, the generally higher growth responses in acid treatments may indicate the beneficial effect of a low concentration of aluminium on the uptake and translocation of phosphorus when nutrients are at low concentrations (Figure 4.1) (Ryan *et al.* 1986). This effect can only be realized when aluminium is in an acid solution making it available and the interaction possible.

The better performance of *A. biglandulosum* under acid conditions, regardless of nutrient level, concurs with the arguments of Webb (1953). Webb indicates that aluminium accumulators perform best on acid sites. *A. biglandulosum* was not able to be confirmed as an accumulator in this study. This does not, however, necessarily exclude it from such potential, as taxa may be facultative accumulators, or they may accumulate Al in tissues other than those tested here. More sampling would be necessary to ascertain whether or not it is the case.

The three species responses to the nutrient regimes applied in this experiment are different. There is evidence to suggest that sensitivity to soil pH is a factor which delimits performance, particularly on infertile substrates. The relative insensitivity of *P. aspleniifolius* helps to explain its broad edaphic range even allowing for other considerations such as vagility and historic factors. On the other hand, *N. cunninghamii* is clearly affected by pH and fertility and this is reflected in its more variable field performance. This result agrees with the findings of Read (1985a) who grew *P. aspleniifolius* and *N. cunninghamii* in field soils and noted that *N. cunninghamii* showed a marked decrease in performance compared to *P. aspleniifolius* on the most infertile soil.

The maintenance of the production of biomass on infertile substrates by *P. aspleniifolius* may be facilitated by a mycorrhizal association (Baylis *et al.* 1963). A mycorrhizal association makes nutrients available (notably phosphorus) which may not normally be available to a plant on acid substrates or on substrates that are inherently low in

nutrients. A mycorrhizal association may also explain the fairly uniform results across treatments. This may be true if the effect of the association out-weighs the biochemical and physiological processes involved in nutrient uptake, particularly the uptake of phosphorus.

Although no capacity for the roots of *P. aspleniifolius* to fix atmospheric nitrogen was detected in this study it is relevant to note that Bergerson and Costin (1964) measured nitrogen fixation associated with the roots of *Podocarpus lawrencei*. They argued that atmospheric nitrogen was fixed in a symbiotic relationship with an endophytic fungus. Although the rate of fixation was slow Barker (1991) measured soil nitrogen levels beneath *P. lawrencei* at greater than 2.4 % after 260 years without fire. Other authors have also studied nitrogen fixation in association with the rhizosphere of conifers and have concluded that nitrogen fixation can be attributed to soil-borne bacteria in the root region rather than endophytic organisms (Silvester and Bennett 1973, Richards 1972). If bacteria in the rhizosphere of *P. aspleniifolius* fix nitrogen, then other species which occupy the same sites may benefit from their association, particularly in the long term, on infertile or burned sites. However, *A. biglandulosum* did not benefit from growing with *P. aspleniifolius* in the competition experiment in the present study.

In the field, it is likely to be the relative abilities of other species, and the ability to avoid the hazards of low nutrients, which determines success on any given site (Grime 1979). This is evident between *N. cunninghamii* and *P. aspleniifolius* where *N. cunninghamii* dominates fertile sites in the field while *P. aspleniifolius* is equally dominant on infertile sites (Figure 4.4).

The correlation between community floristics and soil fertility (Figure 4.3), and the occurrence and abundance of *P. aspleniifolius* and *A. biglandulosum* within the communities that were observed (Figure 4.4), reflects the findings of the first experiment. This co-incidence is unusual as the physiological optimum of a species is not usually achieved nor expressed in the field due to the effects of competition (Gause 1934, Whittaker 1975, Austin 1985). *Pinus radiata* is a good example of the latter when planted as an exotic. However, the depauperate rainforests in Tasmania may support *P. aspleniifolius* and *A. biglandulosum* as members of communities in which they may otherwise have been excluded by competition from species from more diverse communities before Tertiary extinctions (Hill 1989, Jordan *et al.* 1991, Carpenter and Buchannan in prep.). Their presence across a large proportion of their potential niche may include their prime habitat permitting optimum ecological performance (Whittaker 1975).

The effect of a competitor with an identical niche (con-specific) is clearly illustrated by the intraspecific results in the competition experiment (Table 4.6, Figure 4.5). There is a strong tendency for *P. aspleniifolius* and *A. biglandulosum* to perform better in competition with each other than in competition with another plant of their own species. This result strongly reaffirms the concept that unless the use of a resource is stratified in space, or in time, then competition will occur and performance will decline (Hutchinson 1958).

In the most productive forests (sites 1 and 2, Figure 4.4), the trend towards monoculture has produced a simple canopy below which coexisting species are restricted by shading to the most shade tolerant taxa (ferns). The increased diversity in the subdominant and shrub strata on the lower fertility sites (Figure 4.4, Table 4.4) may be derived from the low habitat productivity. Grime (1979) argues that in low fertility environments, tree sizes are restricted to below sizes which could exert major dominance thus allowing coexistence with increasing diversity. Inherent infertility may also restrict below ground competition. The rapid growth of above ground biomass necessary for the production of photosynthates is dependent upon rates of nutrient uptake, which are dependent upon root development, all of which are restricted by low nutrient availability (Grime 1979). The result of this negative feedback is more space in the habitat for coexistence.

In depauperate forest formations, such as Tasmanian rainforest, competition may still be limiting distributions. The results of experiments 1 and 2 indicate that *P. aspleniifolius* and *A. biglandulosum* may be excluded from callidendrous forests by the faster growing *Nothofagus cunninghamii* (see Read 1985a) but otherwise are not displaced from communities by competition.

The relatively infertile habitats of the implicate and thamnic forests are those in which *P. aspleniifolius* and *A. biglandulosum* most commonly coexist. As such, Grime's premise of low competition on such sites includes a plausible explanation for the spatial stratification of the nutrient resource.

The effect of competition for nutrients in the rhizosphere may be a major determinant of the spatial relationships of plants both inter- and intraspecifically. In the field, established trees of *P. aspleniifolius* and *A. biglandulosum* are distributed in a random fashion (Table 6) in relation to each other. No measure of the spatial relationship between the canopies was attempted. However, as *P. aspleniifolius* is often taller than *A. biglandulosum* the effect of competition for light may impart a large affect on the spatial arrangement of establishment of *A. biglandulosum*. To comment on the degree to which

the photosynthetic response to light may affect the distribution and status of these species requires field measurement of the photosynthetic responses to various situations.

4.4.1 Conclusion

Phyllocladus aspleniifolius and *Anodopetalum biglandulosum* have different physiological responses to substrate fertility and pH. The biomass productivity of *P. aspleniifolius* was insensitive to nutrient and pH status while *A. biglandulosum* performed best in acid treatments. *P. aspleniifolius* demonstrated differences between the growth responses of the provenances inasmuch as the height increment of the high fertility basalt provenance was insensitive to a decrease in fertility, while the height increment of the low fertility provenance was greatest in high nutrient treatments. Both provenances of *N. cunninghamii* performed best in high nutrient treatments. In the field, the performance of all species is reflected by their physiological response. *P. aspleniifolius* and *A. biglandulosum* being found more abundant on sites of low fertility or low soil pH, and *N. cunninghamii* dominating the high fertility sites. However, both *P. aspleniifolius* and *A. biglandulosum* co-exist across a broad range of soil conditions indicating that neither species is severely confined by its physiological attributes to a narrow realized niche but rather are able to fill a large part of their potential niche.

The effect of competition between *P. aspleniifolius* and *A. biglandulosum* was weaker than the effect between conspecifics. However, *P. aspleniifolius* and *A. biglandulosum* tend to be spatially separated in the field more than would be expected due to chance.

P. aspleniifolius did not fix atmospheric nitrogen and aluminium accumulation was not detected in *A. biglandulosum*. However, further work is required, including more rigorous sampling from a range of soil types to determine the potential or otherwise for *A. biglandulosum* to accumulate aluminium. The apparent broad ecological amplitude of both species may be attributable to low competition in a floristically depauperate forest estate.

Chapter 5. Photosynthetic gas exchange responses of *Phyllocladus aspleniifolius* and *Anodopetalum biglandulosum* in the sun-canopy, gap and understorey environments.

5.1 Introduction

Morphological and physiological properties of plants play an important role in determining the relative success of species within communities. The competitive sorting and arrangement of species within communities is fuelled at the most fundamental level by competition for, and efficient use of, photosynthetically active radiation.

In forests, the light intensity varies between the canopy, where the intensity is often far in excess of a plants photosynthetic capacity, and the forest floor, where it may fall to levels too low for plants to grow at all. Light intensity varies horizontally, from undisturbed areas to disturbed areas of the forest (Chazdon & Fetcher 1984) and with structural differences imposed by the mosaic of forest types and ages in which a tree may grow (Torquebiau 1988). The availability of light also varies temporally with the diurnal and seasonal cycles and with the incidence of cloud (Field 1988). Within the extremes of such variation natural selection favours plants whose form and physiology are able to maximize the net rate of energy capture (Givnish 1988). Such maximization allows plants to reproduce and compete for space (Horn 1971).

The variability in the forest environment has often been simplified to address the question of exposure to either sun or shade (Berry 1975, Boardman 1977, Bjorkman 1981, Read 1985b) and also temperature (Bjorkman 1981, Read 1985a). However, measurement of the responses of single leaves to a range of environmental variables under controlled conditions may be of limited relevance in elucidating the physiological determinants of ecological success (Field 1988). The arrangement and properties of leaves in the canopy, the canopy shape, and resource allocation of photosynthates will directly affect a plant's performance and hence its niche in a community (Givnish 1988). Hence, plant responses to light have been investigated in the field for ecological significance (Horn 1971, Bjorkman *et al.* 1972, Bazzaz & Carlson 1982, Pearcy 1987, Givnish 1988, Doley *et al.* 1988, Kuppers 1989).

A focus on the variation in the field light environment and on plant responses to it will extend mechanistic studies to ecologically relevant contexts (Field 1988). Assessment of the capacity of a species to utilize light, is therefore, useful in the question of community dynamics and species coexistence. Clearly then, it is desirable to measure the light

environment and the photosynthetic performance of a species at different times and positions in the community structure to determine the range of its photosynthetic performance. From this state of knowledge, valid comparison can be made between species that coexist in terms of their status in the dynamics of the community.

Aims

In this chapter the photosynthetic gas exchange of *Phyllocladus aspleniifolius* and *Anodopetalum biglandulosum* will be compared and contrasted at the sun-canopy, in the understorey and gap environments. The aim is to assess the degree to which the photosynthetic performance of the different phenological stages in the three environments is reflected in the phytosociology and population dynamics of *P. aspleniifolius* and *A. biglandulosum*.

5.2 Materials and Methods

Physiological observations were made on three specimens of both *Anodopetalum biglandulosum* and *Phyllocladus aspleniifolius* growing in the forest. The specimens included a mature sun-canopy tree, an understorey sapling and gap phase regrowth of each species.

Five leaves were labelled on each plant. All leaves were randomly selected from fully expanded, current seasons growth which were all located in the outer canopy. The same leaves were used throughout the experiment except if they were damaged, then a new leaf was selected. Replacement was only required on two occasions. Care was taken to ensure readings were made when the leaf was as near as possible to a natural orientation, although this was sometimes difficult in times of wind gusts.

The sun-canopy position was 12 m above the ground and was accessible using tree climbing ladders to a platform built in the canopy of the *P. aspleniifolius*. The canopy of the *A. biglandulosum* was within reach from the same platform. The leaves of the two understorey specimens were at two metres above the ground and below a subcanopy at four metres above the ground; they were 10 m apart and thus were in different light environments. The gap phase individuals were in a gap measuring 15 m across. The *P. aspleniifolius* was a seedling 0.25 m tall while the *A. biglandulosum* leaves were on sprouts from a fallen stem. Resprouting is the typical response of *A. biglandulosum* in gap phase regrowth (See chapter 7). All individuals were within an area less than 25 m across.

Measurements were made on eight days: March 7th, 8th, 12th and 13th and in July on the 11th and 27th. Seasonal precipitation had been near average and rain fell over night on the 6th and 11th of March. On the 11th of July a heavy frost occurred and all specimens were frosted until after 11 am; the gap was frosted all day. Light drizzle fell intermittently for much of the 27th of July. The leaves were dried with a soft absorbent cloth before measurements were made.

Five sets of measurements per day were made in March between 700 and 1700 hours and three sets per day were made in July between 900 and 1500 hours. Rates of carbon dioxide exchange were measured using an Analytical Development Company (ADC) portable infra-red gas analyser (LCA-2 IRGA) connected to a Parkinson leaf chamber. Dry CO₂-free air was pumped across a leaf in the leaf chamber at a rate of 300 ml s⁻¹ using an ADC air supply unit (ASU (MF)). Light intensity and air temperature were measured simultaneously using sensors which were built into the leaf chamber. Relative humidity, due to transpiration, was measured by a sensor fitted to the exhaust of the leaf chamber. After allowing about 30 seconds for the instrument to reach stability, results were calculated every four seconds and averaged over a one minute observation period. The calculated variables used in this study were the CO₂ exchange rate (mmol m² s⁻¹) and the stomatal conductance (mol m² s⁻¹). Calculation of the CO₂ exchange rate was adjusted to take into account the absorption of CO₂ by water vapour in the chamber due to transpiration.

Total nitrogen was measured in the leaves of *P. aspleniifolius*, *A. biglandulosum* and *Nothofagus cunninghamii*. The five leaves from each position used for physiological measurements were used for total nitrogen measurement. Because single leaves provided insufficient material for accurate analysis, additional leaves of the same age and from the same spray of growth were included to obtain sufficient dry leaf material. Leaves of *N. cunninghamii* were also assessed to provide a basis for comparison with the dominant tree in Tasmania's rainforests. The leaves were collected from similar situations to the other species at the same site. The method used for measuring total nitrogen was described in chapter 4.

The anatomy of the leaves of *P. aspleniifolius* and *A. biglandulosum* from the three light environments were studied in detail. Hand cut sections were stained. These were viewed at x 400 magnification under a light transmitting microscope and drawn with the aid of a drawing tube. A drawing tube transmits an image from the field of view to a drawing board next to the microscope, allowing the specimen to be traced accurately.

Leaf surfaces of *P. aspleniifolius* and *A. biglandulosum* from sun and shade were examined and photographed using a scanning electron microscope. The size of stomata was measured and the density of stomata was estimated (average of two leaves) from the areas photographed.

5.3 Results

5.3.1 Leaf characteristics

All three species orientate their leaves in a similar manner. The specific leaf weights reflect increasing leaf area and diminishing leaf thickness from sun to gap and finally shade specimens of *P. aspleniifolius* and *A. biglandulosum* (Table 5.1, Figure 5.1). The leaf anatomy (Figure 5.1) illustrates poor palisade mesophyll development in the sun leaves of *P. aspleniifolius* and *A. biglandulosum*. The gap phase leaves possess similar or better palisade development than the sun canopy while the shade leaves are predominantly spongy mesophyll. Other leaf attributes are typical of sun and shade leaf anatomical responses such as thin cuticles in the shade environment and a leaf thickness gradient from sun to shade. *A. biglandulosum* displays a hypodermis below the epidermis on the adaxial side; this is best developed in the gap specimen and absent from the shade specimen. *P. aspleniifolius* possesses large scleroid cells in the leaf matrix which are not apparent in the leaves of *A. biglandulosum*. Stomatal densities are higher in the shade than in the sun environments (Table 5.1, Figure 5.2).

5.3.2 Leaf nitrogen

(See Table 5.1).

There is significant variation between the species' sun-canopy leaves although there is no difference in the leaves of the shade environment. *A. biglandulosum* has significantly less leaf nitrogen than the other species in the gap phase regeneration. In the case of *A. biglandulosum*, the gap phase material is from shoots that sprouted from dormant buds after the gap formed, and so have a mature root system.

Intraspecies analyses indicate no difference in leaf nitrogen content between situations for *A. biglandulosum* while *P. aspleniifolius* contains highest N% in the gap and lowest at the sun canopy. *Nothofagus cunninghamii* has highest leaf nitrogen in the gap phase regeneration with no distinction between the other two positions.

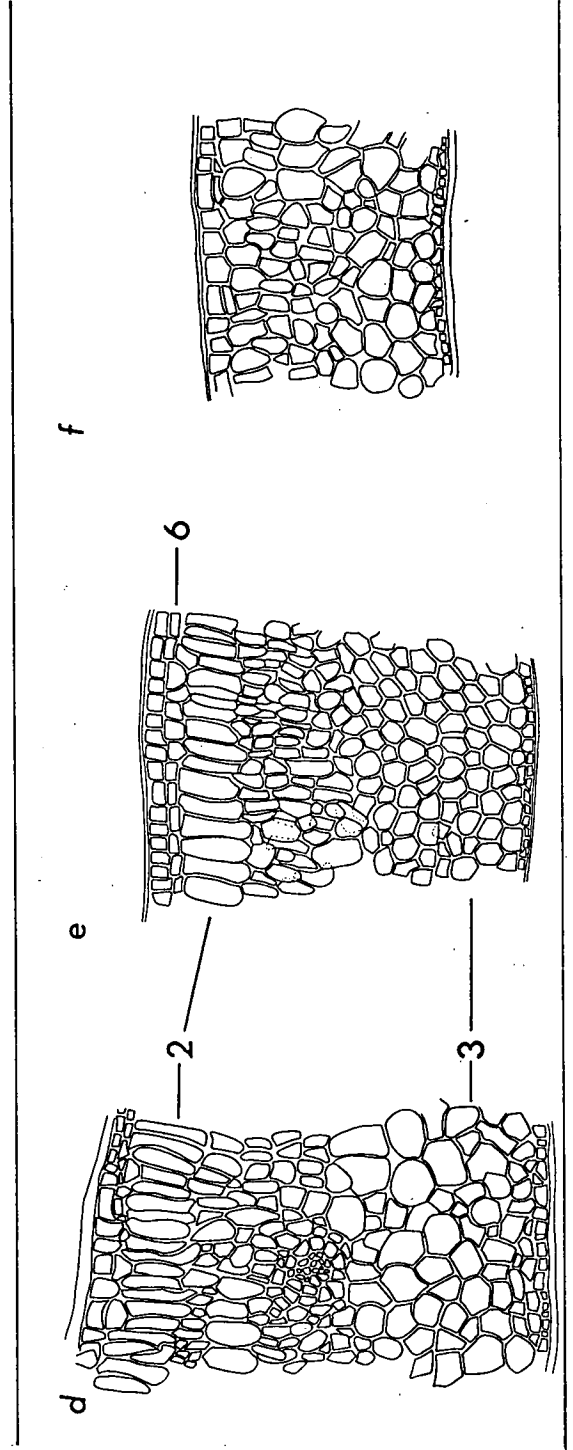
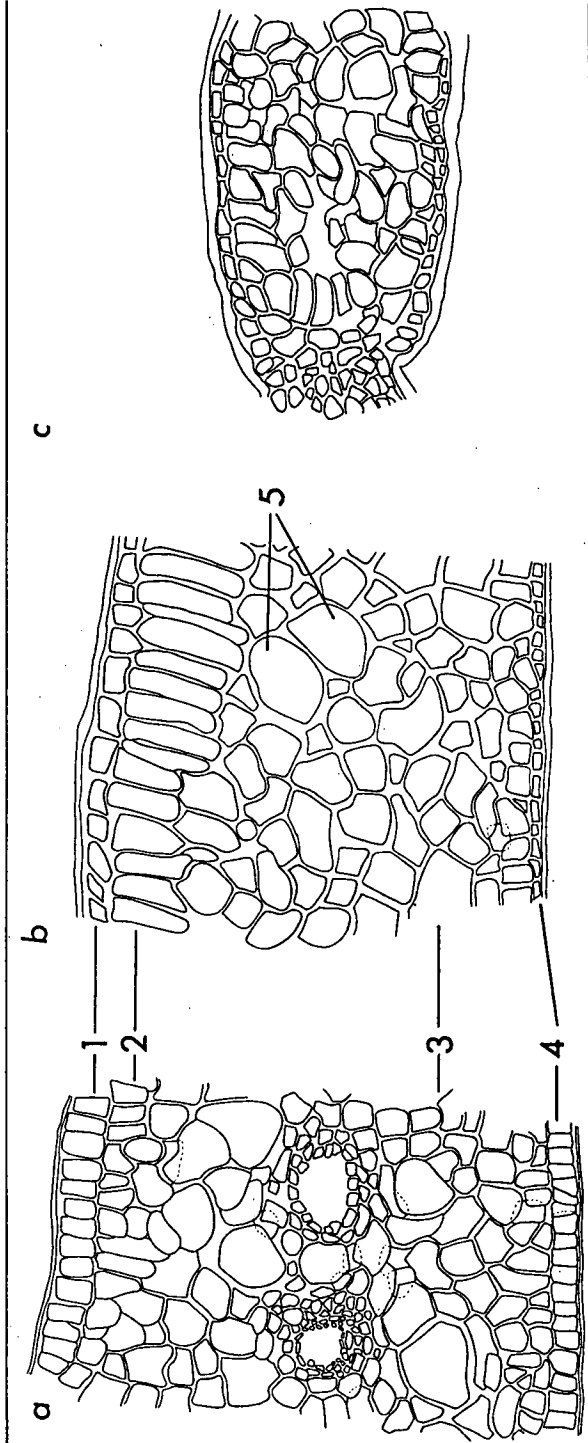
Figure 5.3 illustrates the relationship between leaf nitrogen and the maximum rate of CO₂ exchange measured for each leaf. There is no significant difference between the sun and gap situations for either species (Wilcoxon sign rank test), however, it should be noted that the maximum rates measured are not indicative of the light saturated rates. In the case of *P. aspleniifolius*, the highest rates were consistently measured in the high nitrogen gap leaves (Figure 5.6), and it would, therefore, be expected that they would have higher light saturated photosynthetic rates than the low nitrogen sun-canopy leaves.

5.3.3 Environmental characteristics

Air temperatures indicate differences between the gap and sun-canopy environments. The sun canopy of *P. aspleniifolius* consistently experiences higher ambient temperature than both the shade and gap environments. The shade environment of *A. biglandulosum* is coolest but there is no consistent difference between the sun and gap environments (Wilcoxon signed rank test, $P < 0.05$). The net result, over all days, is that *A. biglandulosum* leaves, in the sun and gap canopies, are operating under similar temperature conditions while those of *P. aspleniifolius* are operating under dissimilar temperature conditions.

In the sun and gap environments, the leaf temperatures of both species are maintained at or very close to ambient temperature when maximum daily ambient temperature is below about 16° C (Figure 5.4). Leaf temperature exceeds ambient by an increasing amount as ambient temperatures approach the maximum levels recorded (Figure 5.4). The leaves of *P. aspleniifolius* in the sun canopy, in particular, are between 2 and 3° C above ambient air temperature. The net result is that under the highest ambient temperatures measured the temperature of the sun canopy of *P. aspleniifolius* was up to 9° C higher than the gap canopy. The *A. biglandulosum* sun canopy reached only 5° C higher than the gap canopy.

Figure 5.1. Cross sections of phylloclades of *P. asplenifolius* (top) and leaves of *A. biglandulosum* (bottom) from three canopy positions. a, d sun canopy; b, e canopy in gap, c; f canopy in shade. Key to numbers: 1 palisade mesophyll; 2 spongy mesophyll; 3 abaxial epidermis; 4 adaxial epidermis; 5 hypodermis; 6 sclerids.



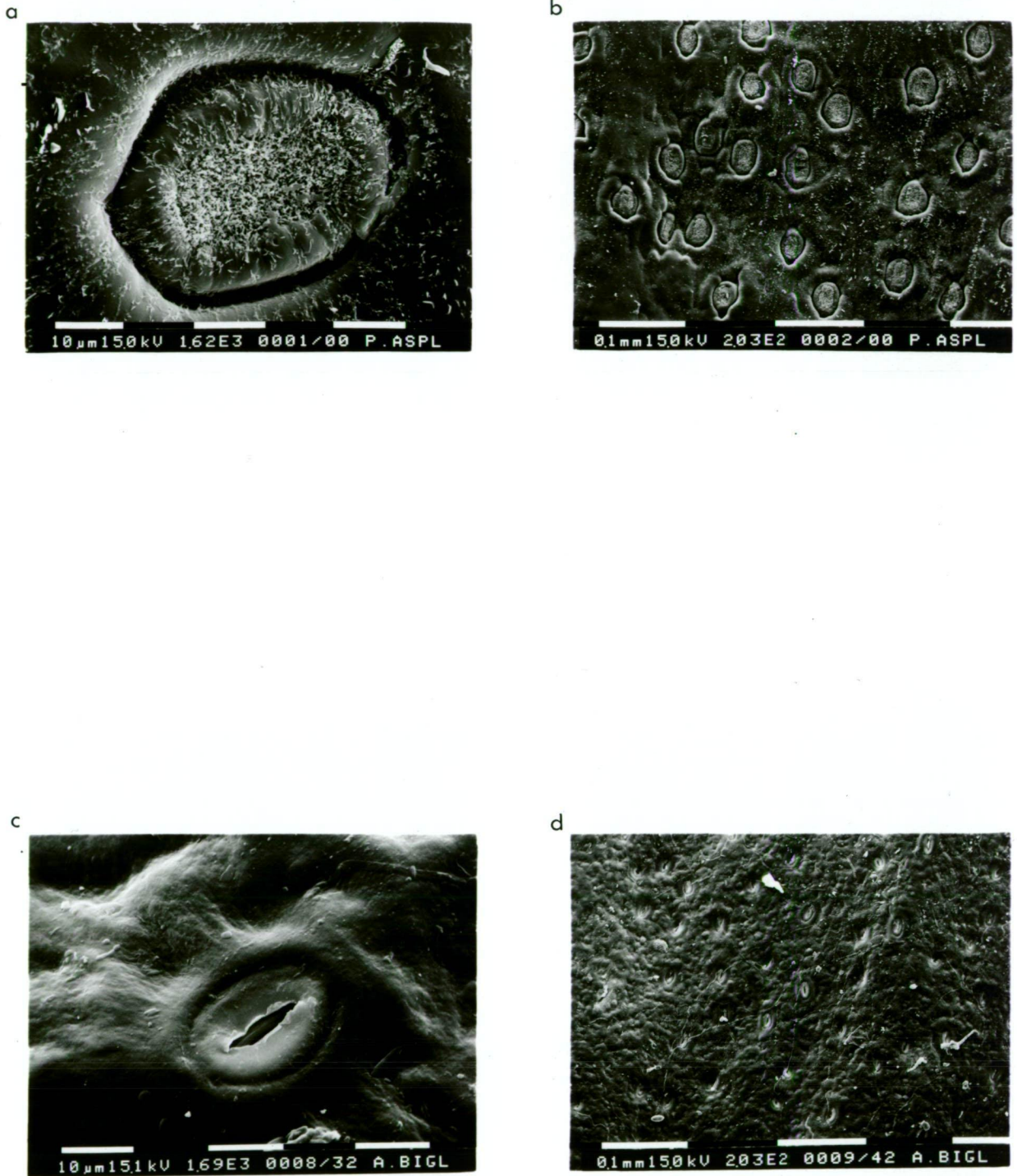


Figure 5.2. Scanning electron micrographs of leaf adaxial surfaces of *P. aspleniifolius* (a, b) and *A. biglandulosum* (c, d) showing the size and density of stomata on leaves from sun canopies.

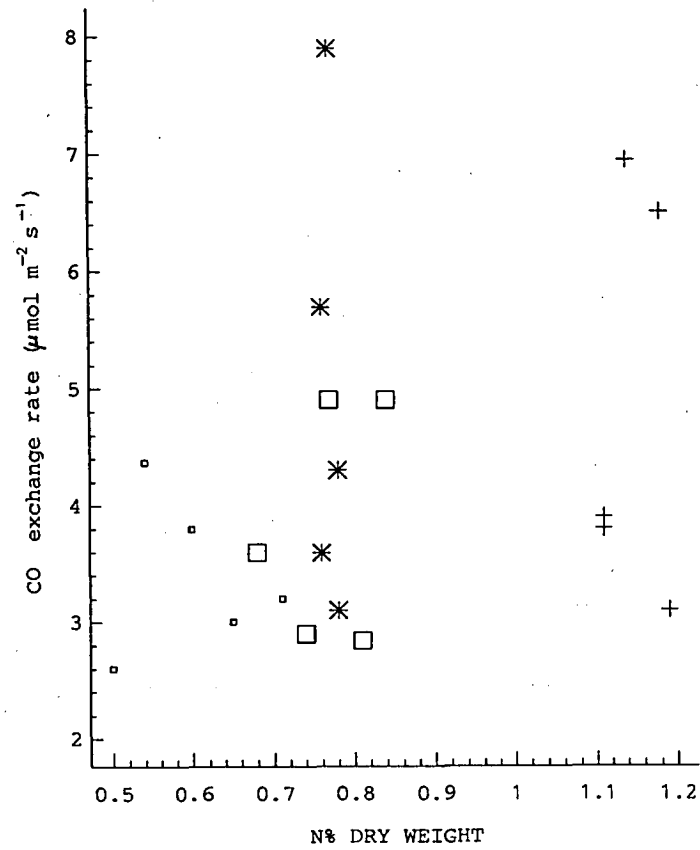


Figure 5.3. The maximum rate of photosynthesis measured for each of five leaves plotted against the nitrogen (% dry weight) content of the leaves for *P. aspleniifolius* and *A. biglandulosum*. *P. aspleniifolius* gap +, sun canopy □; *A. biglandulosum* gap *, sun canopy ◻.

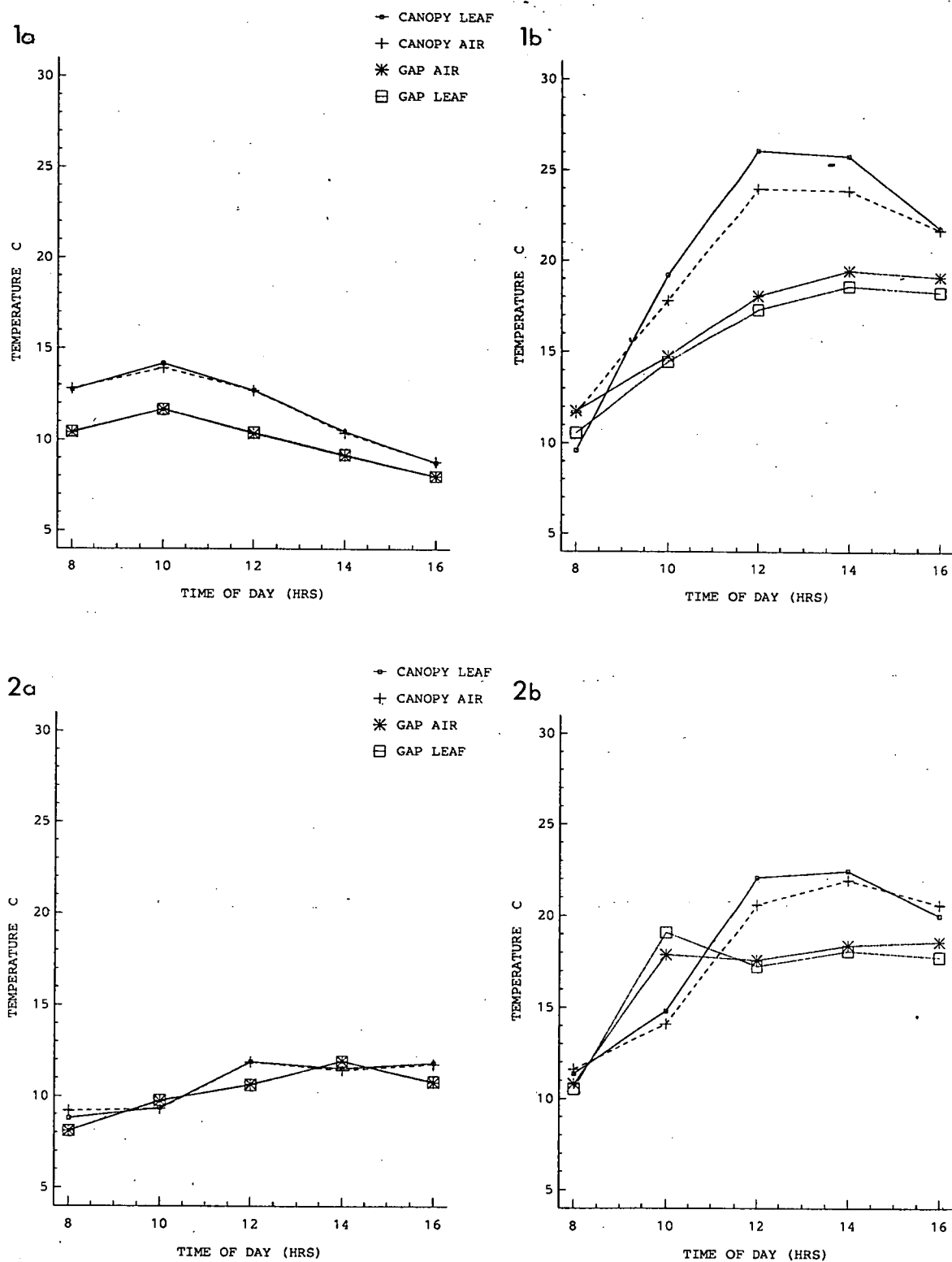


Figure 5.4. Leaf and ambient air temperatures ($^{\circ}\text{C}$) during the course of a days measurement period from the suncanopy and gap canopy. 1a. *P. asplenifolius* one day after rain and 1b, two days after rain; 2a. *A. biglandulosum* one day after rain, and 2b two days after rain.

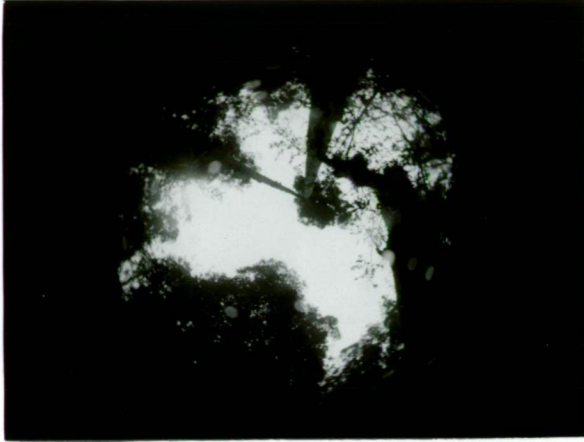
Table 5.1. Leaf characteristics of *P. aspleniifolius*, *A. biglandulosum* and *N. cunninghamii* in three environments (Env.). Leaf angle represents mean degrees from the vertical, n=20, N % (standard error). Different subscripts indicate significant differences: letters indicate intraspecies differences between situations and numbers indicate differences between species in similar situations. Spearman's Rank Analysis, $P < 0.01$.

Species	Env.	Leaf angle	Weight (g/cm ²)	Area (cm ²)	Stomata cm ²	N (%)
<i>P.asp</i>	sun	25	0.027	3.07	10 500	0.60(.04) _{a1}
	gap	51	0.020	5.58	-	1.14(.02) _{b1}
	shade	87	0.014	6.23	15 300	0.90(.04) _{c1}
<i>A.bigl</i>	sun	40	0.021	1.47	28 200	0.76(.00) _{a2}
	gap	38	0.015	2.30	-	0.77(.03) _{a2}
	shade	97	0.010	3.60	34 800	0.81(.01) _{a1}
<i>N.cunn</i>	sun	35	0.017	0.45		0.91(.02) _{a3}
	gap	43	0.013	0.48		1.14(.01) _{b1}
	shade	84	0.009	0.62		0.90(.01) _{a1}

5.3.4 Photosynthetically Active Radiation

Figure 5.5 illustrates the the nature of the forest canopy above the the gap and understorey environments. The level of photosynthetically active radiation (PAR) recorded at the sun-canopies is not impeded by surrounding forest canopy once the sun has risen above the canopy horizon. The level of PAR at the sun-canopies of both species was higher than the PAR recorded in the gap and in the understorey (Figures 5.6 and 5.7). The maximum (average of five measurements) levels of radiation received in all environments varied with the cloud cover and the season.

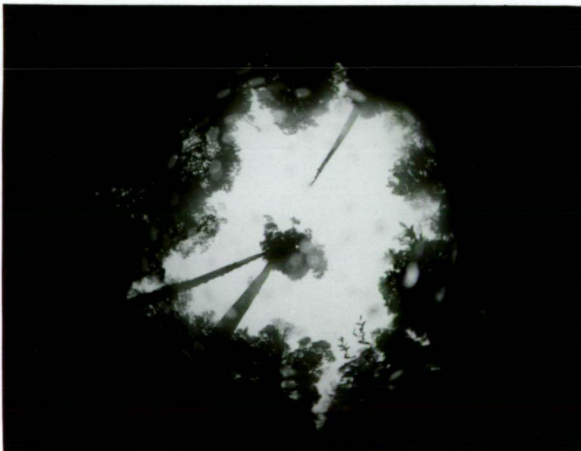
1a



1b



2a



2b

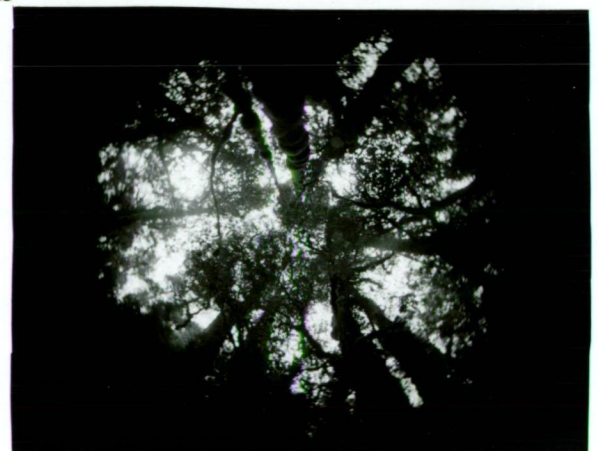


Figure 5.5. Canopy photographs illustrating the amount of over head cover. 1a. *P. aspleniifolius* in the gap environment, 1b. *P. aspleniifolius* in the shade environment; 2a. *A. biglandulosum* in the gap environment, 2b *A. biglandulosum* in the shade environment.

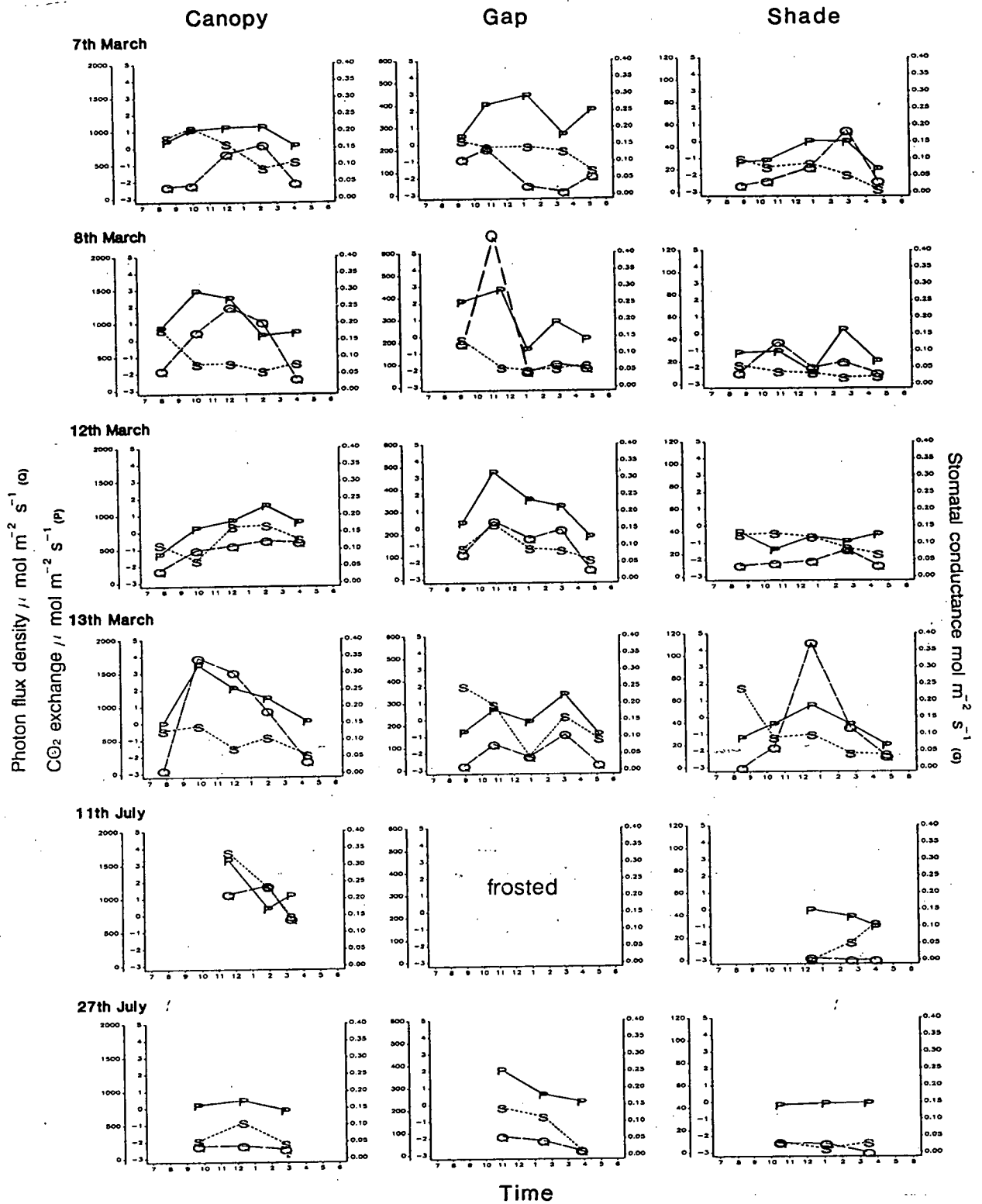


Figure 5.6. The photosynthetically active radiation measured as photon flux density (Q), apparent photosynthesis as CO₂ exchange rate (P), and stomatal conductance (S) for *Phyllocladus aspleniifolius* in three micro-environments; canopy, gap and shade (left to right), on six days (top to bottom).

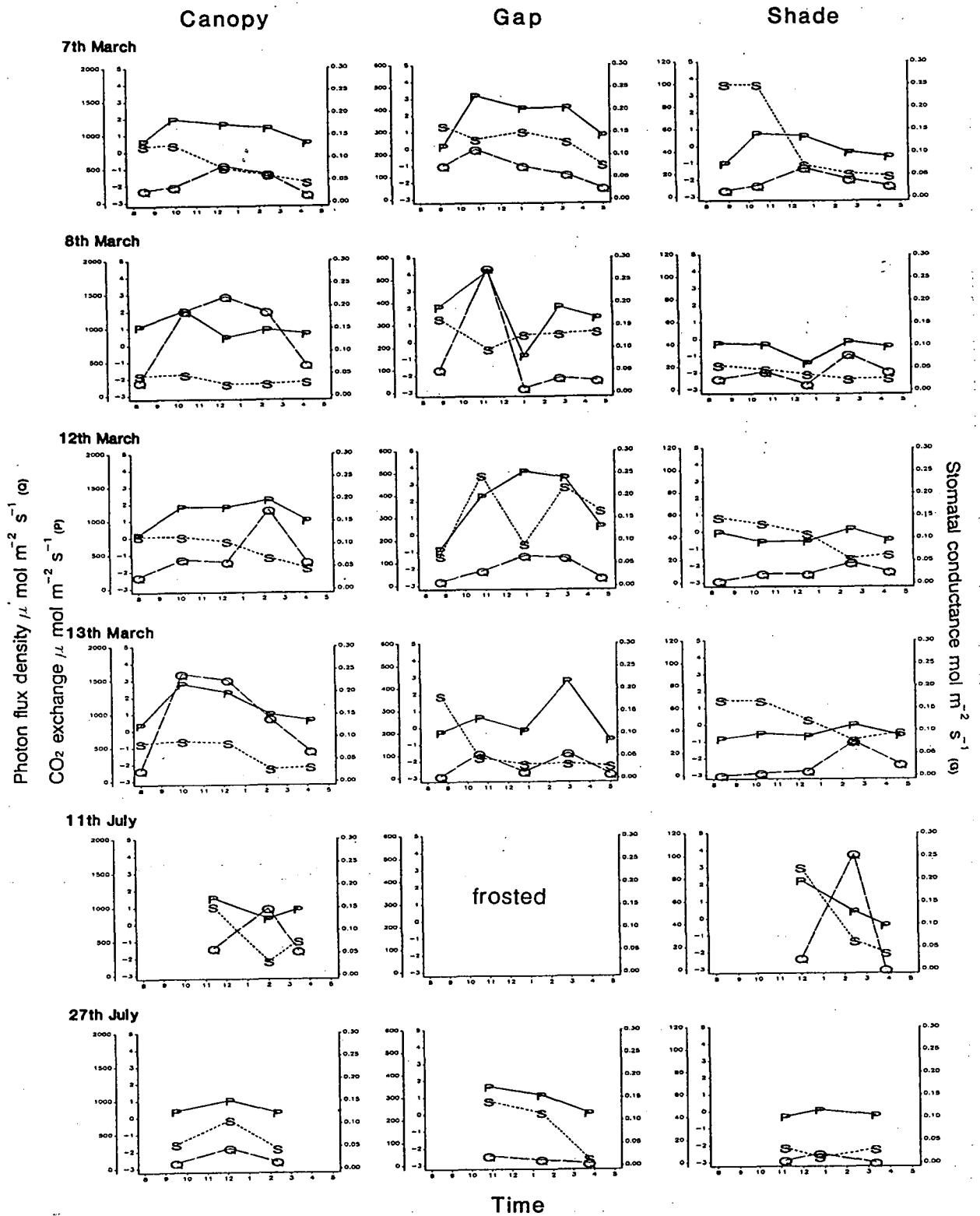


Figure 5.7. The photosynthetically active radiation measured as photon flux density (Q), apparent photosynthesis as CO₂ exchange rate (P), and stomatal conductance (S) for *Anodopetalum biglandulosum* in three micro-environments; canopy, gap and shade (left to right), on six days (top to bottom).

Summer

On the 13th March (Figures 5.6 and 5.7), a clear sunny day, the PAR incident at the orientation of the leaves reached 1 596 and 1 724 mmol m² s⁻¹ at the *P. aspleniifolius* and *A. biglandulosum* sun canopies respectively. These levels represent 72.5% and 78.4 % of total incoming PAR; these differences probably reflect leaf angles, *A. biglandulosum* being slightly more exposed (Table 5.1). Maximum levels reached in the gap environment were 110 mmol m² s⁻¹ (5%) for *P. aspleniifolius* and 160 mmol m² s⁻¹ (7.2%) for *A. biglandulosum*. In the understorey environment, the maximum levels of PAR were 30 mmol m² s⁻¹ (1.3%) and 112 mmol m² s⁻¹ (5.1%) although the latter reading was affected greatly by a single high value and is typically about 70 mmol m² s⁻¹ (3.2%) for *A. biglandulosum*.

On the 7th March, a cloudy day, the maximum levels of PAR received at the sun canopies were reduced to 546 mmol m² s⁻¹ (24.8 %) and 668 mmol m² s⁻¹ (30.3 %) for *P. aspleniifolius* and *A. biglandulosum* respectively. In the gap environment, however, PAR increased to 150 mmol m² s⁻¹ for (6.8%) *P. aspleniifolius* and 230 mmol m² s⁻¹ (10.5%) for *A. biglandulosum*. In the understorey environment the level of PAR was at least maintained for *P. aspleniifolius* at 30 mmol m² s⁻¹ (1.3%) and increased for *A. biglandulosum* to 170 mmol m² s⁻¹ (7.7%). A similar pattern was evident between other sunny and cloudy days in March and between sunny and cloudy days in the winter month of July. These data indicate the effect of diffuse light on cloudy days resulting in a more even distribution of light.

Winter

A decline in incident PAR is evident in winter. On the 11th July, after a severe frost followed by a sunny day, the maximum levels of PAR recorded at the sun canopies were 986 mmol m² s⁻¹ (44.5 %) and 1 190 mmol m² s⁻¹ (54.1 %) for *P. aspleniifolius* and *A. biglandulosum* respectively. The maximum levels recorded in the gap environment were 10 mmol m² s⁻¹ (0.45 %) and 20 mmol m² s⁻¹ (0.9 %) for the two species respectively. In the understorey environment, the maximum recorded level was 102 mmol m² s⁻¹ (4.6%) for *P. aspleniifolius*. This higher level is probably a result of a lower solar angle producing side lighting through the uneven canopy. *A. biglandulosum* received 10 mmol m² s⁻¹ (0.45%).

On the 27th July, the weather was heavily overcast with intermittent drizzle. Maximum levels of PAR recorded at the sun canopies were reduced to 300 mmol m² s⁻¹ (13.6%) for

P. aspleniifolius and $190 \text{ mmol m}^{-2} \text{ s}^{-1}$ (8.6%) for *A. biglandulosum*. In the gap environment, *P. aspleniifolius* received a PAR maximum of $42 \text{ mmol m}^{-2} \text{ s}^{-1}$ (1.9%) and *A. biglandulosum* received $84 \text{ mmol m}^{-2} \text{ s}^{-1}$ (3.8%). In the understorey the maximum levels were $8 \text{ mmol m}^{-2} \text{ s}^{-1}$ (0.36%) and $8.8 \text{ mmol m}^{-2} \text{ s}^{-1}$ (0.40%) respectively.

5.3.5 Physiological responses

5.3.5.1 Stomatal Conductance

The diurnal changes in stomatal conductance (S) for six days (Figures 5.6 and 5.7) indicate some differences in the responses between the species in the three environments. For both species, S tends to decline during the day in all positions but sometimes shows a small recovery in the late afternoon. Photosynthesis decreases in the afternoons of the summer days, the 8th and 13th of March (two days after rain), even though PAR is higher than saturation level (Figures 5.6 and 5.7). This is likely to be reflecting increasing water deficit and declining S. Stomatal conductance is higher in the gap than at the sun or shade canopy on all days for *P. aspleniifolius*. Stomatal conductance tends to be lowest in the shade for *A. biglandulosum* but there is no clear difference between the gap and the sun-canopy (Figure 5.3).

5.3.5.2 Stomatal conductance and photosynthesis

Figure 5.8 confirms the differences between the environments but also illustrates the relationship between CO_2 exchange rate and S for two selected days; one day after rain and two days after rain. The three canopy responses are distinct for *P. aspleniifolius* and indicate the large fall in S at the sun-canopy two days after rain. For *A. biglandulosum* S is relatively resistant. Comparatively high S values at low or negative CO_2 exchange rates were measured early in the morning under low light and may reflect ameliorated vapour deficits although these were not measured. The data indicate a complex relationship between S and CO_2 exchange rate which may be expected to be linear when below light saturation.

5.5.5.3 Stomatal conductance and light intensity

The controlled response of stomata to photon flux density (Q) is a triangular hyperbola (Jarvis & Mansfield 1981). The data in this experiment reflect only the correlation between Q and S under the influence of field variability. The data indicate a weak linear relationship for both species one day after rain for the sun-canopy and gap

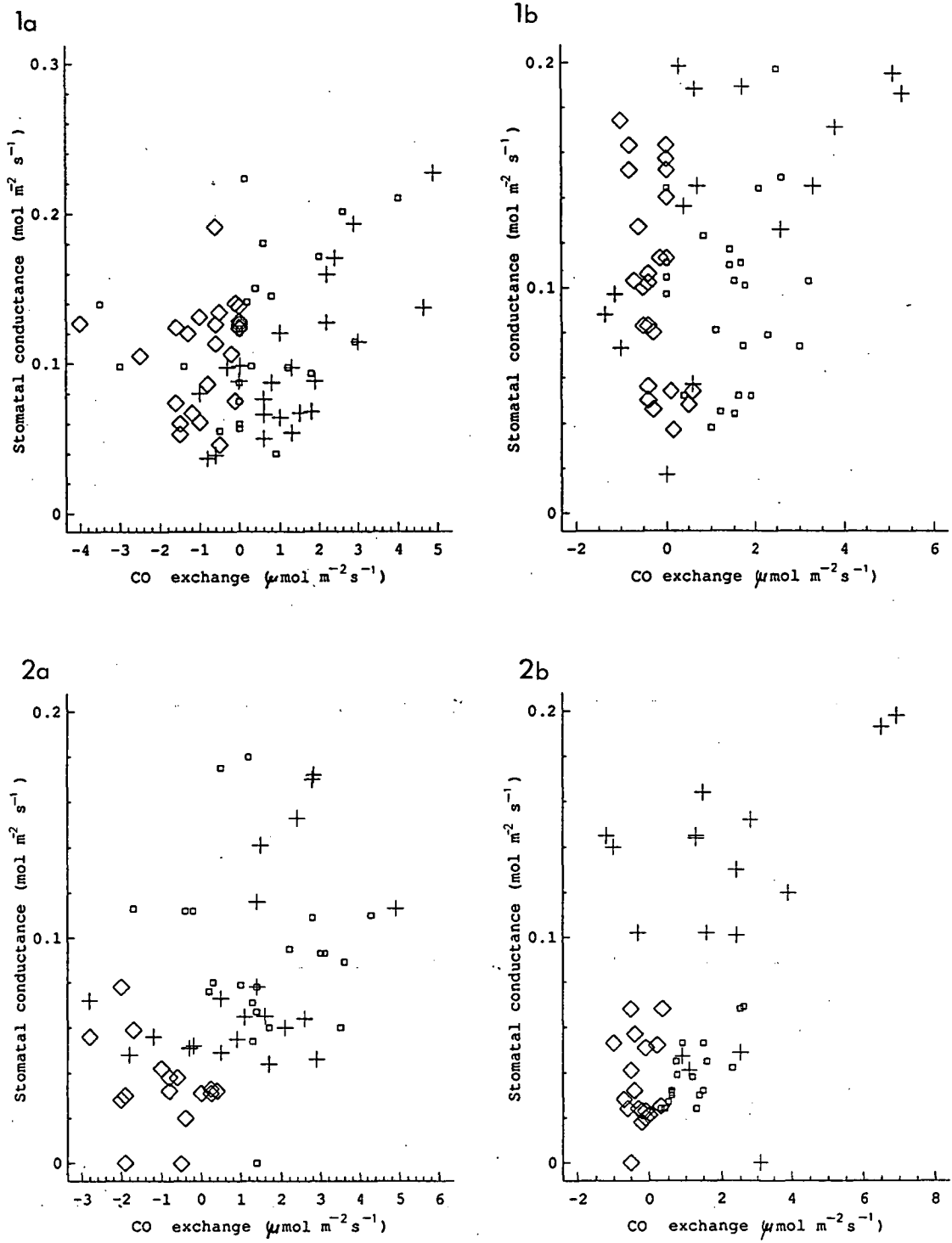


Figure 5.8. Stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$) versus CO₂ exchange rate in three canopy positions for a. *A. biglandulosum* and b. *P. aspleniiifolius* on two selected days 1a,b one day after rain and 2a,b two days after rain. \square sun-canopy, $+$ gap-canopy, \diamond shade-canopy.

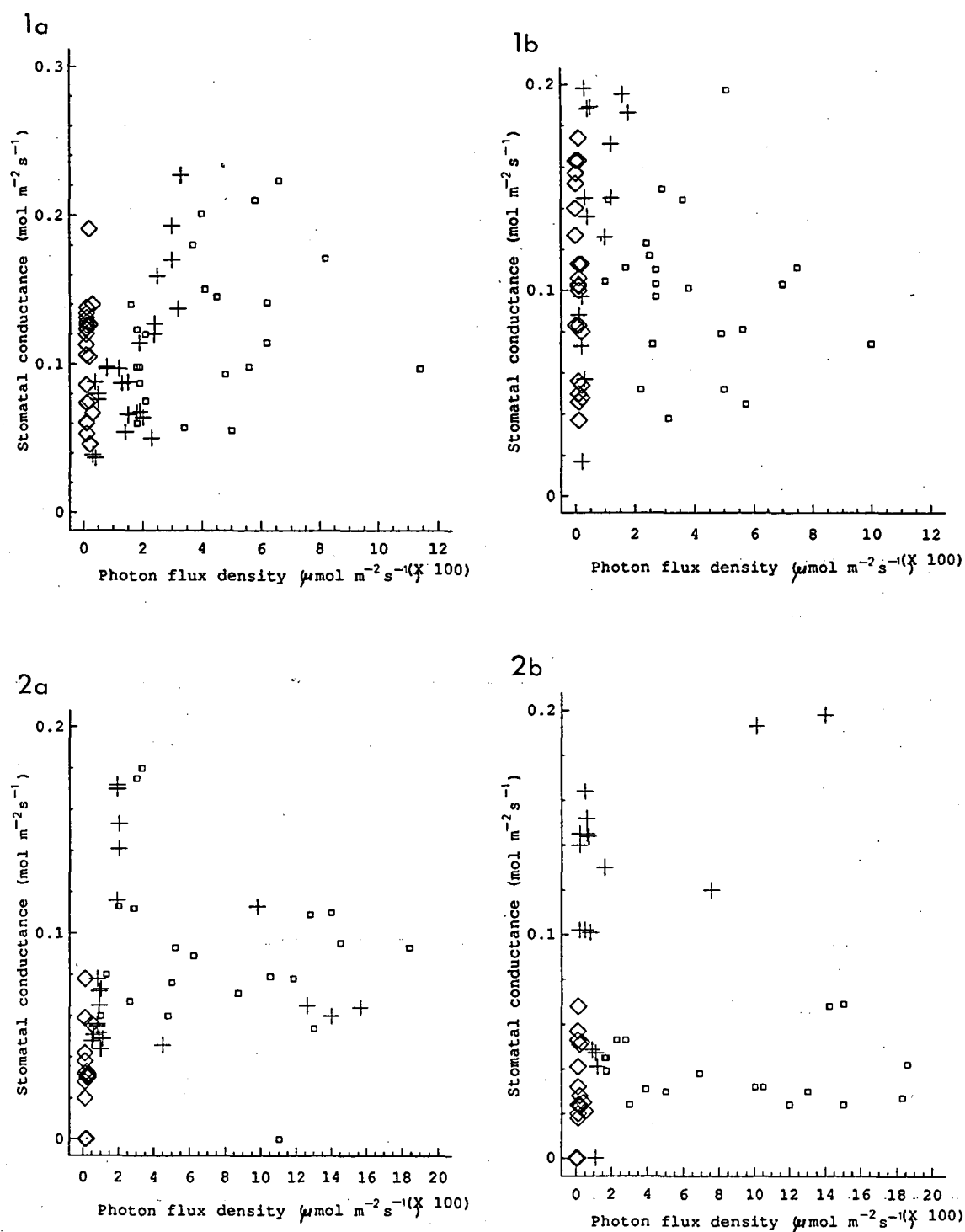


Figure 5.9. Stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$) versus photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for a. *A. biglandulosum* and b. *P. asplenifolius* on two selected days. 1a and b, one day after rain and 2a and b, two days after rain. \square sun-canopy, $+$ gap-canopy, \diamond shade-canopy.

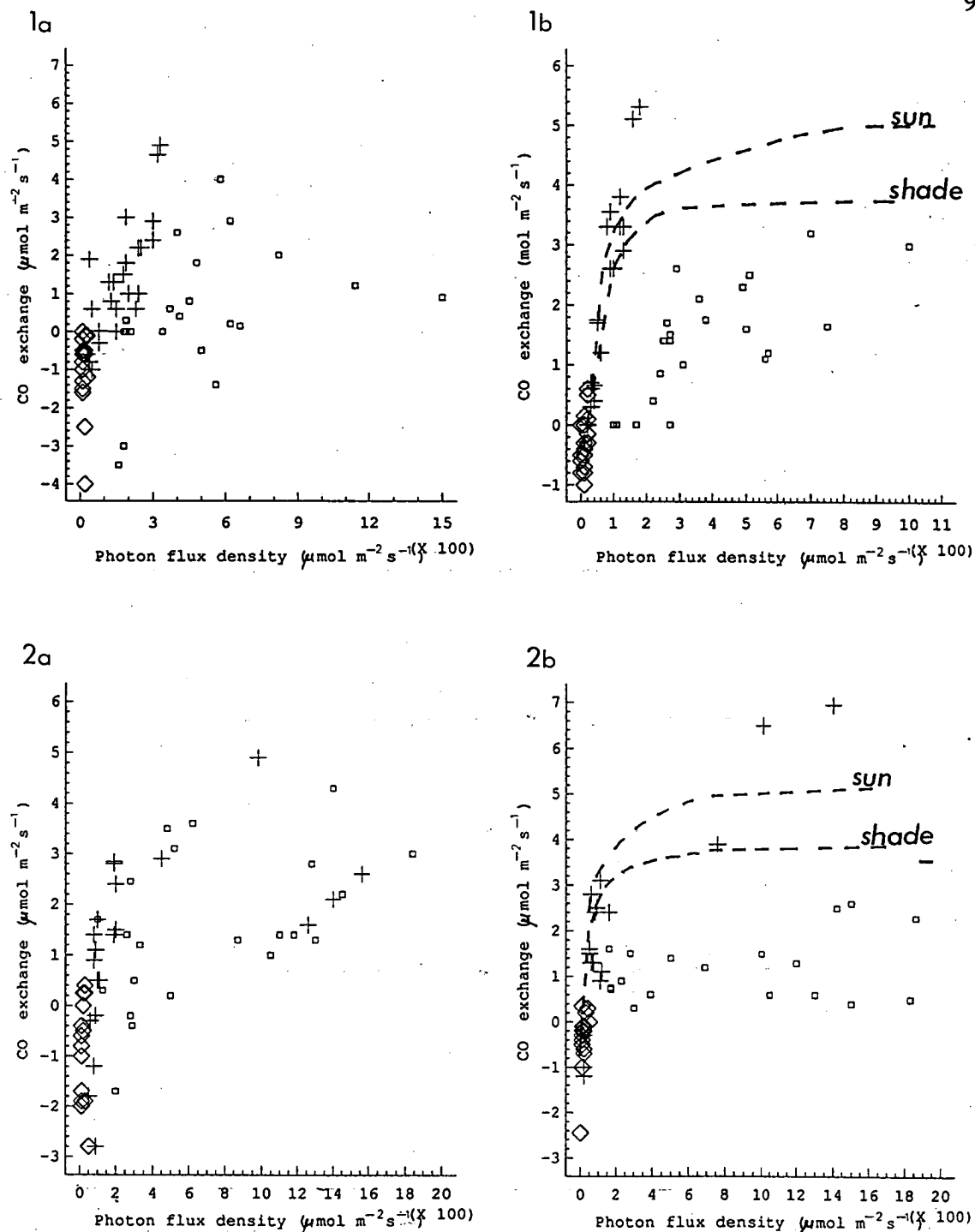


Figure 5.10. CO₂ exchange rate (μmol m⁻² s⁻¹) versus photon flux density (μmol m⁻² s⁻¹) for a. *P. aspleniifolius* and b. *A. biglandulosum* on two selected days. 1a, and b, one day after rain, 2a and b, two days after rain. The superimposed broken lines represent the light response curves of Read (1985b), sun plants + shade plants, □ sun-canopy, + gap-canopy, ◇ shade-canopy.

environments. The narrow range of Q in the shade limited the usefulness of the shade response for further interpretation. Two days after rain, however, the response of S to Q is low and flat for both species at the sun-canopy, while the plants in the gap maintain relatively high S under predominantly lower Q (Figure 5.9 c,d).

5.3.5.4 Rates of Photosynthesis

Figures 5.6 and 5.7 illustrate the course of CO_2 uptake (P) compared to the photon flux density (Q). From these time series diagrams it can be seen that there is a strong correspondence between the fluctuations in Q and P in all the environments and for both species except, on the 11th July when P and Q were out of phase after a severe frost overnight. The gap environment remained frosted all day and CO_2 exchange was not measured. Overall, maximum rates recorded on the winter days were lower than in summer, except in the understorey where Q was higher, or at least maintained, in winter.

On sunny days, *A. biglandulosum* recorded maximum rates (average of five leaves) of photosynthesis in the sun-canopy. The rates reached in the gap were comparable but were reached under considerably lower Q . The absolute maximum rate for *A. biglandulosum* was $7.9 \text{ mmol m}^{-2} \text{ s}^{-1}$ attained at $1810 \text{ mmol m}^{-2} \text{ s}^{-1}$ at the sun-canopy.

P. aspleniifolius responded similarly on the 13th March and produced an absolute maximum rate of photosynthesis of $4.37 \text{ mmol m}^{-2} \text{ s}^{-1}$ at $1850 \text{ mmol m}^{-2} \text{ s}^{-1}$. On the 8th March, also a sunny day, the highest rates were reached in the gap with an absolute maximum of $6.94 \text{ mmol m}^{-2} \text{ s}^{-1}$ measured when Q was $1400 \text{ mmol m}^{-2} \text{ s}^{-1}$.

For both species, photosynthesis was greater in the gap than at the canopy in the afternoon on days when the air temperature rose above 16°C and the radiation load exceeded $1000 \text{ mmol m}^{-2} \text{ s}^{-1}$ at the sun-canopy. This corresponds with a decrease in stomatal conductance and a fall in the sun-canopy rates of photosynthesis. Q remained well above saturation levels at the sun-canopy.

On cloudy days, the maximum rates of photosynthesis for both species occurred in the gap environment. The gap environment experienced lower Q than was measured at the sun-canopies. These days were characterised by Q being reduced to less than $600 \text{ mmol m}^{-2} \text{ s}^{-1}$ on average throughout the day at the sun-canopy. *A. biglandulosum* reached an absolute maximum rate of photosynthesis of $4.2 \text{ mmol m}^{-2} \text{ s}^{-1}$ at $260 \text{ mmol m}^{-2} \text{ s}^{-1}$ and *P. aspleniifolius* reached $3.9 \text{ mmol m}^{-2} \text{ s}^{-1}$ at $180 \text{ mmol m}^{-2} \text{ s}^{-1}$.

During the low Q levels of the 27th July both species again recorded the highest rates of photosynthesis in the gap under lower levels of Q than were measured in the canopy. No gap measurements were made on the 11th July due to frosting.

Rates of photosynthesis in the understorey were generally very low for both species, only once exceeding $1 \text{ mmol m}^2 \text{ s}^{-1}$ (*P. aspleniifolius* 11th July). The low sampling frequency was not sufficient to quantify sunfleck activity in this environment. However, a net positive carbon gain may occur for a few hours during the middle of the day in the summer months without sunfleck utilization.

In the winter understorey environment *P. aspleniifolius* was only able to record positive CO_2 gain under the higher and more diffuse light conditions on the cloudy 27th July compared to 11th July which was sunny. Under these conditions Q averaged $20 \text{ mmol m}^2 \text{ s}^{-1}$. *A. biglandulosum* responded similarly but only maximum rates were positive while average rates remained negative.

Figure 5.10 illustrates the relationship between Q and photosynthesis in the three situations on selected days; one day after rain and two days after rain. The relatively high rates of photosynthesis at lower Q are evident for both species in the gap environment although the difference is more pronounced for *P. aspleniifolius*. Absolute rates are highest in the gap environment for *P. aspleniifolius* on both days; this is less clear for *A. biglandulosum*. The response of photosynthesis to increasing Q at the sun-canopy is flat for *P. aspleniifolius* two days after rain (Figure 5.10). The response of stomatal conductance (Figure 5.9) is also flat and may indicate that S is limiting P . Two days after rain, *A. biglandulosum* maintains a positive P response to Q until light saturated. The broken lines indicate the controlled light response curve of Read and Hill (1988) for *P. aspleniifolius*.

5.4 Discussion

5.4.1 Light

The light environments measured at the three locations are marginally higher than those reported from South American tropical rainforest (Chazdon & Fetcher 1984, Kwesiga *et al.* 1986) but are comparable with those measured by Turton (1990) in Australian tropical rainforest. These results do not entirely concur with Lowman (1986), who concluded that the cool temperate rainforests allowed more light to pass through the canopy than tropical rainforest. However, large variability in the structure of different Tasmanian rainforest communities may account for this discrepancy. Lowman (1986) did not indicate the effect of diffuse light on cloudy days in the understorey, which was important in this study, and is also important in tropical rainforests (Chazdon & Fetcher 1984, Torquebiau 1988) and in tropical cloud forest (Huber 1972).

In the present study, the light levels incident at the sun-canopy were reduced considerably by cloud, and resulted in a greater day to day variation than in the understorey or in the gap. The daily fluctuation in PAR due to cloud cover is considered more important than seasonal variation in tropical rainforest (Chazdon & Fetcher 1984). However, the present study shows a significant drop in the PAR incident at the leaf in winter, and this may distinguish the cool temperate rainforests' seasonality in the light environment.

5.4.2 Stomatal conductance

Environmental variation over a period of days, such as in water supply or temperature, has been shown to influence photosynthesis in rainforest trees (Doley *et al.* 1988) and temperate conifers (Beadle *et al.* 1985a).

Levels of stomatal conductivity in *P. aspleniifolius* and *A. biglandulosum* were generally very low but marginally higher than levels measured by Langenheim *et al.* (1984) for *Agathis*. Langenheim *et al.* suggested that the low conductivity may be due to low stomatal frequency. Hill and Carpenter (1991) describe reduced stomatal frequency as a feature of Australia's cool temperate conifers which distinguishes them from tropical species. They suggest that reduced stomatal frequency is an evolutionary response to selection pressures such as dry glacial periods. Figure 5.8 illustrates the generally higher stomatal conductance of both species in the gap environment which may in part be attributed to higher stomatal density. The lowest levels of stomatal conductance were

recorded in the understorey but no limitation to CO₂ uptake was detected. It has been suggested that in the understorey of tropical rainforests low S may have more to do with carbon gain than with high water use efficiency (Bjorkman *et al.* 1972, Pearcy 1987). This contention has been supported by Cowan (1982) who suggests that stomatal restriction of gas exchange in response to high CO₂ concentration in the mesophyll may produce optimal assimilation rates with respect to water loss. The low levels of S in the understorey in this study may therefore reflect light-limited rates of photosynthesis which require only minimal rates of gas exchange.

Beadle *et al.* (1985b) illustrated a well defined relationship between photosynthesis and stomatal conductance at high saturation deficits in Scots Pine. This relationship did not exist at low saturation deficits. Saturation deficit was not measured in the present study but photosynthesis was observed to decline steeply in *A. biglandulosum*, and also in *P. aspleniifolius* at above light saturation levels. This occurred on the second afternoon after rain on both the 8th and 13th March. The decline in performance coincided with decreasing S at the sun-canopy, and probably reflects an increasing saturation deficit resulting in photosynthesis being limited by gas exchange rates in the sun-canopy.

Unexplained controls on the rate of photosynthesis under field conditions probably reflect the effects of wind and air temperature on leaf temperature. The leaf temperature in the sun-canopy of *P. aspleniifolius* was 3 to 4° C above ambient and reached 5° C greater than the optimum temperature for this species reported by Read (1985) and other Australian temperate rainforest trees (Hill *et al.* 1988). Although the optimum for *A. biglandulosum* has not been determined, the leaf temperature rose to less than 2° C above ambient. Beadle *et al.* (1985) showed that the response of P to Q was a clear function of leaf temperature in *Pinus sylvestris* (a temperate conifer) and was severely impeded above 25° C.

Two days after rain, the stomatal conductance of *P. aspleniifolius* (S) remained at least an order of magnitude higher in the gap than at the sun-canopy. The maintenance of S for *P. aspleniifolius* probably reflects the high temperature differential between the sun and gap environments for this species and its consequent effect upon vapour deficit and photosynthetic efficiency. Stomatal conductance of *A. biglandulosum* fell in the gap environment, however, the maintenance of photosynthesis under lower S may be attributed to the light intensity being well below saturation and demonstrates the relative stability of this environment for photosynthetic performance compared to the more exposed sun-canopy.

In the winter measurements, S varied little and photosynthesis appeared to be light controlled except after a severe frost. Although soil and air temperatures in Tasmania are unlikely to fall as low as those in continental regions a severe frost may still affect the rate of physiological responses. Makroß (1972) showed that several days of warm temperatures are required for spruce to have a positive CO_2 uptake in winter.

5.4.3 Assimilation Rates

Assimilation rates of both species were relatively low compared to tropical species (Langenheim 1984) and compared to light-saturated levels under controlled conditions for canopy dominants in Tasmania (Read 1985). Read reported light-saturated photosynthesis for *P. aspleniifolius* of about $5 \text{ mmol m}^{-2} \text{ s}^{-1}$ at a PAR level of about $500 \text{ mmol m}^{-2} \text{ s}^{-1}$. In the present study, a few absolute maximum rates measured on single leaves were higher than the light-saturated level reported by Read (1985) for *P. aspleniifolius*. This suggests that while the field potential is higher than that indicated by Read, environmental parameters other than light generally limit the photosynthetic rate to considerably lower levels. Furthermore, the generally lower level of PAR in Tasmania's winter months and on its many cloudy days is likely to be reflected in leaf morphogenesis (Kwesiga *et al.* 1986) and subsequently a lower photosynthetic capacity than may otherwise be expected.

The rates of photosynthesis between the three environments did not reflect the distribution of PAR. It was common for the rates in the gap to be higher than the rates in the sun-canopy at lower levels of PAR, even though the gap environment rarely experienced saturation levels. Assimilation rates were sensitive to relatively small changes in PAR in the gap and particularly in the understorey where PAR only occasionally fluctuated by more than $20 \text{ mmol m}^{-2} \text{ s}^{-1}$. Chazdon and Fetcher (1984) also reported sensitivity of assimilation rates in tropical rainforest, but it was restricted to the understorey and did not extend to gaps. The response in this study may be influenced by the size of the gap, which generally limits PAR levels to below saturation. The sensitive response of the plants is more akin to that of a shade plant, but it should be remembered that the rates in the gap were also often higher than the sun-canopy, suggesting that light saturated rates may also be higher. The highest rates measured for both species were recorded under high levels of PAR; the difference being that it was recorded for *P. aspleniifolius* in the gap environment and for *A. biglandulosum* in the sun-canopy.

Read (1985) reported that in a controlled experiment using wildlings grown for one year in sun, compared to wildlings grown for one year in shade, that *P. aspleniifolius* produced a maximum photosynthetic rate, on a leaf area basis, in the sun-raised plants. Doley *et al.* (1988), studying a tropical rainforest tree in Queensland, and Schulze *et al.* (1977), studying temperate forest species, demonstrated that the physiological characteristics of leaves from various canopy positions are different to those of mature sun-canopy leaves. Doley *et al.* (1988) and Schulze *et al.* (1977) suggest that subcanopy and understorey leaves exposed to extended sunflecks and patches responded similarly to sun-canopy leaves. This is not, however, demonstrated in the present study as the leaves in the gap environment often performed at higher rates than the sun-canopy leaves, as well as responding more sensitively to changing PAR.

Bazzaz and Carlson (1982) found that the light responses of species typical of different successional environments were related to the light environments experienced at such stages. Although this may have been expected, they also found that early successional species (light demanding) had a greater capacity to acclimate to variability in the light regime, and hence to better utilize the light conditions in which they grow. This greater physiological flexibility, relative to late successional species, may be related to the level of environmental variation characteristic of the habitat.

The data presented here suggest that that species are light demanding but exhibit a great deal of plasticity in performance, particularly in the gap environment. Such plasticity may reflect an adaptation to regeneration and growth under moderate but highly variable levels of PAR. These conditions are likely to be experienced in tree-fall gaps, in regrowth rainforest and in subdominant canopies similar to those where both of these species are commonly found.

Read (1985b) suggests that, in *Nothofagus* dominated rainforest, the relative growth rate of *P. aspleniifolius* is reduced in comparison to other canopy dominants by its low specific leaf area. From this point, she concludes that *P. aspleniifolius* is limited to an early successional role by a reduced ability to compete for light. However, the diversity of forest structures within the range of *P. aspleniifolius* and the plastic response to light suggests that a range of field performances should be anticipated.

Furthermore, the nutrient physiology of species is often a delimiting factor with respect to distribution of species and communities (Grime 1979). A strong correlation between leaf nitrogen and leaf photosynthetic capacity is well known (Field 1988, Thompson *et al.* 1988, Givnish 1988) and as such may, in part, determine regeneration status. In the

present study, Table 5.1 and Figure 5.3 indicate the influence of nitrogen content on P_{max} and the higher leaf nitrogen content of *Nothofagus cunninghamii* at the sun-canopy. Working with *Flindersia brayleyana*, Thompson *et al.* (1988) demonstrated that the photosynthetic capacity was highest for plants grown under high nitrogen regimes and under medium light intensity. Furthermore, plants grown with high nutrients and low light performed better than those of low nutrients and high light. Thompson *et al.* described these results as being nutrient dependant responses of leaf cell development, particularly the depth of palisade. Similar relationships exist between leaf nitrogen and palisade depth for *P. aspleniifolius* and *A. biglandulosum* (Figure 5.1, Table 5.1). As such, species which are best suited to fertile sites, such as *N. cunninghamii* (Read and Hill 1988), would be expected to have higher leaf nitrogen and higher P_{max} on those sites. However, the competitive advantage would be lost on low nutrient sites if such species could not extract or use the limited resources more efficiently than other species at these sites, including *P. aspleniifolius* and *A. biglandulosum*.

The relatively high leaf nitrogen of *P. aspleniifolius* and *Nothofagus cunninghamii* in the gap environment may indicate the effect of a nutrient flush which is alleged to follow gap-forming disturbances on nutrient poor sites (Ewel *et al.* 1981). The uniformity of leaf nitrogen content in *A. biglandulosum* is attributed to the vegetative nature of its proliferation in gaps which remains dependant upon established root systems and nutrient sinks in the surviving biomass. Although the nutrient data in the present experiment are limited, the apparent differentiation may better attribute the relative success of species in the process of community dynamics to nutrient physiology, and, hence, the relative fertility of the forests substrate (see also Chapter 4). This question requires more detailed, specific consideration.

This experiment has demonstrated a high degree of plasticity in environmental responses of *P. aspleniifolius* and *A. biglandulosum*. Such variation in the photosynthetic capacities of the three phenological situations poses interesting ecological questions. Besides physiological adaptations of leaves which maximize the light harvest (Berry 1975, Bjorkman 1981, Kwesiga *et al.* 1986) and nitrogen use efficiency (Field 1988), crown dynamics which present efficient photosynthetic displays of leaves are likely to have an equally significant impact on light harvest (Horn 1971).

The adaptability of a species crown in terms of architectural development may influence its dominance and abundance as the species develops in tandem with community succession. This may be particularly important in floristically simple rainforests, such as in Tasmania, where much of the spatial variation in the forests mosaic is structural.

Stewart (1988) indicates that similar variation in North American temperate forest mosaic influences the floristic composition of the understorey.

Torquebiau (1988) argued that species regulate their own heights to maximize light interception. This suggests that stratification of forests has some adaptive significance and may partly explain the great structural diversity of Tasmania's rainforests as well as the variable crown characteristics of species within them.

A quantitative description of crown architecture and development, in conjunction with the above results, may therefore provide useful information concerning a species changing status in response to community structure and dynamics.

Chapter 6. Phenology of seedfall, germination and survival in *Phyllocladus aspleniifolius* and *Anodopetalum biglandulosum*

6.1 Introduction

For plant species to co-exist they must be able to regenerate successfully within the same community, taking advantage of suitable opportunities as they occur in space and through time (Pickett 1980). The level of success at all stages in sexual reproduction is an important determinant of the future status of a taxon within a community (Watt 1947). A high degree of success at this critical life-stage often confers an advantage in the competition for space.

Opportunities for regeneration in forests, whether stimulated by disturbance, climate or the availability of suitable microsites, may only be taken advantage of if seed is present where and when an opportunity is presented. The co-existence of *P. aspleniifolius* and *A. biglandulosum* requires that suitable opportunities for regeneration recur for each species within its life-span. Consequently, the factors that affect the availability of seed interact with the opportunities in a probabilistic way. These factors include the timing and success of seed production and the ability to disperse the seed. Seedling survival in the presence of other species further delimits possibilities for co-existence (Pickett and White 1985). Differences in the pollination success and the timing and quantity of seed produced may distinguish their regeneration niches and, hence, determine the relative regeneration opportunities. Shared pollinators, shared dispersal mechanism and similar seasonality may reduce reproductive success and induce competition for space.

In rainforests, the regeneration of shade-intolerant species, such as *P. aspleniifolius* and *A. biglandulosum*, may involve disturbances at various scales of time and space. Disturbance of the forest canopy or soil may stimulate regeneration if seed is stored in the soil seed bank. The storage of viable seed in the soil increases the probability of regenerating in response to temporally stochastic disturbance events. Disturbances may also reduce regenerative success where and when it results in the physical disruption of seedlings. Susceptibility to early frosts, drought and animal foraging are particular threats to seedlings which may influence their relative survival rates and, hence, coexistence. During development, phenological attributes such as the timing and period of foliar development will affect the competition for space between canopies.

P. aspleniifolius is a dioecious gymnosperm and is dependent upon well-dispersed seed for regeneration. Its seed production varies from year to year, with notable mast years

(Read 1989). In contrast, *A. biglandulosum* produces bisexual flowers and is wind-dispersed. These contrasting characteristics are likely to be reflected in the population dynamics where opportunities for regeneration depend upon the distribution of seed (Horn 1974), the germination characteristics of seed and the physiological needs of the seedling (Grubb 1977a).

The aim of this chapter is three-fold:

1. to describe the foliar and fruiting phenology and seed shed of *P. aspleniifolius* and *A. biglandulosum* and to determine how this might affect the regeneration and maintenance of the species;
2. to test the hypotheses that animal predation affects the survival of *Anodopetalum* seed, and that animal disturbance of the soil and litter affects the survival of seedlings of both species; and
3. to consider the effect of substrate disturbance upon the germination of seed and the survival of seedlings.

6.2 Materials and methods

6.2.1 Reproductive Phenology

Four sites at which the species co-occur from 600 m to 1 030 m at Mt Field (42° 41' S, 146° 40' E) in Tasmania were used to observe shoot extension, leaf expansion and sexual development of *P. aspleniifolius*. Previous observations have shown that *A. biglandulosum* does not flower when it is not part of the canopy. For this reason only one of these sites was suitable for observation of the phenology of this species. Two trees of each sex for the dioecious *Phyllocladus* (4 total) and four trees of *Anodopetalum* were observed at each site. Eight branches were tagged on each tree; two high outer canopy; two high inner canopy; two low outer canopy; and two low inner canopy. If the canopy was emergent (site 1 *Phyllocladus*), only two in the outer and two in the inner canopy were tagged.

The trees were observed weekly during sexual development between November and March and fortnightly during foliar development in this period. The stages of development that were recorded at each site included the following for each species where appropriate:

- | | |
|------------------------|---------------------------|
| 1. Foliar bud swelling | 8. Fruit development |
| 2. Foliar bud burst | 9. Fruit ripening |
| 3. Shoot extension | 10. Strobili development |
| 4. Leaf expansion | 11. Pollen shed |
| 5. Leaf senescence | 12. Micropile receptivity |
| 6. Floral bud swelling | 13. Cone development |
| 7. Floral bud burst | 14. Cone ripening |
| and flowering | |
| 15. Seed fall | |

When 50% of the foliar observations for any stage of development were positive, a branch was considered to be at that particular stage of development. When 50% of the branches reached a particular stage of development a tree was considered to be at that stage. When 50% of the trees were positive the population were considered to be active in the same particular stage of development. In the course of sexual observations, a population was considered positive from the first to the last indication of activity for a particular stage but for fruit ripening the foliar rules were applied.

6.2.2 Foliage phenology of *Phyllocladus* Transplants.

Twenty plants each from a highland (750 m a.s.l.) and twenty plants from a lowland (60 m a.s.l.) population were collected for a provenance trial. Five plants from each provenance were transplanted to four locations on an altitudinal transect. The locations were 60 m a.s.l. in a Hobart shade house, and 220 m, 740 m and 1 030 m a.s.l. at Mt Field. Each specimen was planted randomly in a matrix covering 1m x 1m and a grazing exclosure was erected over them. Only foliar development was monitored as the plants were not sexually mature. These plants were observed at the same times as the *in situ* phenology described above. The initial height was measured and the growth in centimetres was measured in 1990, 1991 and 1992. The total growth of the two provenances was compared using a multi-factor ANOVA with initial height as a covariate, and altitude and provenance as factors.

6.2.3 Seed traps

Eight seed traps were located in four communities at different locations to gain an estimate of the intensity and duration of seed fall over a two year period. The catchment area of each trap was 1 m² and these were placed beneath the canopies of female *P. aspleniifolius* and *A. biglandulosum*. During the first year, the traps were emptied every fortnight throughout the year. During the second year, the traps were emptied every fortnight until a nil result was obtained. During the third year, only six traps were monitored as restricted access and disturbance to the traps disrupted collection times. The seeds were counted and the litter was weighed and described in terms of species leaf composition and abundance.

6.2.4 Climatic correlation

The climate at Maydena (42° 41'S, 146° 37'E) from 1978 to 1991 was analysed in a time series in search of correspondence between climatic attributes and mast seeding years. The two most recent mast seeding years recorded for *P. aspleniifolius* and other rainforest trees were assessed. The average monthly minimum temperatures (°C), the average monthly maximum temperatures (°C) and the average monthly rainfall during the growing season (October to March) from 1978 to 1990 were tabulated. The 13 years of climatic averages were compared to the thirteen year mean, and each variable for each month was determined to be equal to the mean (m), below the mean (-), or above the mean (+). The growing seasons were then characterised as cool if more than three of the six months were below average maximum temperatures and warm if more than three of

the six months were above average. The growing season was considered dry if more than three of the six months of the growing season recorded below average rainfall and wet if more than three months were above average.

6.2.5 Dispersal

Ten seeds of *P. aspleniifolius* and 10 seeds of *A. biglandulosum* were dropped 5.5 m through still air. The time taken for the last of the 10 seeds to complete the fall was recorded and the procedure was repeated 10 times for each species with 10 independent sets of seeds. The distance that a seed is able to be carried by wind was calculated using the formulae;

$$V_t = Y1 - Y2 / T(Y1 - Y2)$$

$$D = V_w * H / V_t$$

where: V_t = terminal velocity (m s^{-1})
 Y = distance of fall (m)
 T = time taken to fall Y (seconds)
 D = approximate distance dispersed (m)
 V_w = velocity of the wind (m s^{-1})
 H = height of dispersal point (m)

6.2.6 Disturbance and animal exclusion

This experiment was designed to test the effect of ground disturbance on germination, and the effect of animal digging and grazing on the survival of *P. aspleniifolius* and *A. biglandulosum* seedlings.

Twelve exclosures were erected in four communities. Two communities were in the northwest of the state ($41^{\circ} 13'$, $145^{\circ} 22'$), one on basalt and one on a quartzite substrate. The other two communities were in the southwest ($42^{\circ} 48'$, $146^{\circ} 25'$), one on dolorite and one on a quartzite substrate. Nine of the sites were used to monitor both *P. aspleniifolius* and *A. biglandulosum* while the three basalt sites were used to monitor *A. biglandulosum* only. This was because seedlings of *A. biglandulosum* normally are rare, and these particular sites supported seedlings of *A. biglandulosum* but not *P. aspleniifolius* at the time of the experiment. The overwood was cleared to ensure that light was not limiting germination. The exclosures and adjacent exposed areas were paired and the pairs were independently located in the communities. Each sample site (exposed or enclosed) measured $2\text{m} \times 2\text{m}$ and was divided into 6 sections of equal size arranged in a block of 2×3 . The three sections considered to be most disturbed during construction of the

exclosures were thoroughly scarified using a mattock to produce a disturbance effect, while the other three sections were left undisturbed. The exclosures were completely covered with 1 cm galvanised mesh which was buried to 10 cm around the perimeter. The corners of the exposed areas were marked using steel pickets.

The sites were initially recorded in July 1989, and then monitored for germination and subsequent survival at the end of summer in 1990, 1991 and 1992. The positions of survivors were recorded so that they could be distinguished from the next season's germinants.

To avoid pseudo-replication, the total number of germinants and the total number of survivors under each treatment (i.e. total in three sections) at each site were used in analysis. The data were log transformed and then the treatments were compared across the twelve sites in a multifactor ANOVA.

6.2.7 Disturbance and temperature effects

This experiment was designed to test the effects of substrate disturbance and overwintering on the germination of *P. aspleniifolius* and *A. biglandulosum*.

Peat was removed to a depth of 10 cm from 13 sites in the Mt Field and Frodshams Pass regions in May 1990. The peat from each site was cut into four pieces each measuring 0.1 m². Two pieces were each thoroughly disturbed and mixed before being placed in 0.1 m² trays. The other two pieces were placed in trays without being disturbed. One tray from each treatment and from each site (13 sites X 2 treatments) was kept in a shade house at ambient temperature while the other set was kept in a glass house where the minimum temperature was not allowed to fall below 8° C. All of the trays were watered regularly. The outer 5 cm around the perimeter of the trays was excluded from sampling to avoid edge effects. The germinants within the treatment area were counted in 1991 and 1992.

6.2.8 Seed predation of *A. biglandulosum*.

After the 1989 seed trap collections, it was evident that much of the seed produced by *Anodopetalum* was being predated. An experiment was designed to determine what was responsible for the predation and what proportion of the seed was predated.

In 1990, three treatments were imposed on flowering branches. The treatments were intended to provide three levels of protection from predators: no protection (the branch was tagged 30 cm from the apex); limited protection, a 30 cm long gauze bag (1.5 mm mesh); and complete protection, a 30 cm long calico bag. The bags were tied over the ends of the branches and were securely bound to the branch to prevent insects from entering the bag. The flowers on each length of branch were counted and no significant difference in the number of flowers between treatments existed. The treatments were thrice replicated on each of three trees at two times. Time one was the 2nd of February during early flowering, and time two was the 6th of March during late flowering/early fruit set. All branches were collected on the 4th of April. The number of unproductive flowers, the number of healthy fruit, predated fruit and the number of seeds were all recorded. Potential predator species were also identified.

The experiment was repeated in 1991 but time one was brought forward to before floral bud burst and the treatments were imposed a second time at peak flowering. These modifications were deemed necessary after analysis of the first year's data.

The rates of predation were expressed as percentages of the total number of fruit. These values were transformed using the arcsin transformation, and a multi-factor ANOVA was performed. Records of zero fruit, and consequently zero predation, were excluded from the analysis.

6.3 Results

6.3.1 Phenology

6.3.1.1 *P. aspleniifolius* foliar phenology

Figure 6.1 indicates that the timing of bud-swell is latest at the highest sites. The timing of the bud-swell phase was delayed in the spring of 1990 by about three weeks at the highest sites but was approximately the same as 1989 at the lowest sites. The length of the bud swell period was between one and four weeks, and generally longer at higher altitude.

Shoot extension began three to four weeks later at the highest altitude, however, the period of shoot extension only varied by one week between the sites and was not related to altitude. Phylloclade senescence began at the end of the shoot extension period and involved phylloclades ranging from four to twelve years old (annual node counts). The oldest phylloclades were found on trees growing in full sun.

Phylloclade expansion began two weeks earlier at the lowest site than at the highest site. The total time period over which foliage development occurred was clearly longer at the highest compared with the lowest sites, being nine weeks compared to three weeks, and was similar in both years.

6.3.1.2 *P. aspleniifolius* sexual development

The onset of male strobili development was staggered between the lowest and highest sites by one week in 1989 and two weeks in 1990 (Figure 6.2). Male strobili development took from 14 days at 660 m (1989) to 35 days at 1 030 m (1990). The period over which pollen was released varied between 11 days at 600 m (1990) and 24 days at 840 m (1990). Across all sites, pollen release spanned five to six weeks with an overlapping period between all sites in 1989 and between the lowest three sites in 1990. The number of male strobili varied between sites and years. In 1989, all male trees had large numbers of strobili on each branch. In 1990, strobili were rare at 600 m and at 840 m (closed sites) and although common at 660 m and 1 030 m (open sites), the numbers were considerably less than in 1989.

Female strobili development generally began one or two weeks before pollen release and was staggered in a similar manner to male strobili development in 1989. In 1990 cones

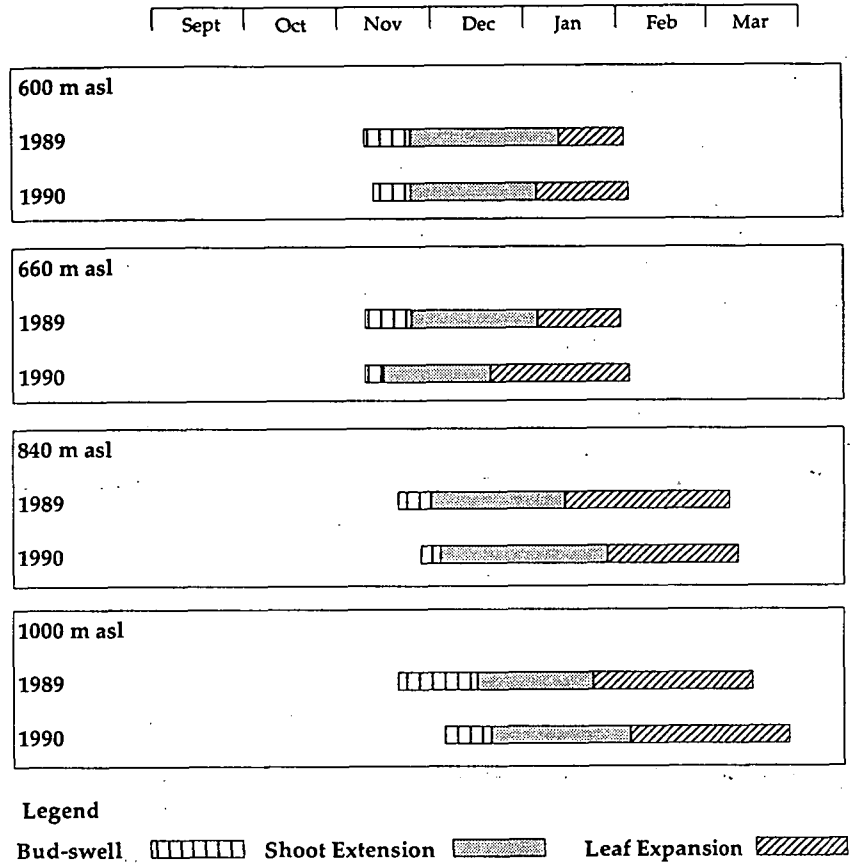


Figure 6.1. The timing and period of bud-swell, shoot extension and leaf expansion for *Phyllocladus aspleniifolius* at 4 sites along an altitudinal gradient in 1989 and 1990.

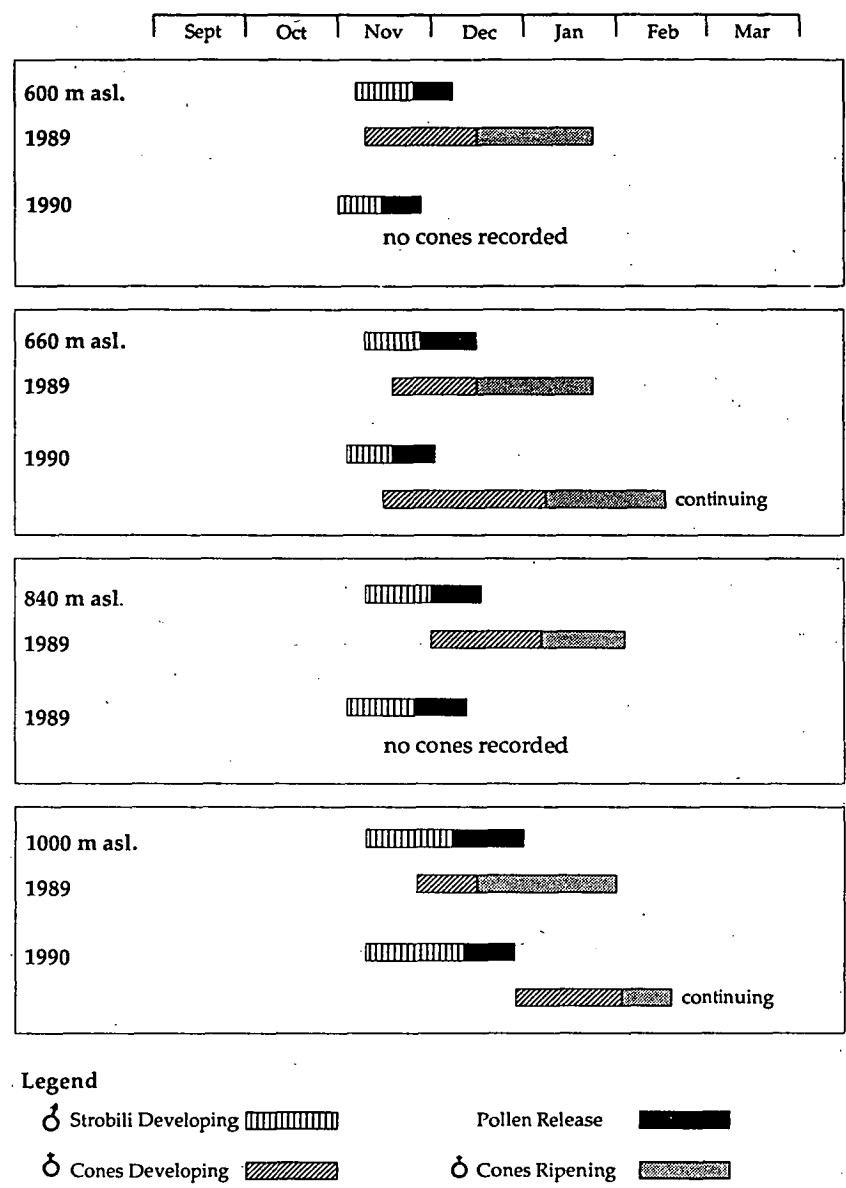


Figure 6.2. The timing and period of male and female cone development and pollen release for *Phyllocladus aspleniifolius* at 4 sites along an altitudinal gradient in 1989 and 1990.

were not recorded at 600 m and 840 m and were rare at 660 m and 1 030 m. The development period ranged from three weeks at 1030 m (1989) to six weeks at 660 m (1990) and the ripening period varied from four to seven weeks. The length of the ripening phase was not directly related to altitude.

6.3.1.3 *P. aspleniifolius* transplants

In 1989, bud-swell began in the highland transplants before the lowland transplants at the two lowest sites, and the lowland transplants began before the highland transplants at the two highest sites (Figure 6.3). The period over which foliage developed ranged from 9 to 13 weeks and had no relationship with altitude, nor were there any differences between the populations. The development period was, however, considerably shorter for the transplants than for any of the trees measured *in situ* at any altitude in this study. The latter ranged from 12 to 17 weeks.

In 1990, the highland transplants began and finished development before the lowland transplants in each case (Figure 6.3). The development period was similar to 1989 in range (9 to 13 weeks) and both the highland and lowland transplants varied by only +/- one week compared to 1989.

The growth rates of each provenance indicate significant differences between the sites with the 740 m site supporting the highest rates for both provenances. The lowland plants grew faster than the highland plants at all but the highest altitude including, the altitude from which the highland sample was collected (740 m) (Table 6.1, Figure 6.4).

6.3.1.4 *A. biglandulosum* foliar phenology

Bud swell occurred in the same period for *A. biglandulosum* as for *P. aspleniifolius* in both years, and was delayed by about one week in 1989 compared to 1990. The shoot extension period was equal to the leaf expansion period and continued for about six weeks in both years (Figure 6.5).

6.3.1.5 *A. biglandulosum* sexual development

Floral buds are axillary and can be seen as soon as the opposite leaves separate after foliar bud burst. The buds continued to expand for six weeks before flowering. Flowering began one week earlier (mid December) in 1990 than in 1989 and lasted for three weeks, one week less than in 1989 (Figure 6.5). Nectar flow was observed when the

flowers were fully open and native bees (*Exoneura bicolor*) were seen visiting flowers and carrying pollen loads. The period from the first appearance of fruit until seed-fall began was six weeks in 1989 and eight weeks in 1990.

Table 6.1. ANOVA, means and standard errors (se) of the total growth (mm) of five plants each from lowland and highland provenances planted at four altitudes (m) asl

Source of variation	SS	d.f.	MS	F	P
COVARIATE					
INITIAL HEIGHT	1678.4	1	1678.4	1.9	0.178
MAIN EFFECTS					
A:PROVENANCE	1623.3	1	1623.3	1.9	0.187
B:ALTITUDE	64142.2	3	21380.7	25.3	0.000
INTERACTIONS					
AB	14166.1	3	4722.0	5.5	0.005
RESIDUAL	20271.5	24	844.6		
TOTAL (CORRECTED)	123792.97	32			

7 missing values excluded.

All F-ratios are based on the residual mean square error.

Altitude (m)	Provenance	Growth (mm)	(SE)
60	Lowland	115.3	(16.8)
60	Highland	79.6	(18.8)
220	Lowland	129.2	(19.0)
220	Highland	74.1	(15.0)
740	Lowland	206.2	(15.0)
740	Highland	154.2	(16.1)
1030	Lowland	28.5	(5.9)
1030	Highland	52.4	(13.3)

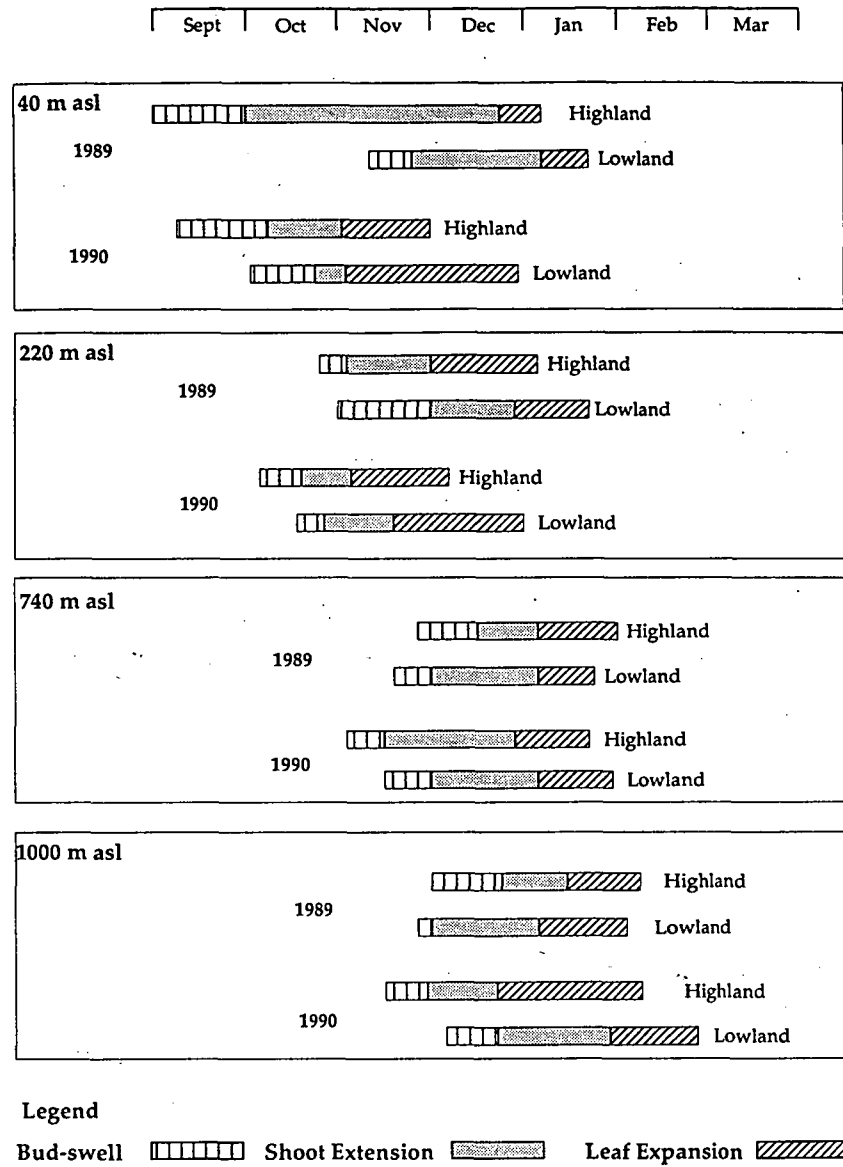


Figure 6.3. The timing and period of bud-swell, shoot extension and leaf expansion for transplants from a highland (750 m) population and a lowland (60 m) population of *P. asplenifolius* along an altitudinal gradient in 1989 and 1990.

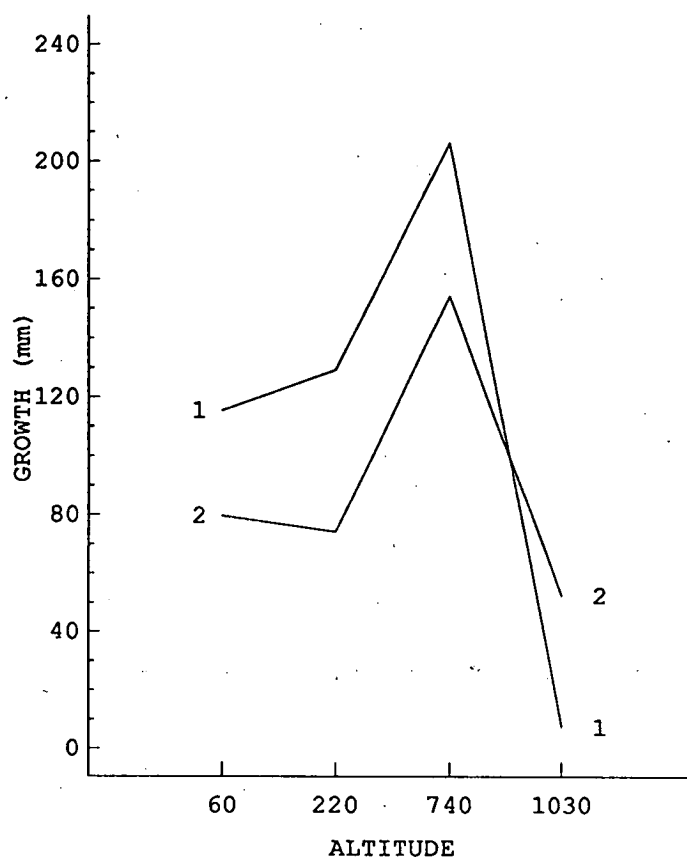


Figure 6.4. A plot of the vertical growth (mm) of two provenances of *P. aspleniifolius* along an altitudinal gradient. Sites were Hobart (60 m) and Mt. Field (220, 740 and 1 030 m); (1) a lowland provenance and (2) a highland provenance .

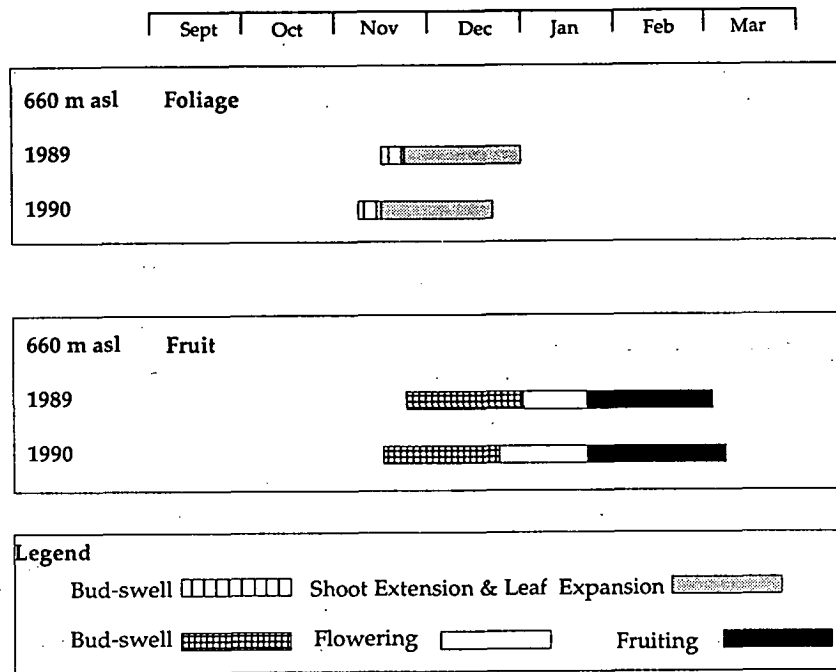


Figure 6.5. The timing and period of foliar development and sexual development for *A. biglandulosum* at one site in 1989 and 1990.

6.3.3 The fate of the seed

6.3.3.1 Seed Dispersal

Seed from *P. aspleniifolius* began to fall at Mt Field in mid-February 1989, one month earlier than at the other sites. In 1990, the seed began to fall in mid-January at Frodshams Pass, two weeks earlier than at the other sites. *P. aspleniifolius* produced variable amounts of seed between the sites in 1989. In 1990, and particularly 1991 (Appendix 4) the traps generally captured considerably less seed than in 1989, a mast seeding year (Figure 6.6a). However, traps 2 and 3 captured more seed in 1990 than in 1989.

The seed of *Anodopetalum* began to fall in late March at Frodshams Pass and two weeks later at the other sites in 1989. In 1990 seed-fall began in early February at Hopetoun and one month later at Frodshams Pass. *Anodopetalum* also produced more seed in 1989 than in 1990 and 1991. However, only two traps caught more than 20 seeds in any fortnight and the same tree was the most productive in each year (Figure 6.6b). Most seeds had small holes bored into them or were shrivelled.

Both species shed most seed in the first month but seed continued to fall at a much lower rate until September in 1989 and May in 1990 for both species (Figure 6.6a,b). The low sampling intensity at any site precluded estimates of the overall density of seed fall.

The seed and aril (connected at time of dispersal) of *A. biglandulosum* weighs 3.67^{-3} g on average, compared to 2.81^{-3} g for the seed of *P. aspleniifolius* without its aril. The seed of *A. biglandulosum*, inside its papery aril, is able to disperse about 500 m from a 20 m tall tree when aided by a wind velocity of 100 km/h compared with about 130 m for *P. aspleniifolius* (Figure 6.7). However, *P. aspleniifolius* is dispersed much further by birds.

Casual observation of *A. biglandulosum* revealed that many fruit had been removed by parrots and were scattered on the ground beneath the branches. Of ten trees that were observed, 80% of the fruit were scattered on the ground and the "soft" seed had been removed (Figure 6.8).

The analysis of the Maydena climate between 1978 and 1991 (Figure 6.9) indicates that the mast years of 1982 and 1989 were associated with similar climatic patterns (Table 6.2). In both cases, the mast year and its previous year were warm and dry. These were the only consecutive warm and dry years during the 14 year period.

Table 6.2 . The number of months during the growing season (October to March) in which average minimum and maximum temperatures and rainfall were below the average - or above the average + for the years 1978 to 1991. Each variable is summarised as (-) or (+) dependant upon the condition of the majority of months. The season is summarized based on the average state of the maximum temperature and rainfall as cool if average maximum temperature is below average in a majority of growing season months and warm if it is above average for a majority of months. And similarly wet or dry depending on the monthly average rainfall in the growing season. (m) = moderate, where the number of months during the growing season which are below and above average is equal. * Bold indicates mast years.

YEAR	MINIMUM -, +	MAXIMUM -, +	RAINFALL -, +	DESCRIPTION
1978	5, 1 (-)	4, 2 (-)	3, 3 (m)	COOL MODERATE
1979	2, 4 (+)	4, 2 (-)	4, 2 (-)	WARM DRY
1980	3, 3 (m)	3, 3 (m)	3, 3 (m)	MODERATE
1981	3, 3 (m)	1, 5 (+)	4, 2 (-)	WARM DRY
1982	4, 2 (-)	0, 6 (+)	4, 2 (-)	WARM DRY*
1983	2, 4 (+)	4, 2 (-)	5, 1 (-)	COOL DRY
1984	5, 1 (-)	4, 2 (-)	5, 1 (-)	COOL DRY
1985	5, 1 (-)	4, 2 (-)	2, 4 (+)	COOL WET
1986	4, 2 (-)	4, 2 (-)	2, 4 (+)	COOL WET
1987	6, 0 (-)	5, 1 (-)	1, 5 (+)	COOL WET
1988	3, 3 (m)	2, 4 (+)	5, 1 (-)	WARM DRY
1989	1, 5 (+)	1, 5 (+)	4, 2 (-)	WARM DRY*
1990	1, 5 (+)	3, 3 (m)	2, 4 (-)	MODERATE WET
1991	3, 3 (m)	5, 1 (-)	3, 3 (m)	WARM MODERATE

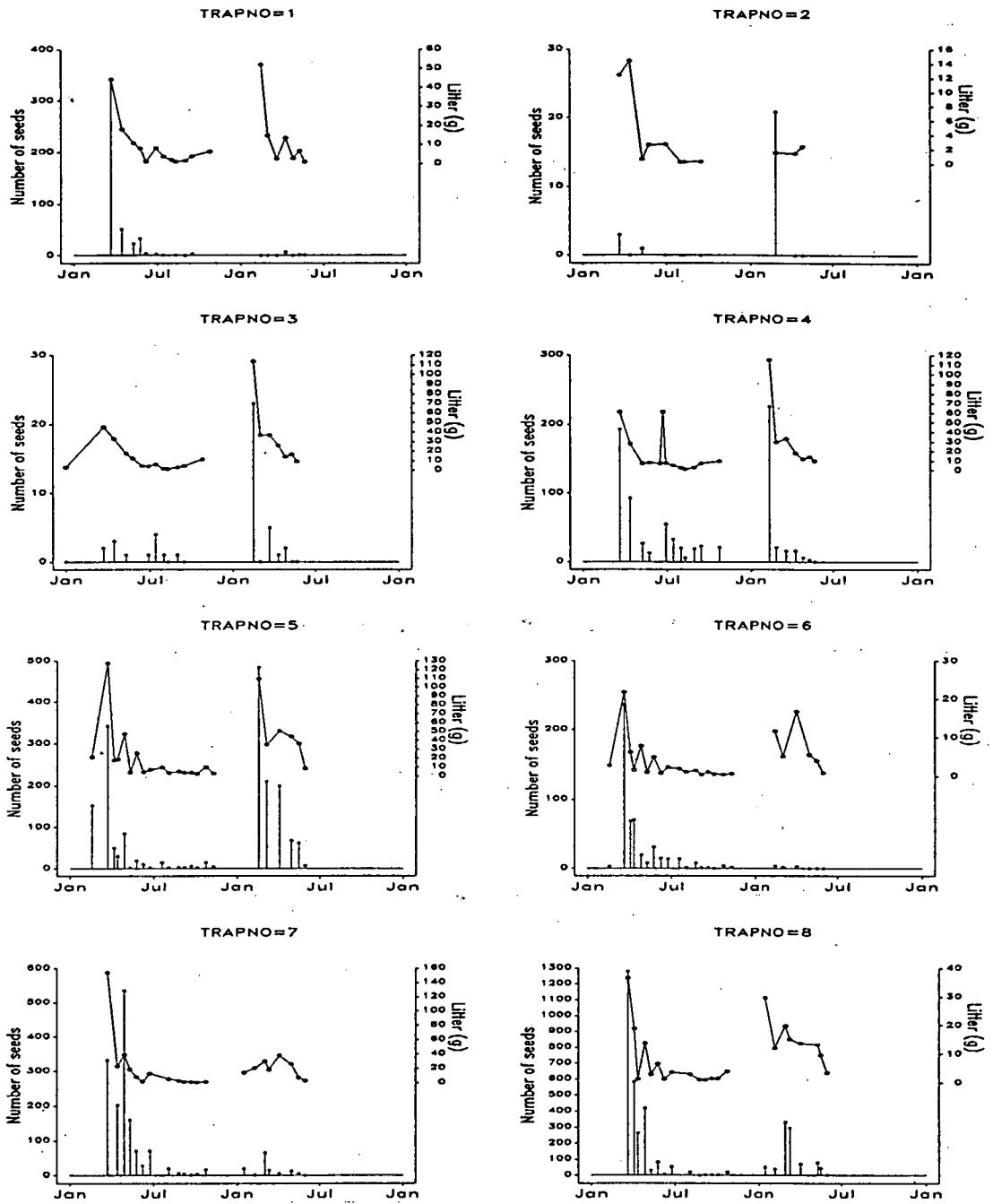


Figure 6.6a. The number of *P. aspleniifolius* seeds and the weight of litter (g) caught in eight 1 m² seed and litter traps at four sites in 1989 and 1990. 1 and 2 Hopetoun Rd., 3 and 4 Bennets Spur, 5 and 6 Mt Field, and 7 and 8 Frodshams Pass.

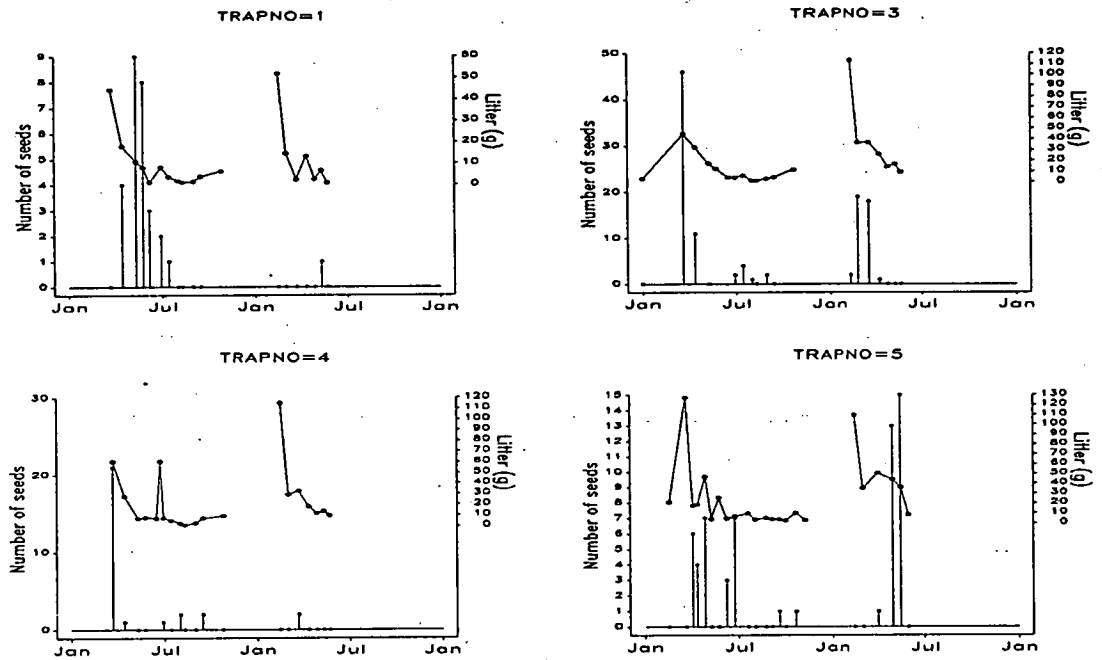


Figure 6.6b. The number of *A. biglandulosum* seeds and the weight of litter (g) caught in four 1 m^2 seed and litter traps at three sites in 1989 and 1990. 1 Bennets Spur, 2 and 3 Hopetoun Rd., and 4 Mt Field.

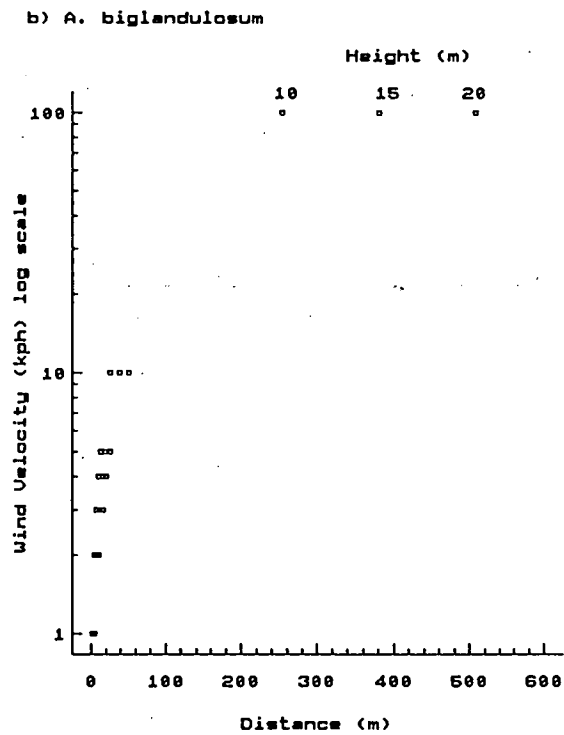
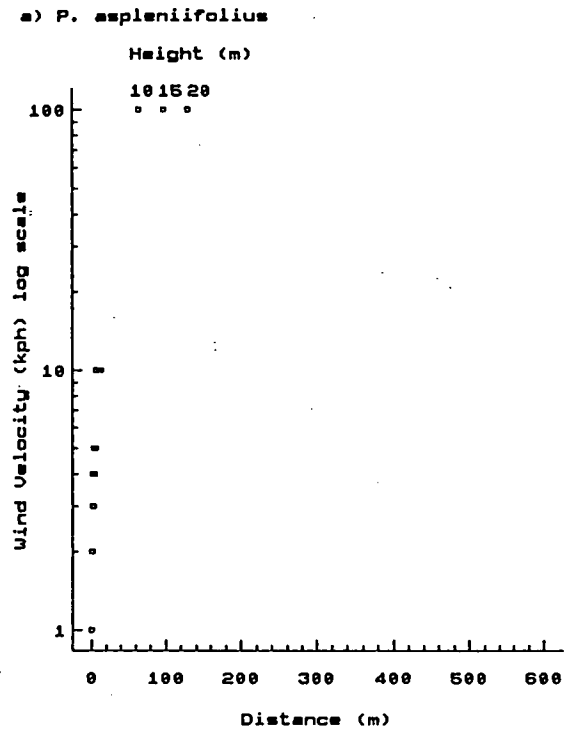


Figure 6.7. The estimated dispersal distances (x axis) for the seed of (a) *P. aspleniifolius* and (b) *A. biglandulosum* under the influence of wind velocities ranging from 1 to 100 k/h (y axis) falling from 10, 15 and 20 m above the ground (top).

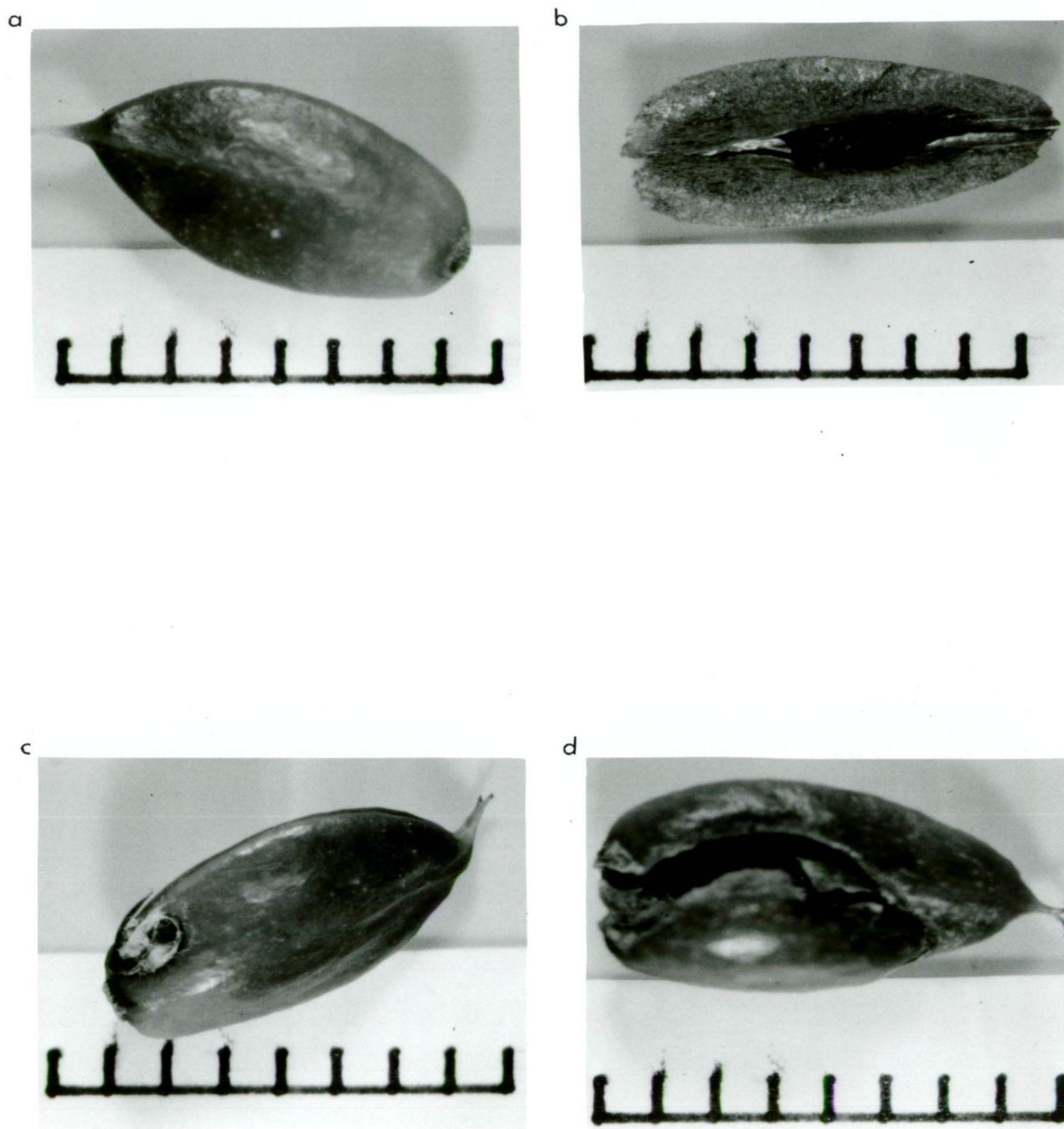


Figure 6.8. Photographs of green *A. biglandulosum* fruit showing a. a single fruit, b. the papery aril with a single seed attached in the centre, c. fruit with an exit holes of the moth larve *Neoherminias* sp. (Tortrichedae), and d. the fruit after being removed and the seed eaten by parrots. Scale = 1 cm.

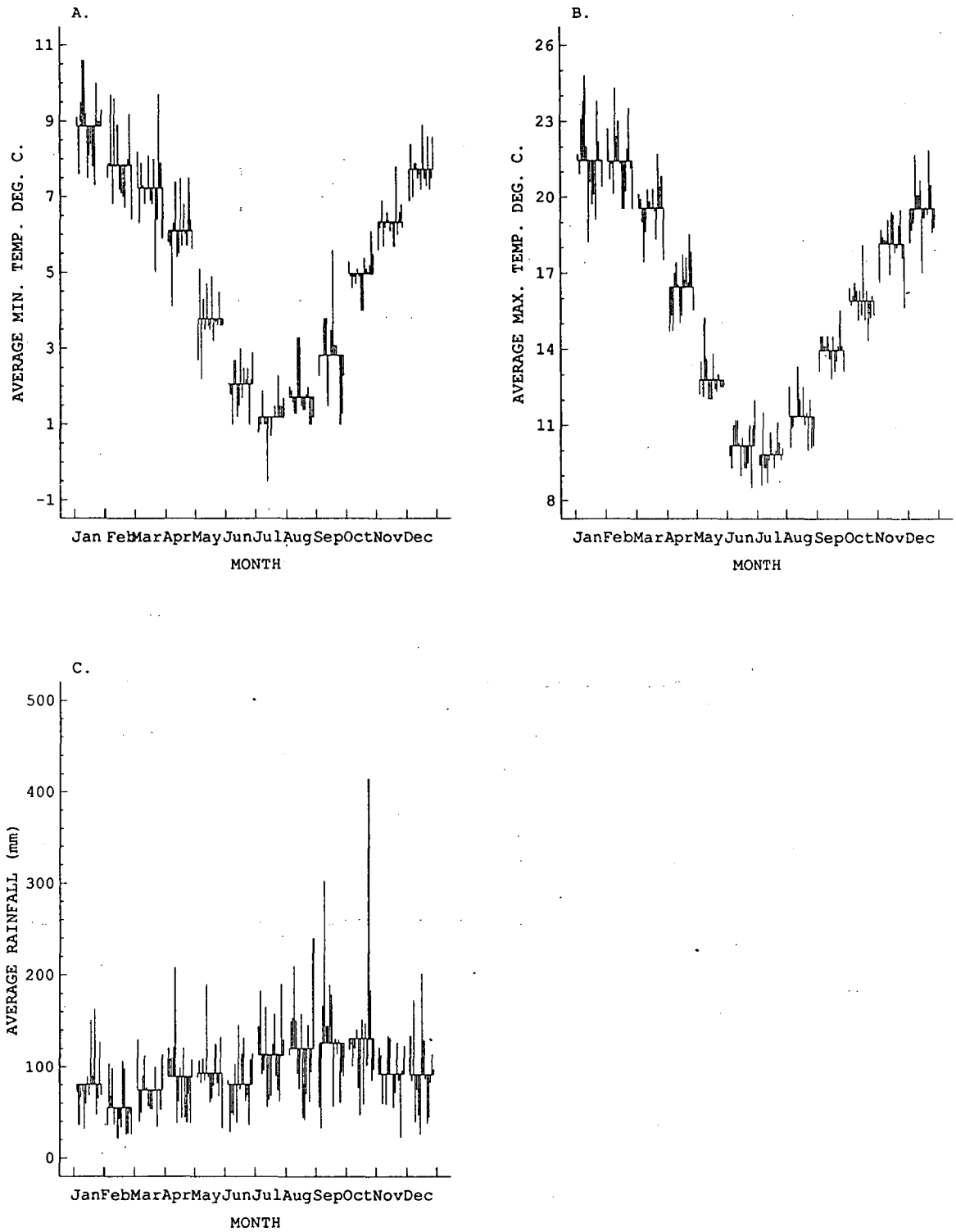


Figure 6.9. Seasonal sub-series plots of 13 years of climatic averages at Maydena, near Mt. Field between 1978 and 1990. A. average monthly minimum temperature $^{\circ}\text{C}$; B. average monthly maximum temperature $^{\circ}\text{C}$; C. average monthly rainfall (mm). All values are absolute and the length of the lines indicate the distance from the 13 year mean which is indicated by the horizontal interval.

Table 6.3. ANOVA, means and standard errors (se) of the number of (a) *P. aspleniifolius* and (b) *A. biglandulosum* germinants on disturbed and undisturbed ground both inside and outside enclosures over three years (1989-1991). And Anova, means and standard errors (se) of the number of survivors in 1990 and 1991 of (c) *P. aspleniifolius* and (d) *A. biglandulosum*.

6.3 (a)

Source of variation	SS	d.f.	MS	F	P

MAIN EFFECTS					
A:YEAR	59422.3	2	29711.1	5.9	0.003
B:DISTURBANCE	49.3	1	49.3	0.1	0.921
C:EXPOSURE	5390.4	1	5390.4	1.0	0.300
INTERACTIONS					
AB	17.7	2	8.8	0.1	0.998
AC	8007.0	2	4003.5	0.8	0.450
BC	3547.7	1	3547.7	0.7	0.409
RESIDUAL	487432.1	98	4973.7		

TOTAL (CORRECTED)	563866.9	107			

0 missing values excluded.

All F-ratios are based on the residual mean square error.

Mean germination *P. aspleniifolius*

Treatment	1989	1990	1991
	\bar{x} (se)	\bar{x} (se)	\bar{x} (se)

Disturbed	4(1)	55(18)	8(2)
Undisturbed	3(1)	56(35)	9(3)
Enclosed	3(1)	36(15)	10(3)
Exposed	3(1)	74(36)	7(2)

Table 6.3 continued

6.3 (b):

Source of variation	SS	d.f.	MS	F	P

MAIN EFFECTS					
A:YEAR	17.98	2	8.99	9.14	0.001
B:DISTURBANCE	0.55	1	.55	0.56	0.461
C:EXPOSURE	2.25	1	2.25	2.28	0.132
RESIDUAL	136.65	139	0.98		

TOTAL (CORRECTED)	157.00	143			

0 missing values excluded.

All F-ratios are based on the residual mean square error.

Mean germination *A. biglandulosum*

Treatment	1989 \bar{x} (se)	1990 \bar{x} (se)	1991 \bar{x} (se)

Disturbed	0.8(.2)	0.4(.2)	0.4(.1)
Undisturbed	0.6(.2)	0.2(.1)	0.3(.1)
Enclosed	0.7(.2)	0.3(.2)	0.2(.1)
Exposed	0.8(.3)	0.4(.2)	0.1(0.1)

6.3 (c)

Source of variation	SS	d.f.	MS	F	P

COVARIATES					
GERMINATE NUMBER	6289.1	1	6289.1	10.6	0.001
MAIN EFFECTS					
A:YEAR	8835.8	1	8835.8	14.9	0.001
B:DISTURBANCE	22.3	1	22.3	0.1	0.848
C:EXPOSURE	1624.6	1	1624.6	2.7	0.102
INTERACTIONS					
AB	936.5	1	936.5	1.5	0.213
AC	1162.1	1	1162.1	1.9	0.166
BC	6.3	1	6.3	0.1	0.919
RESIDUAL	34283.1	58	591.1		

TOTAL (CORRECTED)	54792.5	65			

6 missing values excluded.

All F-ratios are based on the residual mean square error.

6.3 (c) continued

Mean survivors *P. aspleniifolius*

Treatment	1990 \bar{x} (se)	1991 \bar{x} (se)
Disturbed	1(0.3)	30(6)
Undisturbed	4(0.9)	23(7)
Enclosed	3(0.8)	36(6)
Exposed	2(0.9)	17(6)

6.3 (d)

Source of variation	SS	d.f.	MS	F	P
COVARIATES					
GERMINATE NUMBER	5.60	1	5.60	7.15	0.011
MAIN EFFECTS					
A:YEAR	0.01	1	0.01	0.01	0.921
B:DISTURBANCE	0.01	1	0.01	0.01	0.940
C:EXPOSURE	2.42	1	2.42	3.08	0.087
INTERACTIONS					
AB	0.44	1	0.44	0.56	0.464
AC	0.01	1	0.01	0.01	0.912
BC	0.01	1	0.01	0.01	0.938
RESIDUAL	28.23	36	0.78		
TOTAL (CORRECTED)	36.97	43			

52 missing values have been excluded.

All F-ratios are based on the residual mean square error.

Mean survivors *A. biglandulosum*

Treatment	1990 \bar{x} (se)	1991 \bar{x} (se)
Disturbed	0.3(0.2)	0.3(0.3)
Undisturbed	0.3(0.1)	0.5(0.2)
Enclosed	0.5(0.2)	0.7(0.2)
Exposed	0.1(0.1)	0.2(0.2)

Table 6.4. ANOVA, means and standard errors (se) of the number of (a) *P. aspleniifolius* germinants in disturbed and undisturbed peat in a glasshouse (minimum temperature 8°C) and in a shade-house at ambient temperature in 1990 and 1991. And (b) the number of surviving seedlings from the 1990 germinants.

6.4a

Source of variation	SS	d.f.	MS	F	P

MAIN EFFECTS					
A:YEAR	37.50	1	37.84	41.236	0.000
B:GLASSHOUSE	0.15	1	0.15	0.171	0.684
C:DISTURBANCE	7.65	1	7.65	8.342	0.004
INTERACTIONS					
AB	0.10	1	0.10	0.111	0.743
AC	0.17	1	0.17	0.193	0.666
BC	0.12	1	0.12	0.134	0.718
RESIDUAL	89.01	97	0.91		

TOTAL (CORRECTED)	135.06	103			

0 missing values excluded.

All F-ratios are based on the residual mean square error.

Mean germinates *P. aspleniifolius*

Treatment	1990	1991
	\bar{x} (se)	\bar{x} (se)

Glasshouse		
Disturbed	2.5(0.4)	14.8(6.6)
Undisturbed	0.6(0.3)	10.0(4.1)
Ambient		
Disturbed	2.8(1.2)	11.6(2.5)
Undisturbed	2.5(0.4)	6.9(2.4)

Table 6.4 continued

6.4(b) :

Source of variation	SS	d.f.	MS	F	P

COVARIATES					
GERMINANT NUMBER	28.95	1	28.95	1000.00	0.000
MAIN EFFECTS					
A:GLASSHOUSE	0.02	1	0.02	1.14	0.290
B:DISTURBANCE	0.03	1	0.03	1.79	0.186
INTERACTIONS					
AB	0.03	1	0.03	1.95	0.168
RESIDUAL	0.72	47	0.15		

TOTAL (CORRECTED)	29.75	51			

All F-ratios are based on the residual mean square error.

Mean survivors *P. aspleniifolius*

Treatment	1991
	\bar{x} (se)

Glasshouse	
Disturbed	2.4(1.0)
Undisturbed	1.2(0.8)
Ambient	
Disturbed	2.2(0.5)
Undisturbed	0.6(0.3)

6.3.3.2 Exclosure and disturbance effects.

The multi-factor analysis of variance indicates that neither disturbance of the substrate nor exclosure from animal foraging and grazing, or any interaction between disturbance and exclosure, significantly affected germination of *P. aspleniifolius* or *A. biglandulosum* in 1990, 1991 or 1992 (Table 6.3). A highly significant increase in the number of germinants of *P. aspleniifolius* was evident in 1990, two years after the mast. The number of surviving seedlings was dependent upon the number of germinants in the previous year but was not affected by disturbance or animal foraging.

Similar treatment responses were observed for *A. biglandulosum*. Significantly more seeds germinated in 1990 than in subsequent years. However, low numbers of seeds were produced in all years.

6.3.3.3 Disturbance and temperature effects

Only one germinant of *A. biglandulosum* was recorded and was not included in the analysis. No search for seeds in the peat samples was undertaken.

The multi-factor analysis of variance indicates that there was a significant effect of disturbance and year on the germination of *P. aspleniifolius*. There was no difference in the effect of the over-wintering temperatures nor any interaction between disturbance and environment on the germination of *P. aspleniifolius* (Table 6.4). The survival of seedlings was not affected differentially between disturbed and undisturbed substrates nor between environments. The number of survivors was, however, related to the number of germinants in the previous year.

6.3.3.4 Seed predation of *A. biglandulosum*

Seven pupae were collected from inside fruit in the bagged treatments and three were reared to adult moths, *Neoherminias* sp. (Tortricidae). A caterpillar, of the same species, was recovered from a calico bag. It is probable that the eggs of this species were laid on the flower very early and that the moth may also act as a pollinator.

An interaction between treatment and time of treatment resulted in lower rates of pollination success (measured as the percentage of fruit to the total number of flowers) when exclusion was applied earlier in the second year (Table 6.5a, Figure 6.10a). The branches carrying the highest numbers of flowers displayed the lowest rate of pollination

success. This may indicate that a high number of flowers may overwhelm the pollinator(s). Alternatively, the number of fruit that *A. biglandulosum* can produce may be governed by resource limits to its own energy budget. The percentage of fruit predated was not related to the number of fruit produced. These results suggest that even when large numbers of flowers are produced the predator remains the predominant pollinator, otherwise a decrease in the percentage predated with an increase in the number of flowers and fruit would be expected. Interaction between the time and the treatment significantly effected the amount of fruit predated. The earlier implimentation of exclusion treatments in 1991 (Time 3) resulted in lower proportions of predation (Table 6.5b, Figure 6.10b). The low number of fruit on the exposed branches in 1990 appears to reflect the removal by parrots (*Platycerus caledonicus*).

There was a significant ($P < 0.05$) interaction between treatment and time of treatment on the number of fruit produced. Bare branches carried less fruit than the branches with a gauze bag or cloth bag on them in the first year but carried more in the second year (Figure 6.10c). There was no difference in the number of fruit produced under treatments 1 and 2, at time 1, compared to time 2. The earlier application of treatments in the second year (time 3) resulted in reduced numbers of fruit in the exclusion treatments which correlates with the low pollination success (Figure 6.10a).

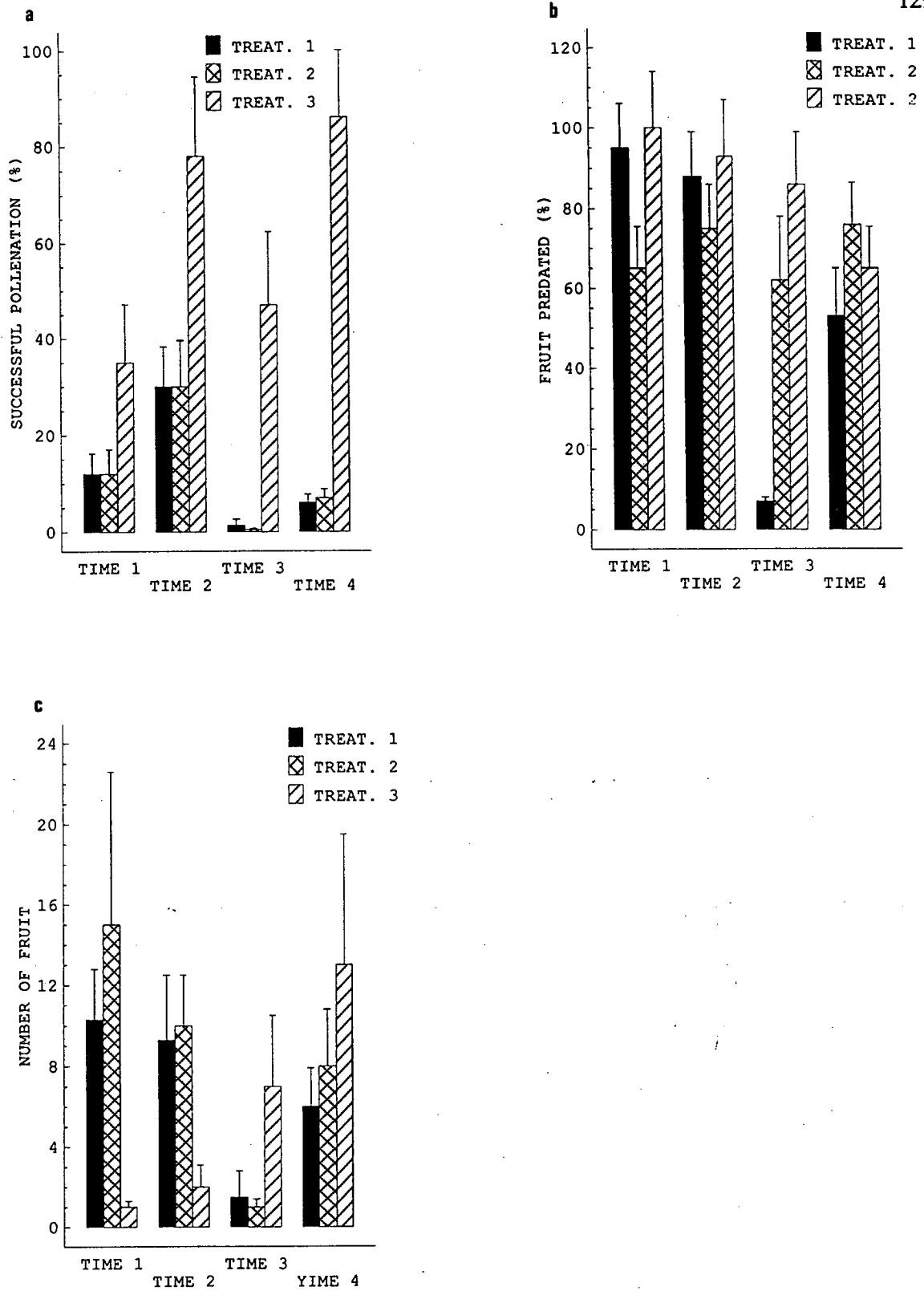


Figure 6.10. Bar graphs showing the mean and standard error of a. the rate of pollination success as a percentage of the total number of flowers that bear fruit, b. the percentage of fruit predated and c. the amount of fruit produced.

Table 6.5. ANOVA, means and standard errors (se) of (a) the rate of pollination success of flowers of *A. biglandulosum* (percentage of flowers that develop into mature fruit) (x), (b) the quantity of fruit produced and (c) the proportion of fruit predated after 3 treatments at 4 times.

6.5 (a)					
Source of variation	SS	d.f.	MS	F	P

COVARIATES					
NUMBER FLOWERS	0.034	1	0.034	0.34	0.566
MAIN EFFECTS					
A: TIME	1.992	3	0.664	6.53	0.001
B: TREATMENT	2.982	2	1.491	14.67	0.001
INTERACTIONS					
AB	2.101	6	0.350	3.44	0.004
RESIDUAL	8.838	87	0.101		

TOTAL (CORRECTED)	21.20	99			

8 missing values have been excluded.

All F-ratios are based on the residual mean square error.

	Pollination Success (%)

Treatment	\bar{x} (se)

Time 1	
Bagged	10 (2)
Gauze	15 (8)
No treatment	35 (12)
Time 2	
Bagged	30 (8)
Gauze	30 (10)
No Treatment	78 (0)
Time 3	
Bagged	1.5 (1)
Gauze	0.5 (.2)
No Treatment	47 (11)
Time 4	
Bagged	6 (1.7)
Gauze	7 (1.8)
No Treatment	86 (9.8)

Table 6.5 continued

6.5(b) :

Source of variation	SS	d.f.	MS	F	P

COVARIATES					
NUMBER OF FRUIT	0.17	1	0.17	0.749	0.399
MAIN EFFECTS					
A:TREATMENT	2.20	2	1.10	4.720	0.012
B:TIME	3.04	3	1.01	4.348	0.007
INTERACTIONS					
AB	3.81	6	0.63	2.719	0.020
RESIDUAL	15.1	65	0.23		

TOTAL (CORRECTED)	21.7	77			

30 missing values have been excluded.

All F-ratios are based on the residual mean square error.

Predation %	

Treatment	\bar{x} (se)

Time 1	
Bagged	95(11)
Gauze	65(10)
No Treatment	100(14)
Time 2	
Bagged	88(11)
Gauze	75(11)
No Treatment	93(14)
Time 3	
Bagged	7(1)
Gauze	62(16)
No Treatment	86(13)
Time 4	
Bagged	53(12)
Gauze	76(10)
No Treatment	65(12)

Table 6.5 continued

6.5(c)

Source of variation	SS	d.f.	MS	F	P

COVARIATES					
FTOT	6.79	1	6.79	6.67	0.011
MAIN EFFECTS					
A:TIME	21.39	3	7.13	7.00	0.001
B:TREATMENT	2.02	2	1.01	.99	0.373
INTERACTIONS					
AB	14.52	6	2.42	2.37	0.035
RESIDUAL	88.58	87	1.01		

TOTAL (CORRECTED)	139.99	99			

8 missing values have been excluded.

All F-ratios are based on the residual mean square error.

6.4 Discussion

In Tasmania, the phenological study of rainforest trees has recently received increasing attention. Hickey *et al.* (1983) investigated *Nothofagus cunninghamii*, *Eucryphia lucida* and *Atherosperma moschatum*. Cullen (1987) and Cullen and Kirkpatrick (1988) observed reproduction of *Athrotaxis selaginoides* and *A. cupressoides*, and considered the controls upon the reproductive ecology of populations. Read (1989) compared the phenology of four canopy dominants, including *P. aspleniifolius*, and tested germination characteristics in the laboratory. Shapcott (1991) worked on *Lagarostrobos franklinii* (Podocarpaceae) in a study of genetic variability within and between populations, and included an assessment of seed dispersal and germination characteristics. These studies contained a range of conclusions with respect to attributes affecting regeneration success. Variation between the species was most apparent in dispersability of seed and annual variation in seed production. Seasonality was similar among the conifers but varied considerably between the angiosperms. *Atherosperma moschatum* flowers in early spring, *Nothofagus cunninghamii* in summer and *Eucryphia lucida* in autumn (Read 1989).

In the present study, bud-burst of *P. aspleniifolius* occurred within two weeks of the time recorded by Read (1989) in 1982. The first appearance of female cones in 1983 and 1984 (Read 1989) was up to two weeks later than in 1989. Regional seed fall in 1989, 1990 and 1991 was also consistent with the times recorded by Read at Mt Field in 1982, 1984 and 1985 (Figure 6.6a). These results indicate that *P. aspleniifolius* displays little phenological variation from year to year. Regular periodicity such as this may be attributed to limits imposed by a short growing season in conjunction with a relatively long foliar

development period. Delayed foliar development of *P. aspleniifolius* has been observed to result in damage to phylloclades by early frosts (pers. obs., Read 1989).

Slow foliar development may also result in the current years foliage being photosynthetically inefficient until late in the summer of the following year. Beadle *et al.* (1985a) found that the current season's needles of Scots Pine are less efficient than the previous season's. In contrast, the leaves of *A. biglandulosum* were fully expanded by the end of the first summer month (Figure 6.5) and presumably were temperature hardened and photosynthetically mature before *P. aspleniifolius*.

The female cones of *P. aspleniifolius* begin to develop before pollen is available from the same site (Figure 6.2). Pollen is being shed from lower sites at the time the micropile becomes receptive. The likelihood of pollination from remote sites is enhanced by the efficient dispersal of pollen on the wind and particularly uphill (Niklas 1985). Successful pollination from remote sites enhances the gene flow from one population to another (Harper 1977). Further enhancement or maintenance of genetic diversity, due to efficient seed dispersal by birds (Kirkpatrick 1977), may play an important role in allowing *P. aspleniifolius* to maintain a broad ecological amplitude. Presumably, the pollination vectors of *A. biglandulosum*, the native bee and a moth, are also able to transport its pollen load but no estimate of distance or efficiency can be made.

Both species shed the largest amounts of seed at the time of peak leaf abscission. The fall of leaves and seeds varied in synchrony and may be attributed to the action of external forces such as wind and rain. Allen and Wardrop (1964) showed that cone dehiscence in *Pinus radiata* was associated with changes in the moisture content which promoted the opening of the cone allowing seeds to fall. The seed of *P. aspleniifolius* is exposed during ripening and ejected from the cone when ripe (Tomlinson and Takaso 1989). However, the cone of *P. aspleniifolius* does not dry before the seed falls and so, presumably, reduction in moisture does not play a role in the ejection of the seed.

In flowering plants which produce a dry dehiscent fruit, such as *A. biglandulosum*, moisture plays a role similar to that observed in *P. radiata* in the opening of the fruit (Fahn and Werker 1972). The synchronous dehiscence of fruit and the abscission of leaves may indicate a similar environmental trigger although the relationship between fruit dehiscence and the environment is not clear (Sedley and Griffin 1989).

Although the timing of seed dispersal was similar in both species, the number of seeds produced varied tremendously (Figure 6.6). The fate of seed is a distinguishing

characteristic between *P. aspleniifolius* and *A. biglandulosum* which may be reflected in the nature and distribution of regeneration. Under the influence of wind, the papery aril surrounding the seed of *A. biglandulosum* carries the seed up to approximately 500 m in strong winds (Figure 6.7). Although this distance is considerably further than that attained by the seed of *P. aspleniifolius* in similar wind conditions, it cannot permit *A. biglandulosum* to cross extensive areas of unfavourable habitat. The effective bird-dispersal of *P. aspleniifolius* seed enables it to reinvade burned areas and to cross large areas of climatically unsuitable habitat. Efficient bird-dispersal of seed is also a feature of the podocarps in New Zealand (Beveridge 1977). There is no evidence that *A. biglandulosum* seed is effectively dispersed by parrots, and so it must be assumed that the "soft" unripe seeds that these birds take are digested (Figure 6.8).

Read (1989) suggests that periodicity in the seed production of *P. aspleniifolius* may allow maximum growth in short growing seasons with significant seed production being confined to seasons when an abundance of assimilate has been stored. In the present study, there is some evidence to suggest that the oscillation from year to year is not necessarily consistent between sites at different locations (Figure 6.6) and that two good years in succession can occur. However, variability in climate may not be geographically coincident, and therefore the seed production may fluctuate from site to site without detracting from Read's basic premise.

P. aspleniifolius produces its male and female cone primordia in the season preceeding development of the fruit (Tomlinson and Takaso 1989). In the New Zealand alpine flora, Mark (1970) reported that the next year's floral primordia formed late in the current growing season to ensure completion of the reproductive cycle in the short snow-free period. Literature from the northern hemisphere concurs with this view. However, in Tasmanian dry sclerophyll vegetation, members of the Fabaceae produce overwintering floral buds in an environment where the reproductive cycle is unlikely to be inhibited by the length of the growing season (Lynch 1992). Thus, it is plausible that the early initiation of floral primordia is an attempt to remain reproductively active as long as possible regardless of the length of the growing season.

The climatic correlation of the two mast seasons, and their previous growing seasons, with warm and dry conditions (Table 6.2) may indicate a climatic stimulus to set fruit. Development of the fruit in the mast season may be dependent upon a suitable climate for the development of the floral initials produced in the previous year. If this does not eventuate the fruit buds may remain dormant. Consequently, a succession of favourable years would be necessary for a mast to be expressed.

Many authors have argued that the phenomenon of mast seed production is an evolutionary response which reduces the proportion of seeds predated in mast years, thus ensuring occasional higher levels of seed will be available for regeneration (Janzen 1971, Waller 1979, Silvertown 1980, Nilsson and Wastljung 1987). This model is known as the predator satiation model and is based on the notion that mast seed production will overwhelm the seed predators and that low seed production in the intervening years will starve them, reducing their numbers and consequent predation. Nilsson and Wastljung (1987) have demonstrated a negative correlation between the increasing number of seeds and the proportion predated and a positive correlation between the number of seeds produced and their viability. For this phenomenon to be most effective, the predator should be a specialist with no alternative food source. For *P. aspleniifolius*, most seed predators are generalist birds (*Cacatua gulerita*, *Strepera fuliginosa* and *Platycercus caledonicus*) with the exception of the rare *Neophema chrysogaster* which specialises on small seeds. For the generalists birds abundant fruit is utilized (pers. obs.) during the same season on alternative species, for example, *Gahnia grandis* and *Cyathodes* spp and alternative food sources are also used. Even if satiation were realised its advantage would not be transferred to dispersal as the rate of dispersal cannot increase if the seed dispersers become satiated (Givnish 1980). Evolutionary relationships, such as predator satiation, may reflect palaeoecologies which involved predators and or pollinators that are now extinct; leaving modern relationships which bear little ecological significance.

Although it is not known whether *A. biglandulosum* produces masts, the results of Nilsson and Wastljung (1987) do not concur with the predation rates of *A. biglandulosum* in relation to fruit abundance. Although the number of fruit is higher on branches with more flowers the proportion of seeds predated does not change (Figure 10, Table 5). If the failure to convert large numbers of flowers to fruit is due to them not being pollinated, then the pollinator is exhibiting a conservative life cycle strategy. Such a strategy may allow it to avoid the "boom and bust" scenario involved in following fluctuations in flowering densities. It appears that mast flowering of *A. biglandulosum* would be advantageous in avoiding seed predation. However, in this case, satiation is not possible as the pollinator is also the predator.

In the absence of long-term soil-stored seed, it would be expected that periodicity in seed production would be reflected in a periodicity in regeneration. The results of the field trial and the glasshouse trial (Tables 6.3 and 6.4) indicate a highly significant difference in number of germinants between years. For *P. aspleniifolius*, these data indicate that the numbers of germinants reflect the mast seed crop of *P. aspleniifolius* two summers

previous. They also support the results of Read (1989) who indicated that with no pretreatment but with daily watering 62% of *P. aspleniifolius* seeds germinated after two winters. Other seed treatments by Read (1989) failed to result in germination. Read suggests that the infrequency of regeneration in rainforest may be related to seed dormancy. Another cause of the inhibition of germination is the requirement for an after-ripening period after seed shed. Because after-ripening is dependent upon metabolic activity to complete embryo development germination cannot be stimulated. An advantage of the delayed germination of *P. aspleniifolius* may be to allow the seed to bury in safe sites such as under the cover of litter or mosses, that may protect the germinant from drought. However, the periodicity of seed production and allied germination may reduce the opportunities for *P. aspleniifolius* to regenerate in the forest due to a lack of seed unless it is stored in the soil for considerable periods. The positive effect of disturbance on germination of seed (Table 6.4) suggests that even though germination cannot be induced in the first year, true dormancy may act as an inhibitor in subsequent years, with soil disturbance breaking the dormancy. Pickett (1980) notes that dormant soil stored seed is beneficial to species dependent upon either large or small scale disturbance to regenerate by allowing them to be present when the regeneration opportunity arises.

The extremely low numbers of *A. biglandulosum* seeds captured in seed traps (Figure 6.6) are the result of poor flower development when growing below a canopy, and extremely high levels of fruit predation (Figure 6.10b, Table 6.5b). The wrinkled seeds that were captured had also suffered predation or premature degeneration, probably indicating embryo or endosperm abortion at some stage of development (Sedley and Griffin 1989). A shortage of viable seed was probably a major cause of the negative results in all of the field and glasshouse germination treatments. Any negative implications of poor seed production for the maintenance of populations of *A. biglandulosum*, or its status in the community succession, are offset by its vegetative means of proliferation and reproduction (Chapter 7) and vegetative recovery after fire (Barker 1990). A shortage of seed must, however, prove a disadvantage for dispersal to and re-occupation of sites after severe fires which kill the root stock. The absence of *A. biglandulosum* from the rainforests of north-east Tasmania may in part reflect poor dispersal characteristics.

Although no effect of exclosure from animal foraging was detected in the present study it has since been noted that animal foraging is often concentrated in tree-fall gaps (pers. obs.) (this study did not consider the effect of foraging in gaps versus understorey) where slow growing seedlings, such as *P. aspleniifolius* and *A. biglandulosum*, could be removed from such an area with significant opportunities for regeneration. This is

particularly true within the range of the introduced Lyrebird which is capable of turning over the forest floor at a rate of one and a half times per annum (Howard 1982).

Differences in the production and survival of seeds are reflected in the numbers of seedlings that germinate each year. For *A. biglandulosum* the compounding effects of low seed survival, lack of seed stored in the soil and the limited dispersal power would reduce the opportunities for regeneration from seed. Thus, while there is no competition between *P. aspleniifolius* and *A. biglandulosum* for pollination or dispersal vectors, *P. aspleniifolius* would be expected to have a competitive advantage at this early life-stage, as greater numbers of seedlings confer a higher probability of survival and so potential domination of a site (Watt 1947).

Variation in the foliar phenology of the *P. aspleniifolius* transplants (Figure 6.3) indicates environmental control in the timing of bud-burst and period of leaf development similar to that of trees *in situ*. The relatively large change in timing from 1989 to 1990, compared to *in situ* trees, suggests that preconditioning by previous environments may be overcome with time, thus indicating phenological plasticity. McGee (1970) showed that bud-break in Red Oak transplants from different altitudes became synchronised after seven years in the new environment. Differences in physiological limits to growth are evident between the two provenances of *P. aspleniifolius* along the altitudinal gradient. Again, these differences may not be genetically fixed, reflecting instead physiological plasticity.

The comparison of the phenology of seedfall, germination and survival in *P. aspleniifolius* and *A. biglandulosum* has illustrated clear and dramatic differences in the early stages of sexual reproduction. One area of similarity is the season of reproductive activity. *P. aspleniifolius* is wind pollinated and *A. biglandulosum* is directly animal-pollinated. Givnish (1980) illustrates a remarkable correlation between breeding system and dispersal syndrome and postulates a pollination/dispersal model to account for the correlation. The model is aimed at maximising reproductive returns in relation to the ecology of pollination and seed dispersal. Although Givnish incorrectly lists *Phyllocladus* as monoecious, the model correctly predicts that this animal-dispersed and wind-pollinated gymnosperm should be dioecious and a mast seed producer. The model correctly predicts that the hermaphrodite angiosperm, *A. biglandulosum*, should be animal-pollinated with wind-dispersed seeds. It suggests that dioecy is favoured in plants that are wind pollinated and animal-dispersed. It is argued that for wind pollinated monoecious plants much of the pollen production falls near the parent and must compete for ovules, whereas when the sexes are separated the efficiency of

fertilisation by pollen on the wind is higher and promotes outcrossing (Maynard Smith 1978) (Figure 6.2). The increased pollination efficiency allows the male reproductive effort to be reduced and an increase in favour of females in the sex ratio (Opler and Bawa 1978), further improving reproductive efficiency. Since animals should prefer (or be attracted) to visit trees with the greatest concentration of fruit, separate female plants may result in higher rates of seed dispersal (and predation) (Givnish 1980). On the other hand hermaphroditism should be favoured among smaller plants where a faithful pollination vector is encouraged to make visits between plants (Givnish 1980). Dioecy is relatively uncommon in angiosperms (Maynard Smith 1978), presumably because the development of the flower has enabled the evolution of direct pollinators (Darwin 1877) increasing the efficiency of pollination within plants. However, in the case of *A. biglandulosum*, where the number of pollinators may be limited, large numbers of flowers counters cross-pollination by overwhelming the pollinator and, hence discouraging visits between plants.

The latitudinal distribution of *P. aspleniifolius* in Tasmania, and the Podocarpaceae generally in the southern hemisphere, does not concur with the logic of the model, as it predicts that animal dispersed gymnosperms should be largely restricted to low latitudes where frugivorous birds and animals are common. Conversely, at higher latitudes windy and cold seasonal climates favour wind-dispersal and wind-pollination. Wind-dispersal is the most common form of dispersal for Tasmanian rainforest dominants including *A. biglandulosum*. However, in New Zealand and Tasmania, the animal-dispersed Podocarpaceae contribute the greatest number of species to the gymnosperm floras. This apparent anomaly may reflect their enhanced chance of survival by efficient migration to refugia and reoccupation of sites, in rapidly changing glacial environments. In New Zealand, McGlone (1985) suggests that deforestation during the onset of the last stadial may have occurred over a period as short as 500 years. The reafforestation of these areas was dominated by the bird-dispersed podocarps although a slow invasion of these forests by the wind-dispersed angiosperm flora is evident. This situation stresses the importance of stochastic and historic influences on the coexistence of alternative breeding systems.

It has been demonstrated that *P. aspleniifolius* and *A. biglandulosum* coexist in a large number of communities and physical environments (Chapters 2 and 3). This chapter illustrates clear differences in the success of seed production and seed and seedling survival. The opportunities for regeneration presented (or limited) by similarities and/or differences in the regenerative capabilities of *P. aspleniifolius* and *A. biglandulosum* are likely to be important determinants of the spatial and temporal coexistence of these

species. The ability of *A. biglandulosum* to maintain populations in a variety of communities from a position of poor competitive ability as a seed regenerator should be reflected in its demographic and spatial status. Furthermore, this should contrast with the relatively efficient seed production, dispersal and soil storage of *P. aspleniifolius*. The resultant population structure and dynamics of these species will be considered separately in the following two chapters.

Chapter 7. *Anodopetalum biglandulosum* : Growth-form and abundance in relation to forest floristics and structure.

7.1 Introduction

The phenological study at Mt. Field indicated that seed of *Anodopetalum biglandulosum* suffers high predation, which is reflected in the low rate of seedling establishment in the forest. The consequent importance of vegetative regeneration to this species may be associated with regeneration opportunities which are spatially or temporally different from those experienced by a well dispersed seed regenerator such as *Phyllocladus aspleniifolius*. The spatial or temporal separation of opportunities for regeneration is essential for coexistence (Hutchinson 1958, Pickett and White 1985) and represents niche stratification. The avoidance of competition at this critical early stage of life is important if competitive exclusion is to be averted.

As illustrated in chapters 3 and 4 (phytosociology and edaphic correlates), *Anodopetalum biglandulosum* is a common component of the shrubby understorey in rainforests on better quality sites, but is also found in the sparse dominant canopy of structurally more complex rainforests (implicate) on less fertile sites. In many locations *A. biglandulosum* forms a dense tangle of stems locally referred to as "horizontal scrub".

The tangle is derived from fallen, once vertical individuals which subsequently proliferate by iterations of collapse and formation of vertical stems. *A. biglandulosum* also has the ability to spread vegetatively by layering and sprouting from the root-system. The ability to draw on stored nutrients and an established root-system allows the proliferation and regeneration at an initially faster rate than regeneration from seed. Similarly, rapid early growth imparts the potential to dominate regrowth rainforest after disturbance. Of particular interest is the effect of proliferation of *A. biglandulosum* on the regeneration of canopy species, particularly *P. aspleniifolius*, in the gap-phase in some *Nothofagus cunninghamii* dominated forests.

The population age or size-class distributions *sensu* the theoretical population growth models of Whittaker (1975) and Harper (1977) may not be useful in describing the stand dynamics of a species that spreads by proliferation, layering and resprouting. In Tasmania, Cullen (1987), Read and Hill (1988) and Gibson and Brown (1991b) have examined size-class distributions to reveal much useful information relevant to rainforest dynamics. However, if much of the variation is due to a process of proliferation and layering, a different approach is required.

Size-class distributions have been interpreted as indicative of different regeneration modes, such as continuous replacement or cohort regeneration (Horn 1974). Both the size-class distribution and the spatial distribution of the sizes indicate specific requirements for regeneration including: the need for gaps (Veblen 1989, Veblen and Stewart 1982, Read and Hill 1988, Gibson and Brown 1991b); soil disturbance (Cullen 1987); or fire (Ashton 1978, Hett and Loucks 1976, Read and Hill 1988). If a species reproduces vegetatively, and/or increases in abundance by proliferation, then the spatial distribution and variation in characteristics of the regeneration and proliferation may reveal similar information to the size-class distributions of other species.

The growth-form of a plant at any point along an environmental continuum will be one phenotypic expression from a potential range of taxon-specific growth forms (Kuppers 1989). For some species, such as *P. aspleniifolius*, the construction of the canopy does not vary, it is tightly deterministic, but for others, such as *A. biglandulosum*, stochastic events result in probabilistic responses (Tomlinson 1982). Furthermore, the light environment influences canopy shape which allows a plant to maximize light interception (Horn 1971, Givnish 1988). Thus, canopy shape should be related to changes in the community's light regime as succession proceeds, or to differences in the light regime between communities. Changes in the light regime may also involve disturbance. Clearly, an ability to recover from disturbance vegetatively, and hence form an appropriate canopy may provide a competitive advantage. The advantage would be gained by an increase in a plant's relative rate of growth, its consequent ability to cover ground area, and to reduce the light below its canopy; this has implications for the regeneration and success of other species, and, hence, coexistence.

This chapter aims to quantify and describe the variation in the growth form and regeneration modes of *A. biglandulosum*, and relate that variation to the structure, floristics and disturbance regimes of rainforest communities. Spatial and temporal patterns of regeneration, the small-scale processes, and specific attributes of *A. biglandulosum* responsible for those patterns will be compared with those of *P. aspleniifolius*.

7.2 Methods

7.2.1 Community data

The data were recorded from 48 quadrats of 100 m² area from various forest types throughout the range of *A. biglandulosum*. The quadrats were located subjectively to sample the range of *A. biglandulosum* habitats and within sites to represent apparent variation. A complete list of vascular plant species was recorded, species outside the quadrat, but nearby, were recorded in the species list to offset the influence of *A. biglandulosum* domination in ordinating the communities by floristics. All species were recorded with modified Braun-Blanquet cover classes: 0= nearby, 1= rare, 2= <1%, 3= 1-5%, 4= 5-25%, 5= 25-50%, 6= 50-75%, and 7= >75%. Structural attributes of the forest were also noted (Appendix 5).

7.2.2 *Anodopetalum* growth-form data

Each stand was classified as one of four forms which were typical expressions of the apparent variation; these were a multi-stemmed "coppice", a single stemmed and suckering shrub form, a tangled scrub form and a monopodial tree form.

The stems of *A. biglandulosum* were categorized into three types all of which could be vertical or non-vertical (Figures 7.1 & 7.2). They were primary stems (1⁰), that is, those that emerge from the ground; secondary stems (2⁰, reshoots) are stems which arise from primary stems in response to the primary stems not being in the vertical position, that is, they are sprouts. Tertiary (3⁰) stems may develop similarly from large secondary stems if they leave the vertical position. Consequently two stem positions were noted, vertical and non-vertical. Non-vertical stems were distinguished as those stems that were curved away from the vertical position more than 45° or else supported 2⁰ stems (Figure 7.1).

The diameters of the three largest stems in each category were measured and averaged. Stem density classes were estimated for each stem category: 1-4, 5-8, 9-15, 16-30, 31-60, 60-100, 100-200, and >200 stems per quadrat. The percent projected foliage cover was estimated in Braun-Blanquet cover classes at three levels in the canopy; greater than 10m, 2-10m and less than 2m (Appendix 5). Total percent cover of *A. biglandulosum* was also estimated in Braun-Blanquet cover classes. These data were intended to produce a three dimensional impression of each stand using the size, type and density of the *A. biglandulosum* stems and the distribution of the foliage.

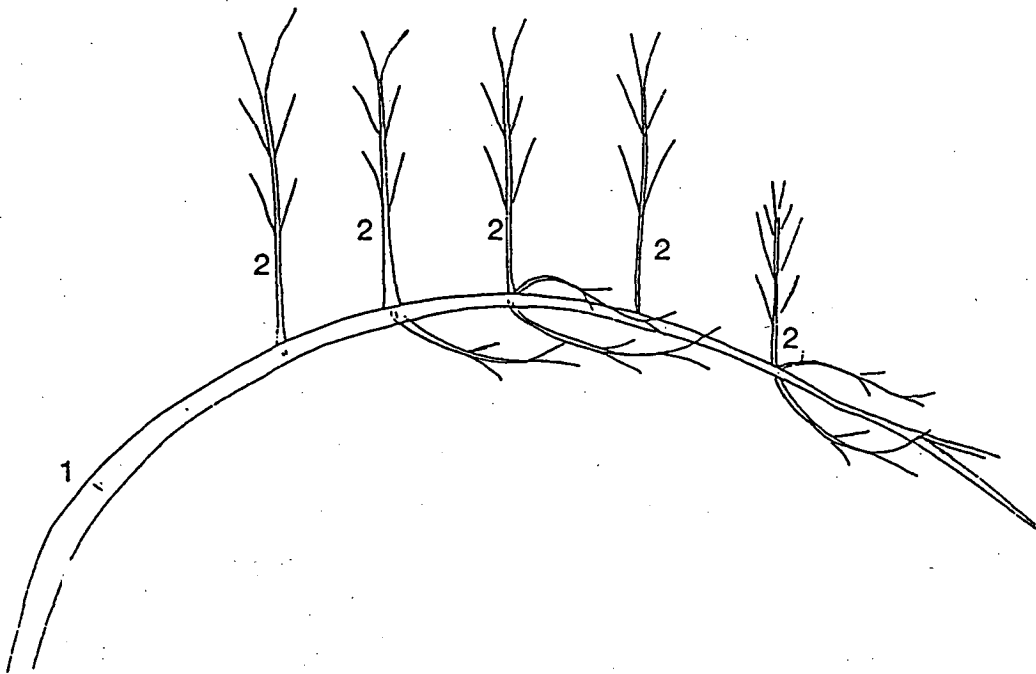


Figure 7.1. An illustration of the nature of secondary stems. They are shown here shooting from the branch nodes of a non vertical primary stem.

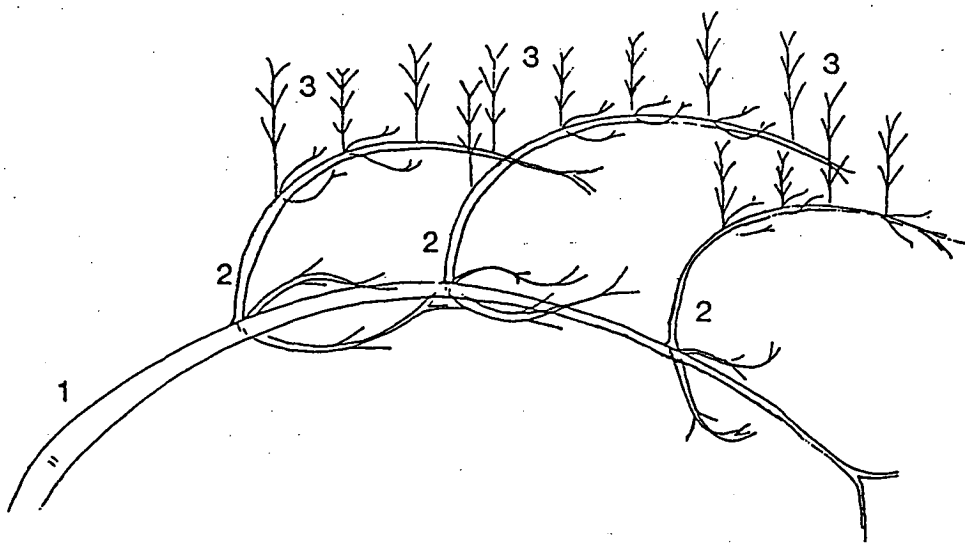


Figure 7.2. An illustration of the development of tertiary stems. These stems develop in a manner similar to secondary stems but arise from secondary rather than from primary stems.

7.2.3 Regeneration characteristics

In each quadrat the presence or absence of various regeneration modes was recorded. Modes of regeneration were assessed as seedlings, reshoots (2^o or 3^o), layering and/or suckering; it was also noted if the plants were ramifying or rooted in the plot. Suckering and reshoots are distinguished by position. Suckers arise from the base of a primary stem whereas reshoots arise from the upper surface of a non-vertical stem. Ramification simply indicates whether stems from outside the plot contribute to the cover of the plot.

7.2.4 Disturbance

Indications of disturbance were noted as present or absent and included pinning, root-failure, bank-failure, and the presence of a gap in the canopy (Appendix 5). The bending of stems is a characteristic growth habit of *A. biglandulosum* and makes the stem susceptible to "pinning", that is, being pushed to the ground by falling trees or branches. Root-failure was ascribed to individuals whose roots had been disrupted under the destabilising influence of bending primary stems and the weight of subsequent 2^o and 3^o stems. Bank-failure was recorded in riparian situations where the stream bank rather than the roots gave way under the same pressures as described above. Canopy gaps were recorded as being produced by tree-fall or by standing dead trees.

7.2.5 The gap-phase response

An area of forest in which *A. biglandulosum* was an important component was sampled to determine the probability of the domination of forest canopy gaps by *A. biglandulosum*. The density of *A. biglandulosum* across the area varied from absent to extremely dense patches. A set of 6 parallel and adjoining belt-transects consisting of 50x50 m quadrats and ranging from 300 m to 500 m long were sampled. Each quadrat was divided into four 25x25 m quadrats and each of those was characterised by its condition. The characteristic conditions were:

1. recent gap is dominated by *A. biglandulosum* regrowth;
2. recent gap is not dominated by *A. biglandulosum* regrowth (clear);
3. patch of dense "oldgrowth" *A. biglandulosum* cover >70%;
4. *A. biglandulosum* present with cover 10%-70%;
5. *A. biglandulosum* present with cover <10% or absent.

The five conditions were tested for their degree of association in 50 X 50 m quadrats using two-way contingency tables. The tables were analysed using Fisher's Exact Probability Test.

Each 25 X 25 m quadrat was further characterised as containing a treefall gap or a gap with a standing dead tree in it. In all cases the standing dead trees were *Nothofagus cunninghamii* killed by the pathogen *Chalara* sp. (Kile and Walker 1987).

7.2.6 Data analysis

All of the data were entered into a computer file for use in the ecological data analysis package DECODA (Minchin 1990).

The floristic data were classified using the polythetic divisive classification program TWINSpan (Hill 1979). This allowed a comparison to be made between the classificatory groups. The comparisons made were; the heights of the dominant canopies, and the differences in height between the dominant and subdominant canopies using a Kruskal-Wallis oneway analysis of variance.

Multi-dimensional scaling (MDS) was used to calculate ordination axes for the floristic data set. This procedure produces axes which are continuous numeric indices of the similarity of sites based on the species present and their percent cover. The growth-form attributes of *A. biglandulosum*, that is, the stem diameters and densities in each stem category were compared, as a multivariate data set, to the first two MDS axes using canonical correlation analysis (CCA) (Gittens 1985). Those categories which produced the highest contribution in the CCA, thus maximizing the correlation, were selected and the CCA was rerun. This analysis, in conjunction with the tabulated field observations, including mode of regeneration and indications of disturbance, allowed a typology of *A. biglandulosum* growth-form to be developed.



The growth-form attributes used in the final CCA were used in a discriminant function analysis to determine whether these characteristics effectively distinguish the observed structural variation in *A. biglandulosum*.

7.2.7 Stem size-class distribution

After the typology had been produced the size-class distributions of two examples of each type were determined. All primary stems were counted and measured in a 10x10 m quadrat or until at least 50 stems were counted. In the latter case, the area covered was also measured.

7.3 Results

7.3.1 Floristic correlation

The CCA illustrates a separation of the sites along the y axis according to the growth form data set. The four forms described in the methods are indicated on the plot (Figure 7.3). The groups are separated along the x axis according to MDS scores. The result of this correlation technique indicates a highly significant relationship between community floristics and the stand growth-form of *A. biglandulosum*, $P < 0.01$. (Table 7.1). The CCA did not include forest structure nor indications of disturbance, and the four types evident in the field can be divided further based on the response of *A. biglandulosum* to these characteristics.

7.3.2 Subdivision of growth-form Data

The floristic axis of the CCA plot indicates a continuum in floristic variation from thamnic to implicate forests. This continuum was classified by the TWINSpan program into groups which contrasted in forest structure (Table 7.2) (Appendix 5). The height of the dominant canopy varied significantly ($P < 0.01$) between the implicate forest (group 2) and the remaining types, including the sclerophyll-dominated forests. The comparison of forest structure between the growth-form groups indicates a weaker relationship ($P < 0.09$). The weaker relationship is due to there being variation in growth-form types (i.e. response and low response) in forests with the same structure. The Implicate low response type has a significantly lower canopy than all others while the implicate coppice tends to occur in the sclerophyll dominated implicate forests and this is reflected in the greater height of the *Eucalyptus* species present at those sites. The "emergent" eucalypts amongst the Implicate Coppice are similar in height to the dominants amongst most other types.

Where a sub-canopy is present its height does not vary significantly ($P > 0.1$) between the TWINSpan groups. The greater difference in the heights of the dominant and subcanopies in the thamnic TWINSpan groups compared to the implicate groups is a reflection of much taller dominant species in the former groups. These trees produce a major impact on the subcanopy when they fall.

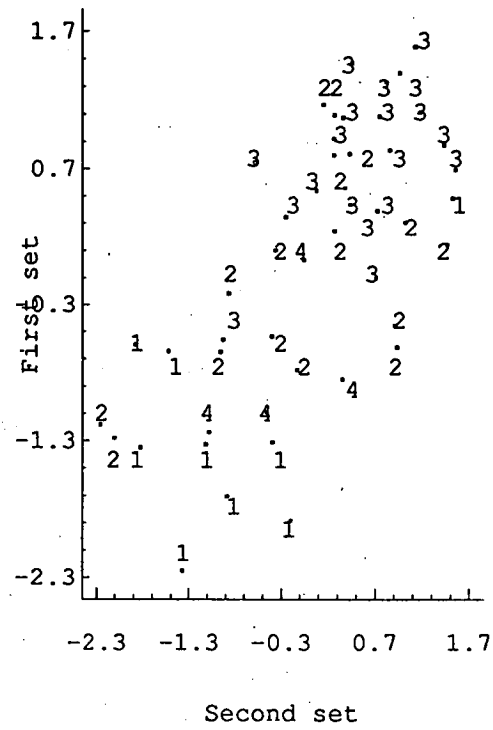


Figure 7.3. Canonical correlation analysis of the multivariate floristic data set versus the multivariate growth-form data set. Canonical correlation = 0.678, $p < 0.01$. The four forms described in the text are indicated, 1. coppice, 2. shrub, 3. scrub, 4. monopodial tree.

Table 7.1. A summary of the canonical correlation between selected growth-form attributes and the first two MDS axes.

Number	Eigenvalue	Canonical Correlation	Chi-Square	D.F.	Sign. Level
1	0.4705	0.6860	31.164	12	0.002
2	0.0928	0.3046	4.139	5	0.529

Coefficients for Canonical Variables of the First Set

Diameter Vertical 1°	0.06616	0.26814
Diameter Nonvertical 1°	0.78405	-0.70664
Diameter Vertical 2°	-0.36602	-0.06786
Density Vertical 1°	-0.75730	-0.49046
Density Vertical 2°	-0.12157	0.06965
Density Vertical 3°	-0.25908	0.77884

Coefficients for Canonical Variables of the Second Set

MDS axis 1	0.99984	0.03521
MDS axis 2	0.00487	-1.00045

Table 7.2. Kruskal-Wallis analyses of the relationship between the TWINSPAN groups (a) The height of the dominant canopy. (b) The difference in the height between the dominant and subdominant canopies. (c) The relationship between the growth-form typology and the height of the dominant canopy.

a.

TWINSpan Group	Count	Average	Average Rank	Homogeneous Groups
2	10	15.10	10.55	A
3	11	20.81	22.18	AB
5	6	24.50	28.50	B
6	5	25.60	32.30	B
4	10	26.60	32.05	B
1	6	27.66	28.91	B

Test statistic = 15.85 Significance level = 0.007

b.

TWINSpan Group	Count	Average	Average Rank	Homogeneous Groups
2	5	7.20	8.00	A
3	4	9.00	10.5	A
4	8	12.25	12.93	AB
5	2	14.00	18.5	AB
6	4	15.25	16.75	AB
1	4	21.25	22.12	B

Test statistic = 9.14 Significance level = 0.10

c.

TWINSPAN	Count	Average	Average	Homogeneous
Group			Rank	Groups

2	5	13.60	8.3	A
6	5	20.00	20.6	AB
3	11	22.18	24.0	B
1	9	23.00	25.6	B
5	4	23.00	26.5	BC
4	10	24.60	28.7	BC
7	4	32.50	35.62	C

Test statistic = 10.71 Significance level = 0.09

Table 7.3. Percentage frequencies of indications of disturbance and of modes of regeneration among four forms which distinguish seven types from 48 sites based on floristic, structural and growth-form characteristics: Disturbance- root-failure (ROOT), pinning (PINN), stem-bending (BEND), bank-failure (BANK), tree-fall gap (GAP); Regeneration- stem suckers (SUCK), seedlings present (SEED), ramification (RAM), layering (LAY), primary stems rooted in the quadrat (ROOT). See text for explanations of each. Form: 1. Coppice, 2. Single-stem shrub, 3. Tangle, 4. Monopodial tree. Types: 1. Implicate Coppice, 2. Implicate Low Response, 3. Thamnic Low Response, 4. Thamnic Response Scrub, 5. Gully Scrub, 6. Thamnic Scrub, 7. Monopodial. (see Table 7.4).

FORM	TYPE	DISTURBANCE					REGENERATION				
		ROOT	PINN	BEND	BANK	GAP	SUCK	SEED	RAM	LAY	ROOT
1	1	0	45	54	0	0	89	22	0	11	100
2	2	50	75	100	0	0	80	20	60	20	100
2	3	70	60	80	10	20	63	27	18	27	100
3	4	56	90	44	0	78	80	10	50	10	80
3	5	100	50	75	50	0	50	25	75	25	100
3	6	20	40	80	0	50	80	20	60	40	100
4	7	60	20	20	0	0	50	75	0	0	100

Table 7.4. Seven types of *Anodopetalum biglandulosum* recognised by growth form and distinguishable by forest type, habitat and/or disturbance regime.

Type	Class	Growth-form	Forest type, habitat/disturbance
Implicate Coppice	1	Coppice	Implicate, fire disturbed
Implicate Low Response	2	Single-stem shrub	Implicate, undisturbed
Thamnic Low Response	3	Single-stem shrub	Thamnic, undisturbed
Thamnic Response	4	Tangle	Thamnic, tree-fall gap in closed forest
Gully Scrub	5	Tangle	Callidendrous creeklines, bank-failure.
Thamnic Scrub	6	Tangle	Thamnic open forest, root-failure, catastrophic.
Monopodial	7	Monopodial	Thamnic/sclerophyll, open forest, catastrophic.

7.3.3 Typology

In the most diverse and structurally complex implicate communities the coppice form is common (Table 7.4, Figures 7.4 and 7.5). It is probable that the coppice is fire induced, although unburnt *A. biglandulosum* has been observed to sucker from the base to produce a cluster of vertical stems in these forests. This form is typed as Implicate Coppice with the coppices typically organised as discrete clumps throughout the community. The coppice form has also been found at one callidendrous site (Figure 7.3) which probably indicates that the multistemmed habit is indeed fire-induced resprouting and not a sclerophyllous growth response similar to the mallee eucalypt habit.

While stem-bending and pinning are prevalent in the implicate forests (Table 7.3) the low, sparse canopy dominants (Table 7.2) produce little disturbance when they fall. Consequently, there is little disruption of the *A. biglandulosum* canopy. Hence, secondary proliferation is limited. Root-failure is also much less common in this type of forest as the individual primary stems do not attain a height and weight sufficient to exert a destabilising force. This form is typed as Implicate Low Response in order to indicate the absence of both disturbance and proliferation.

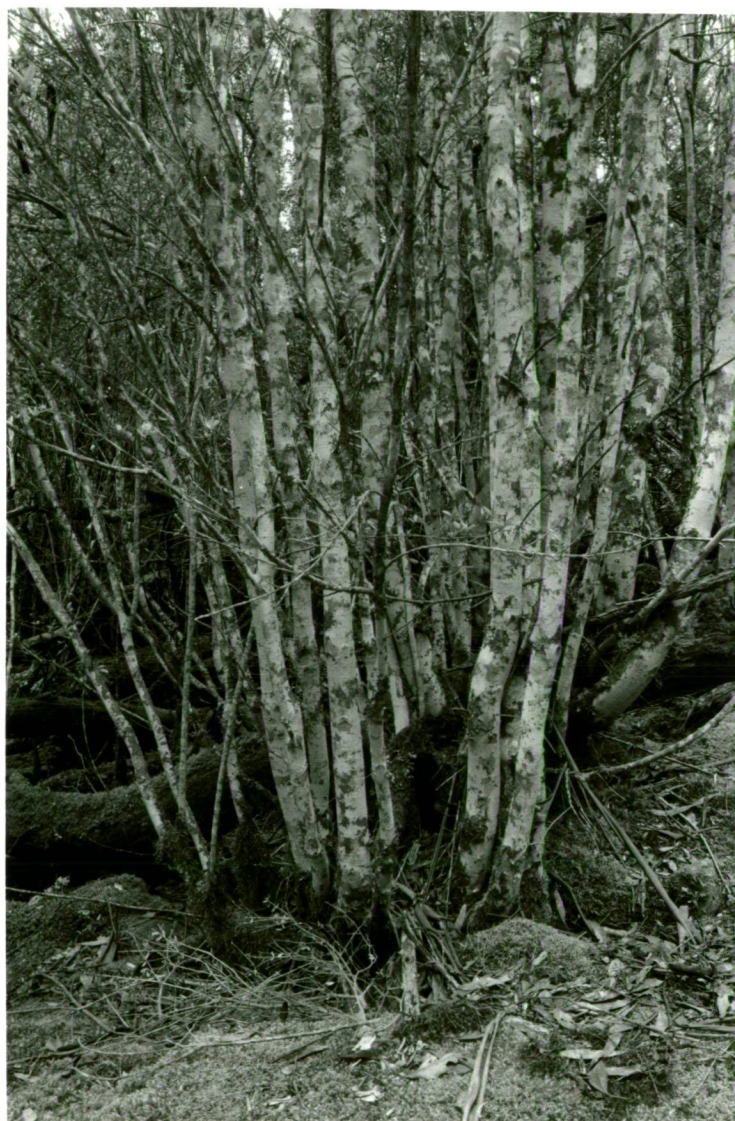


Figure 7.4. The coppice growth form of *A. biglandulosum* in an impenetrable forest.



Figure 7.5. Prolific secondary stem growth of *A. biglandulosum* in response to a tree-fall gap in thamnic forest.

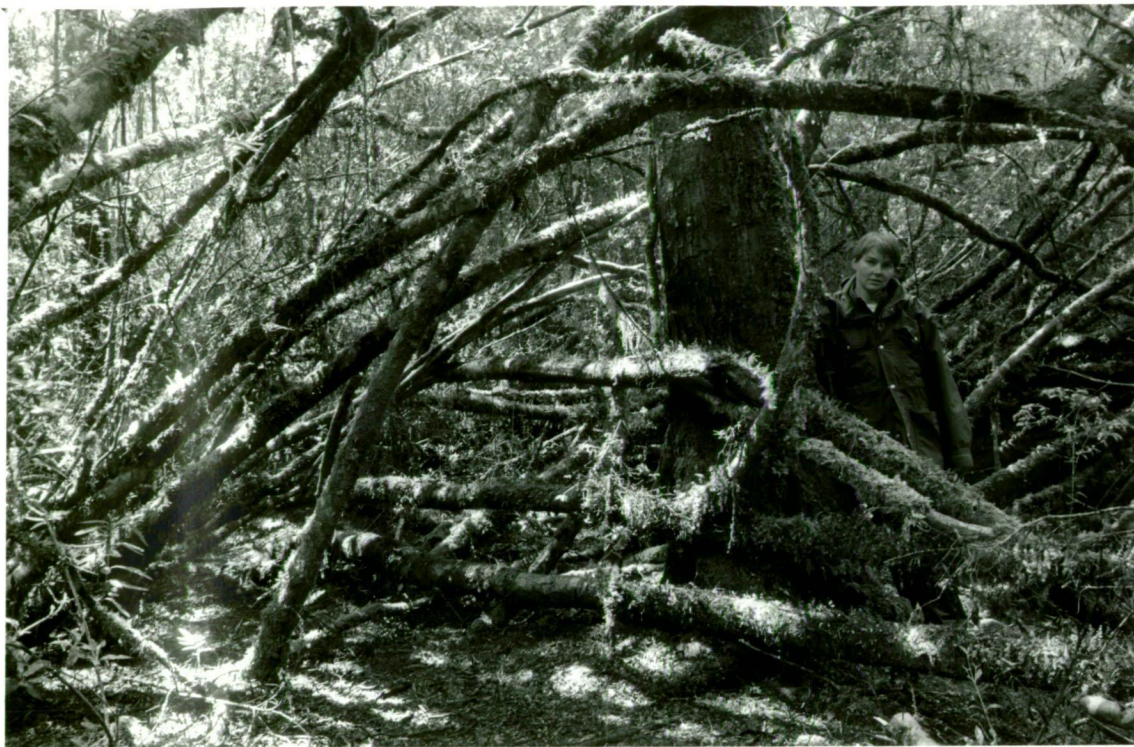


Figure 7.6. The characteristic form of primary stems of *A. biglandulosum* below an undisturbed open canopy dominated by *P. aspleniifolius* in thamnic forest.

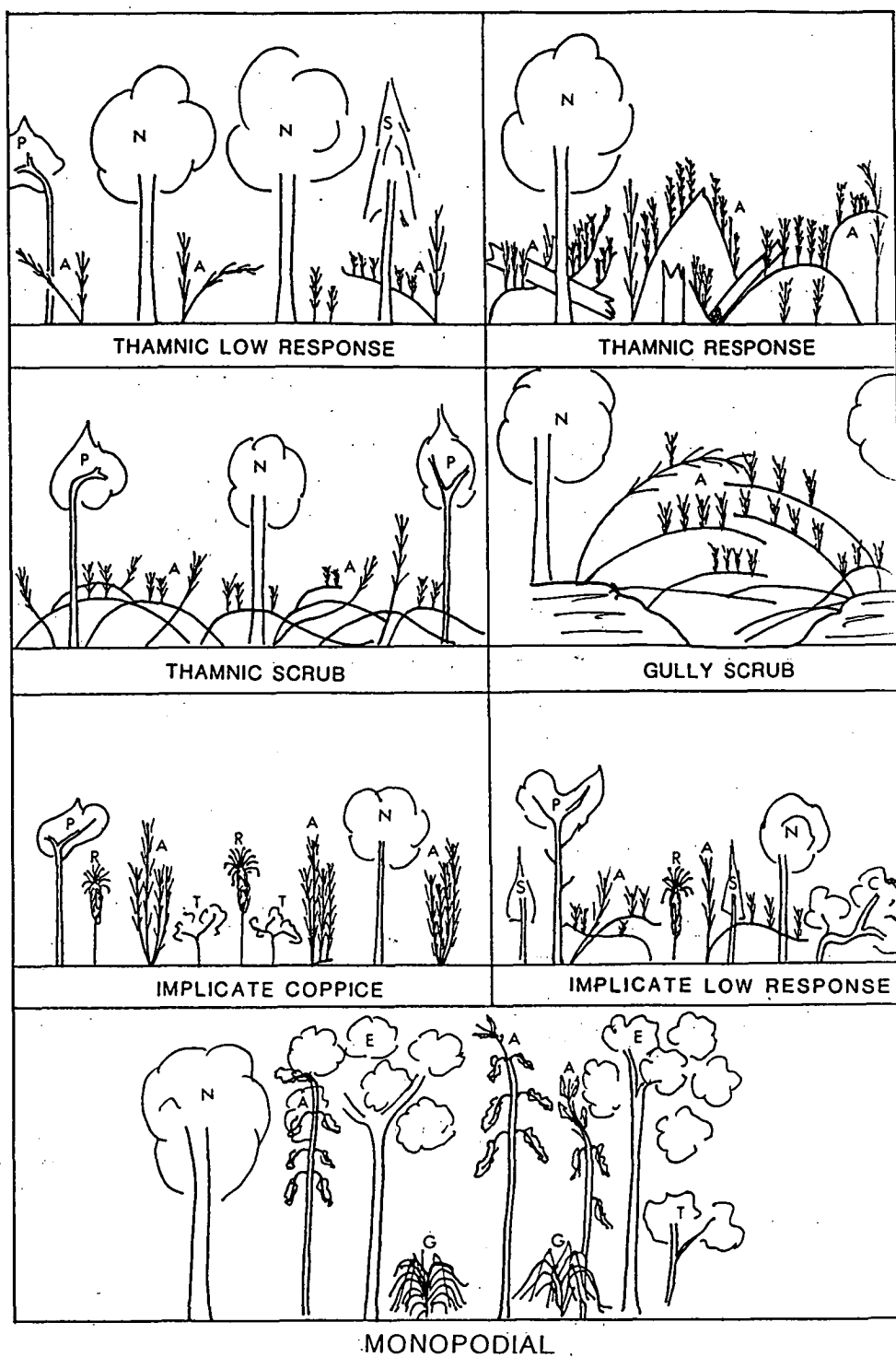


Figure. 7.7. Simplified representations of the seven forest structures and associated forms of *Anodopetalum*. Types are derived from community floristics and structure and architectural variation of *Anodopetalum*. Symbols: A. *A. biglandulosum*, P. *Pyllocladus aspleniifolius*, N. *Nothofagus cunninghamii*, E. *Eucryphia lucida*, G. *Gahnia grandis*, R. *Richea pandanifolia*, T. *Trochocarpa gunnii*, C. *Cenarrhenes nitida*, S. *Atherosperma moschatum*.

A similar form exists in the thamnic forests where tree-fall and canopy senescence are absent (Table 7.4). *A. biglandulosum* occurs as a relatively innocuous understorey component associated with a high percentage cover of canopy dominants. Structurally it can be distinguished from the Implicate Low Response type where *A. biglandulosum* is part of the dominant canopy. This form is typed as Thamnic Low Response.

In the taller thamnic forests with a closed dominant canopy, tree-fall and canopy senescence of the dominants is a major disturbance agent which produces canopy gaps (Table 7.3). The falling trees and branches often pin the bending branches of *A. biglandulosum* which rapidly respond to the disruption and release from limited light by way of prolific secondary growth (Figure 7.6). This mechanism results in variable and patchy development of *A. biglandulosum* into a tangled multi-stemmed scrub (Figure 7.4) and is typed as Thamnic Response Scrub to indicate that the form is promoted by disruption.

A. biglandulosum produces a similar structure to the Thamnic Response Scrub along creeklines, within callidendrous x thamnic forests, where the canopy is often broken due to the absence of dominants growing over the creeks. *A. biglandulosum* is not rooted in the creek-bed and may be absent from surrounding forest. The stems bend out over the creekline which often results in a disruption in the balance of the superstructure and the failure of the roots and the stream bank to support it. The superstructure consequently collapses. There is a secondary growth response leading to areas developing as response scrub. This form is typed as Gully Scrub (Figure 7.4).

Occurring in some thamnic forests is a tangle of *A. biglandulosum* under an open but undisturbed dominant canopy. The relatively high light penetration in this community appears to have allowed *A. biglandulosum* to develop vigorously with some primary stems reaching the canopy and others apparently bending under their own weight and producing a looping tangle (Figures 7.4 and 7.7). In the absence of tree-fall, pinning is less frequent (Table 7.3) and there is less secondary growth response compared with sites having canopy disturbance. This is probably because the light regime remains essentially the same. This has been typed as *Anodopetalum* Thamnic Scrub.

The last growth form is vertical Monopodial *Anodopetalum*. This tends to be found in simply structured forests of various floristic composition; often with a sclerophyll component (Figure 7.4). This type may reflect an intermediate site quality between that of the *Anodopetalum* Thamnic Scrub and the other thamnic types in which *A. biglandulosum* is able to compete successfully for a canopy position. Proliferation and

layering are absent and seedlings are present (Table 7.3). The presence of root-failure among these stands reflects a typical tree-fall mechanism, such as wind-throw, rather than structural destabilisation.

In the discriminant analysis on the original structural data, (Figure 7.8) the sites are identified on the plot by labels which correspond to the typology. The sites cluster into the types described above, albeit with some overlap. The clusters separate in the unplotted third dimension, which is attributed to the disturbance regime and the mode of regeneration (Table 7.3).

7.3.4 Stem size distribution

The stem size-class distributions represent all stems emerging from the ground. Stems less than 1 cm diameter were determined to be either ramets or genets by uprooting the genets, except when cotyledons were present. There was no way of distinguishing ramets from genets in the larger size-classes without excavation. The stem size-classes are represented by two groups: those with the highest frequency of stems being less than 1 cm; and those in which the highest frequency of stems is in a larger size-class (Figure 7.9).

The stem-size distributions in the Thamnic Response, Gully and Thamnic Scrub types are in the first category. These distributions are typical of continuous regeneration. The decrease in stem numbers with size indicates that the smaller stems do suffer density dependent mortality. The smaller stems usually arose in clumps near the bases of the largest stems, or in lines along the length of a layered branch which had become buried.

In the second category of distributions are the Coppice and Low Response types (Figure 7.9e-j). The smallest size-classes are still well represented but the highest frequency of stems is among the middle of the distributions producing bell-shaped or skewed bell-shaped distributions. These distributions may indicate a regeneration event which has produced even or relatively even-aged stands. Some vegetative regeneration by layering and stem suckering is occurring and this may be sufficient to maintain the populations. The distribution k (Figure 7.9) may indicate a steady state where no disturbance is involved. The lack of a major stimulus result in fewer opportunities for seedling regeneration, and consequently, low density dependent mortality. All size-classes are well represented although seedlings are absent. The largest size-classes were clumped, suggesting a similar vegetative origin to the clumps of stems <1cm in diameter. It is also

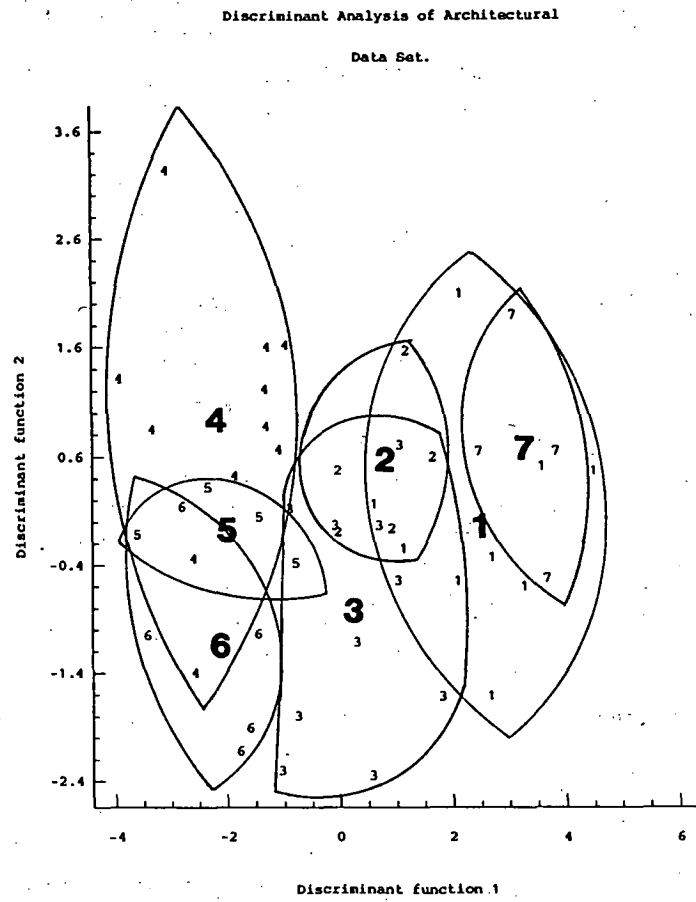


Figure 7.8. Discriminant function analysis of variation in the architectural data set. 1 = Implicate Coppice, 2 = Implicate Low Response, 3 = Thamnic Low Response, 4 = Thamnic Response, 5 = Gully Scrub, 6 = Anodopetalum Thamnic Scrub, 7 = Monopodial. The bold numbers represent group centres

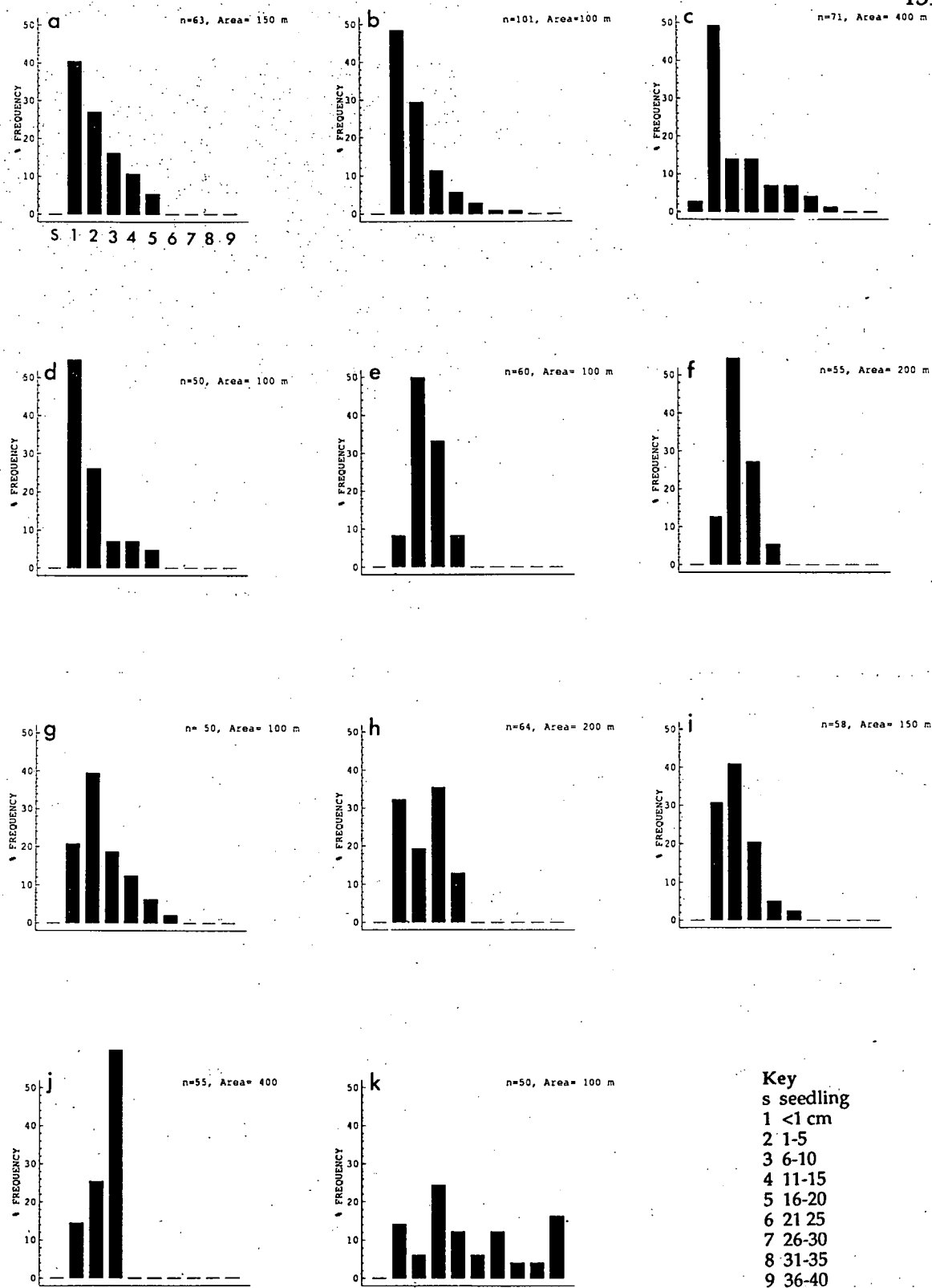


Figure 7.9. Examples of size class distributions from a. Thamnic Response, b. and c. Gully Scrub, d. Thamnic Scrub, e. and f. Coppice, g. and h. Implicate Low Response, i., j. and k Thamnic Low Response.

possible that these large clumps represent regeneration after fire, similar to the Implicate Coppice.

Continuous regeneration can be found in callidendrous/thamnic to implicate/thamnic forest and in gullies. The non-continuous type is also found in callidendrous/thamnic, and in the two implicate types. The similarity in size-class structure between different types of rainforest offers little information that distinguishes the dynamic processes involving disturbance and regeneration. In all types seedlings do not appear to play a role in the maintenance of the population, although they may be important for re-establishment in non-coppice forms after catastrophic disturbances such as fire.

7.3.5 The impact of the gap phase response

Based on the number of tree falls in the entire study area the probability of a tree-fall gap occurring in any quadrant within a 50x50 m quadrat that contains >10% *A. biglandulosum* is 0.62. The probability of gaps that were dominated by *A. biglandulosum* and those that were clear occurring in the same quadrat is lower than might be expected due to chance, i.e. they are negatively correlated. There was a high positive correlation between the status of *A. biglandulosum* regeneration and the nature of the gap. Of the 25 gaps which had no *A. biglandulosum* proliferation 21 were myrtle wilt gaps in quadrats with >10% cover of *A. biglandulosum* and the remaining four were treefall gaps in quadrats with <10% cover of *A. biglandulosum*. Gaps generated by tree-fall in an area in which *A. biglandulosum* is present at cover >10% are dominated by *A. biglandulosum* proliferation.

Myrtle wilt gaps are also spatially associated with the distribution of *A. biglandulosum* throughout the landscape. However, *A. biglandulosum* does not proliferate in gaps generated by myrtle wilt. The lack of disturbance produced in a gap with a standing dead tree (e.g. myrtle wilt) does not promote *A. biglandulosum* proliferation.

In gaps where *A. biglandulosum* proliferates, other canopy dominants are either absent or sparse and tended to be represented by *Atherosperma moschatum* and *Eucryphia lucida*. *Nothofagus cunninghamii* was abundant in clear gaps and *P. aspleniifolius* was also commonly found there.

The positive spatial correlation between all gaps dominated by *A. biglandulosum* and areas with significant cover of *A. biglandulosum* (Table 7.5) reflects the strategy of

vegetative proliferation. Furthermore, this association suggests that invasion of the gaps by seed is ineffective, at least with regard to domination of regrowth in isolated gaps.

Table 7.5. Fisher's Exact Probability of two events occurring in the same 50x50 m quadrat. n=54 quadrats. Negative spatial correlations are indicated (-), positive spatial correlation indicated (+).

	Clear gap	Dense <i>Anodo.</i>	<i>Anodo.</i> >10%	<i>Anodo.</i> <10%
<i>Anodo.</i> gap	-0.003	+0.046	+0.016	-0.000
Clear gap		0.138	+0.027	+0.000
Dense <i>Anodo.</i>			0.490	-0.037
<i>Anodo.</i> >10%				-0.002

The distribution of patches of dense *A. biglandulosum* is marginally significant in its association with tree-fall gaps dominated by *A. biglandulosum*. The patches are distributed randomly with regard to areas with >10% *A. biglandulosum* cover and negatively with regard to areas of cover <10%. These patches of dense *A. biglandulosum* have only a sparse canopy of dominant species above them and often contain the remnants of large fallen trees beneath them. This suggests that these dense patches may indicate old tree-fall gaps which have become dominated by *A. biglandulosum*. The association with treefall gaps may indicate a causal relationship with one gap leading to another by opening the canopy to wind. The randomness and size of the patches in the landscape also favours the hypothesis that they indicate old gaps. It may otherwise be expected that they would be related to particular parts of the landscape or be more extensive.

The analysis of the size of dense patches of *A. biglandulosum* (Table 7.6) indicates that they are significantly larger than either myrtle wilt gaps or tree-fall gaps. If the patches have originated from tree-fall gaps, their large size may indicate that only the largest tree-fall gaps become dominated by *A. biglandulosum*. Alternatively, a significant edge effect may be operating and causing *A. biglandulosum* to respond to increased light at the margins of tree-fall gaps.

Table 7.6. Analysis of variance and table of means with Multiple Range analysis for gap type by gap size (m). X in separate columns indicates a statistically significant differences.

Analysis of variance

Source of variation	SS	d.f.	Mean square	F-ratio	Sig.
Between groups	1.18	2	0.591	4.502	.014
Within groups	9.328	71	0.13		
Total (corrected)			10.51	73	

Type	Count	Average	Std. Error	Sig.
Wilt	21	13.52	1.24	A
Tree-fall	30	12.93	0.74	A
Dense Patch	23	17.00	1.09	B
Total	74	14.36	0.57	

7.4 Discussion

The continuous and complex variation in the structure of the rainforest is associated with floristic variation (Figure 7.3, Table 7.1). Both structure and floristics are related to the physical environment (Brown *et al.* 1991) (Chapter 3). In the present study, apparent differences in processes between implicate and thamnic forests have resulted in different responses which produced a number of forms of *A. biglandulosum*. To what extent the forms reflect selection, and are genetically controlled, is not known. However, the forms can be subdivided and contrasted on the basis of site, the type and degree of disturbance, and the nature of regeneration or proliferation.

It is the thamnic forests which support the largest trees with closed canopies over a definite shrub layer (Jarman *et al.* 1991). Consequently, tree-fall in these forests causes great disruption to the dominant canopy and the understorey vegetation. In the implicate forests, which support trees of smaller stature over a poorly defined stratum of shrubs, tree-fall is less effective in producing gaps, and understorey disturbance. Thus, it appears that the structure of the forest influences the disturbance regime and its consequent regeneration patterns.

Root-failure is another important small scale process which is a result of the canopy development producing imbalance, but it also stimulates further proliferation. Clearly, the response to disturbances, such as tree-fall and root-failure, is an opportunistic one, but the "natural" bending of stems which also results in proliferation is a genetically determined growth habit (Tomlinson 1982).

For a "sun" plant to maintain a canopy position it must grow as tall as its co-dominants in the forest canopy. In some cases a species may be excluded due to genetic limits to its vertical growth. The expression of a relatively fixed plant height is genetically determined. Givnish (1981) suggests that in temperate forest understories the height that co-existing plants attain tends to include them in the same strata. Similar behaviour can be recognized in each strata. *A. biglandulosum* does not generally grow as tall as the forest dominants, but where it does it is monopodial with large diameter trunks, and hence, good structural support (Figure 7.4). On substrates which limit the growth of *A. biglandulosum* to the sub-canopy tall slender stems are unable to support their own weight and results in their flexing. This notion was first suggested by Greenhill (1881), who described the determination of the greatest heights to which a tree of given proportions can grow. In agreement, Niklas and O'Rourke (1982) suggested that the

process of "laying down" is a consequence of the mechanical properties of the wood and is due to the progressive failure of the shoots under their own weight.

The quest for height is induced by the structural development of the community where a high density of stems promotes vertical growth. As structural development proceeds *A. biglandulosum* stems fail, and consequently their position in the forest is altered. As a result *A. biglandulosum* responds to a change in the light environment in its "new" stratum. Other subcanopy and understorey species, such as *Anopterus glandulosus*, *Cenarrhenes nitida* and *Atherosperma moschatum*, are shade tolerant. If a "sun" plant, such as *A. biglandulosum* (Chapter 5), is to successfully fill a place in the understorey then it must increase its canopy area in order to, firstly, capture sufficient photosynthetically active radiation (Givnish 1988) and secondly, to occupy space to prevent shade tolerant species overtopping it. To maximise light interception trees usually present different canopy shapes, with subcanopy trees having wider canopies (Horn 1971). In the case of *A. biglandulosum* its canopy area is increased by secondary growth along the length of the destabilised vertical stems.

Simple physical influences, such as the weight of snow, have also been observed to result in stems bending. These stems remain in the bent position after the snow has melted. Infrequent heavy snowfalls may be sufficient to impart a significant influence upon growth-form. The tall and whippy vertical form and propensity to bend "naturally" makes *A. biglandulosum* susceptible to disturbance by snow. Some other canopy dominants in Tasmania, for example, *P. aspleniifolius*, *Athrotaxis cupressoides* and *Atherosperma moschatum*, have spiral or whorled branches arranged in downward pointing, overlapping layers which produce a conical shape. Conical shapes of this form shed snow efficiently or at least distribute its weight evenly over the canopy, thereby reducing the risk of disruption (Horn 1971).

Secondary and tertiary shoots arise from dormant buds at the branch nodes. They probably overcome apical dominance in response to a light stimulus after the canopy is disturbed or after the vertical stem fails. The new canopy, in the form of numerous vertical secondary or tertiary stems, is formed by a process of reiteration of the single vertical primary stem. This pattern of development is described by Borchert and Tomlinson (1984) as genetically determined. Oldeman (1974) argues that canopy reiteration is an architectural adjustment and is a normal response to disruption. The result is a modified multi-layered canopy, rather than the more typical understorey form represented by the mono-layer (Horn 1971).

The plastic response of an existing canopy to gap creation is unusual. The gap niche is usually occupied either by young understorey trees or by secondary species (Kuppers 1989). In Tasmania, the depauperate rainforest tree flora contains only a few specialist gap colonisers. Thus, there are niche vacancies and opportunities for plants to diversify their niche occupation (e.g. Jordan *et al.* 1991). *A. biglandulosum* is highly plastic in its growth habits and subsequently is able to respond to the range of opportunities presented by the diversified niches.

The Thamnic Scrub is not considered to be related in genesis to a disturbance mechanism but rather reflects deterministic growth in response to the environment. However, the gap phase in such scrub is also likely to be dominated by *A. biglandulosum*. Castro and Santos (1980) distinguished between the deterministic growth habit and the opportunistic response to stochastic events. Castro and Santos described crown development by deterministic growth as "adaptive" and crown re-development by reiteration in response to damage as "traumatic". The traumatic being the reiterative response of a previously dormant meristem which initiates a second version of the initial stem. In the case of *a. biglandulosum*, the deterministic reiteration is similar but is in response to the re-orientation of existing stems. Hence, the capability to reiterate is deterministic but if in response to disturbance it is probabilistic (Tomlinson 1982).

A distinction also needs to be made between regeneration and proliferation. Those sites that were determined to be regenerating continuously (Figure 7.9) were doing so by resprouting in clusters from roots near the base of old stems or by layering. In both of these cases, the axial integrity of the individual is maintained by adding determinate units (Tomlinson 1982) which may persist as "new" individuals. The production of such units was most prevalent in the Thamnic Scrub where there was little disturbance. In contrast, proliferation predominates in the Thamnic Response and adds to the construction of the existing plant. The process is opportunistic in response to tree-fall and does not reproduce an individual.

Seedling regeneration was most prevalent among the Monopodial form (Table 7.3) and was associated with open canopies. However, even where seedlings were present, mortality appears to produce a regeneration gap in the size distribution. Some form of massive disturbance may be necessary for successful seedling recruitment. The well-formed monopodial trees do not fail under their own weight and so the opportunity for proliferation does not arise.

Specht and Morgan (1981) suggest that an equilibrium in the total foliage projected cover (FPC) of the overstorey and understorey is reached in mature communities. They describe the equilibrium as a mosaic of micro-communities with interrelated overstorey and understorey covers, the mosaic being related to the initial patterns of overstorey species or to the development of irregular gaps as the community ages. How long the equilibrium is maintained before the community begins the senescent phase is unknown. They also indicate that if the overstorey FPC is reduced by disturbance the understorey will rapidly compensate for it to maintain the total FPC equilibrium.

It is above type of dynamic process that has been identified with the development of Thamnic Response Scrub compared to the relative stability of the *Anodopetalum* Thamnic Scrub in the present study. It remains to be determined whether the original equilibrium FPC values would be restored in time, or whether a shift in the balance of FPC represents a new equilibrium. The latter case suggests a continuing succession in which the dominant cover would decline and the understorey cover would increase. Certainly the evidence deduced from the analysis of gaps (Tables 7.5 and 7.6) indicates that *A. biglandulosum* will increase in cover, in the understorey, in response to trees falling from the overstorey in forests where it is present in significant density. The successful regeneration of *N. cunninghamii* and *P. aspleniifolius* in myrtle wilt gaps is in agreement with Packham (1991), and suggests that canopy dominants will persist, at least at a reduced density.

A continued succession of this nature suggests that the *N. cunninghamii* dominated thamnic closed-forest may not be a steady-state self-replicating system. In a more extensive study of *N. cunninghamii* dominated forests, Read and Hill (1988) concluded that all were in fact regenerating continuously, and indeed this appears to be the norm. The particular type of thamnic closed-forest in this study appears, however, to be an exception.

The proliferation of *A. biglandulosum* in the gap phase of thamnic forest suggests that a climax forest type would be dominated by *A. biglandulosum*. The fact that this condition is not extensive throughout the landscape may indicate that the succession toward an *A. biglandulosum* climax is truncated. The rejuvenation of the *N. cunninghamii* closed forest would require a catastrophic disturbance in which much of the *A. biglandulosum* were killed.

Fire is the only agent capable of such a rejuvenating process in the Tasmanian landscape within the time scale of centuries. Macphail (1980) suggests that over longer periods

pedogenesis, particularly as a result of nutrient leaching in high rainfall areas, may result in changing community composition. However, in the current study the rate of change appears to favour a shorter term mechanism.

Fire regimes in Tasmanian wet forests which include return periods of less than about 400 years tend to perpetuate the dominance of *Eucalyptus* spp. (Gilbert 1959, Jackson 1968). However, return periods which are longer than the life-span of *Eucalyptus* spp. exclude them from the community (Gilbert 1959, Ashton 1978); except in some high altitude mixed woodland stands on blockstreams (Kirkpatrick and Balmer 1991). A cyclic succession in thamnic forest in which fire is integral may span a period as short as 4-500 hundred years and exclude *Eucalyptus* spp. It is more likely to span between one and two *Nothofagus cunninghamii* generations. This species may live to about 600 years but regenerates in the absence of fire (Read and Hill 1988). Assuming the gap phase starts after one complete life span of 600 years, then a gap phase rate of 1% of total area per year would result in the forest being replaced in 700 years. If one gap in two became dominated by *A. biglandulosum*, the canopy would be replaced by *A. biglandulosum* in 800 years. Whether or not the modification of the canopy would make the forest more prone to ignition is not known. Regardless of this, a hot fire at this stage of succession would return the forest to the beginning of the cycle with *A. biglandulosum* being relatively inconspicuous (See Barker, M 1991). In Chile, Veblen (1982) describes a similar situation in which *Chusquea* bamboos dominate the gap-phase in *Nothofagus* forests. In this case the bamboos are prevented from becoming the climax vegetation by broadscale landscape instability associated with earthquakes which stimulates regeneration of the *Nothofagus* forest (T. Veblen pers. comm.).

7.5 Conclusion.

A. biglandulosum resprouts and layers and does not require disturbance to maintain a population. Where disturbance is experienced, the main feature of its growth response is canopy proliferation. In open rainforests canopy reiteration is common and appears to reflect a deterministic growth habit. In response to disturbance by tree-fall in closed thamnic forests, the reiteration process is so prolific that in some forest types it results in domination of the gap-phase. The progression of gap-phase dominance may result in a successional shift, particularly in the structure of the forest. Although areas of forest in this condition are not uncommon, a more extensive distribution may be limited by a truncated succession. This may result in the forest proceeding from a secondary succession to a mature stage, and then a senescence of the canopy dominants. During

this time *A. biglandulosum* may proliferate before the forest is returned to the beginning of a secondary succession by a catastrophic disturbance, perhaps fire.

Chapter 8. *Phyllocladus aspleniifolius*: the regeneration microsite, population structure and dispersion patterns in Tasmanian forests.

8.1 Introduction

The population ecology of canopy species in Tasmania's cool temperate rainforests has only recently begun to receive significant attention (Ogden and Powell 1978, Read and Hill 1985, Cullen 1987, Cullen and Kirkpatrick 1988, Read 1989, Gibson and Brown 1991b). This is in contrast to New Zealand and South American forests in which numerous studies have been carried out, particularly since 1960 (Wardle 1963, 1969, 1978, Patel 1968, Beveridge 1973, Clayton-Greene 1977, Pook 1978, Veblen *et al.* 1980, Veblen and Stewart 1980, Stewart and Rose 1989, 1990, Norton *et al.* 1988). These studies were conducted at various spatial and temporal scales, and have relied, to various degrees, upon the frequency distribution of size and or age-classes to infer stand history and stand dynamics.

Variation in the physical environment and in stand history provides part of the explanation of population structure. However, it is likely that competition between plants and between populations of plants is relatively more important in controlling community and population dynamics (Grubb 1977a, Woods 1984). Furthermore, as floristic and structural composition changes from one community to another, the competitive relationships of species may change, producing corresponding changes in opportunities for regeneration.

Because regeneration of any species is confined to a particular range of habitat conditions, the extent of those conditions is a major determinant of its geographic distribution (Grubb 1977a). However, within this range there are physiological and biotic factors which affect the regenerative capacity of species and thus their abundance and status. One result of differences between dispersal mechanisms and physiological tolerances of seeds and seedlings is the spatial differentiation of regeneration niches. Recent studies (Christy and Mack 1984, Collins and Good 1987, Harman and Franklin 1989) have produced valuable insights into the needs of particular species for specific microsites for germination and successful recruitment into established communities.

As time passes after large scale disturbance, the biological interactions within communities become more important in terms of the maintenance of populations and changes in the patterns of regeneration (Horn 1974). Different microsites possess various qualities of light, temperature, moisture and nutrition, and different degrees of

protection from seed or seedling predation (Whittaker and Levin 1977). Niche differentiation is most discernible at the early life-stages of seedlings and saplings. It is often emphasised that it is at this stage that the relative abundance and dispersion of a species is determined via the spatial and temporal distribution of suitable regeneration niches (Whittaker 1975, Grubb 1977a, Whittaker and Levin 1977, Harper 1977).

The requirements of each species may vary widely and may include, for example, the need of eucalypts for disturbance by fire to provide a relatively sterile ash-bed to exclude fungal attack of the susceptible seeds (Ashton 1976), or the dependence upon log sites for seedling establishment of species of *Picea* and *Tsuga* (Harman and Franklin 1989). An enormous literature exists which explains the significance of gaps in the recruitment of canopy species, and some authors have also considered the microsites within the gaps (e.g. Veblen 1989).

Compared to the other Tasmanian conifers, *P. aspleniifolius* has a broad ecological and geographic range (Kirkpatrick and Backhouse 1985). The diversity of communities and habitats within this range offers an opportunity to consider the effect of changes in community floristics and structure on regeneration opportunities. This chapter will test the hypothesis that the spatial and temporal distribution of size-classes is dependent upon the spatial and temporal distribution of germination microsites and the dispersal characteristics of *P. aspleniifolius* in Tasmanian forests.

8.2 Methods

8.2.1 Data collection

Fifty sites were surveyed across a variety of rainforest types (Figure 8.1). The area surveyed varied depending upon accessibility and the density of *P. aspleniifolius*. The basic survey unit was a belt-transect measuring 6 m x 50 m (300 m²). Multiple belt-transects were always joined parallel along the entire length up to a maximum area of 1 800 m². The belt-transects were marked down the centre with a 50 m tape-measure and regular 3 m offsets were marked along each side. From within each 3 x 3 m quadrat it was possible to directly read the tape measure, allowing all trees to be mapped to within 0.5 m².

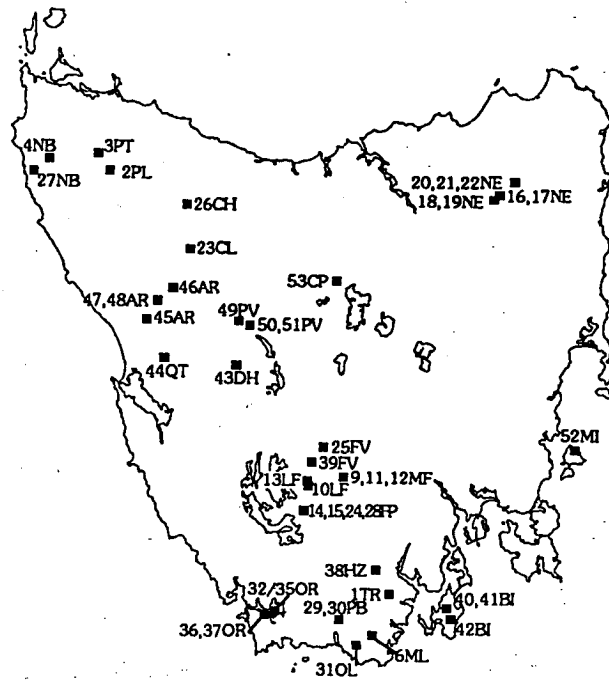


Figure 8.1. The location of sites investigated in this chapter.

The diameter at breast height (dbh) of all species greater than 10 cm was measured and their location was plotted on a grid representing the transects. For *P. aspleniifolius*, all individuals, irrespective of size, were plotted on the grid and diameter at breast height (dbh) if greater than 3 cm. The 3 cm limit was chosen for diameter measurement because the age of such individuals could be determined by counting the nodes (F.Podger CSIRO Hobart, pers. comm.). If an individual was less than 3 cm dbh, and had one or more phylloclades, it was considered to be a sapling. Its height was measured and its age estimated by a count of the nodes along the length of the primary stem. Three years were added to this total to take into account the time taken to produce phylloclades (Read 1985a). This method may incur a small but unknown error by under-estimating age because the nodes are not easily distinguished in the earliest few years of growth. Seedlings were defined as those individuals with no phylloclades and the actual number were recorded if less than 10, or else estimated as classes of ten if greater. The microsite of seedlings was noted in each case (Table 8.1). For saplings and mature trees the microsite was only noted if unmistakably discernible. For example, if a sapling is rooted on the ground it cannot be confidently assigned to either the moss or the litter microsite although clearly germinated on one or the other microsite. Combinations of microsites were also noted. In some cases where saplings appeared to be suppressed, cross-sections were taken for ring counts to confirm the age range in relation to the larger trees, otherwise height/age relationships via node counts were relied upon. The size to age relationship of the dominant trees at or between sites has not been established, however, a comparison of actual age distribution and size distribution was made for one lowland site. The interpretation of size frequency distributions is, therefore, conservative and confounding effects are considered in the discussion.

A list of all vascular plant species and their percent cover (modified Braun-Blanquet: one only=1; <1%=2; 1-5%=3; 5-25%=4; 25-50%=5; 50-75%=6; 75-100%=7) was compiled and ordered for display using the classification programme TWINSpan (Hill 1979). See Appendix 6; the TWINSpan floristic table. Site characteristics appear in Appendix 7 and included for each site is: the presence or absence of gap phase regeneration and or fire scars; the percent cover and depth or size of litter, moss, rock, logs and moss on logs. The height and percent cover of the tallest stratum, subdominant stratum if present, and the lowest stratum were recorded as was the height of the tallest *P. aspleniifolius*. The drainage was recorded as excess, free or impeded. Aspect and slope were measured using a compass and clinometer and altitude was estimated from 1:100 000 topographic maps.

Table 8.1. The microsites recorded for each seedling and sapling less than 3 cm dbh.

Microsite

moss on ground
log on ground
moss on log
litter on ground
stump mound
buttress of another tree
beneath an adult <i>Phyllocladus</i> canopy
tree-fall gap
log in gap
moss on log in gap
litter on ground in gap

For the purposes of analysis, the floristic and population size-class data were numerically indexed using multi-dimensional scaling (MDS). This procedure produces multiple one-dimensional ordination axes of relative similarity between the species assemblages.

8.2.2 Pattern analysis

The methods of Diggle (1983) and Ripley (1977) were used to analyse the dispersion of *Phyllocladus* individuals. Representative quadrats were chosen from the samples to illustrate the variety of patterns observed. The methods of Diggle and Ripley are designed for fully mapped data and allow the statistical significance of any variation from complete spatial randomness (CSR), and the scale of pattern, to be determined. Limitations to the determined scale depend upon the accuracy of the spatial data and the size of the collection area, 0.5 to 12 m for the present study. To test for CSR the method of Diggle (1983) was employed. This method compares the frequency distributions of plant to nearest neighbouring plant, from the mapped data, to a data set generated from points with a frequency distribution representing CSR. Forty-nine simulations enable the statistical significance of any departure of the observed data from CSR to a probability of 0.02.

If a significant deviation from CSR was determined then the method of Ripley (1977) was used to assess the scale of the aggregation or the distances between regularly arranged trees. Ripley's function ($K(t)$) depends upon the number of observations (K) within distance (t) of a given tree. The values of this function derived for every tree in the observed data set were compared to values obtained from simulated data-sets in which there was CSR. The upper and lower limits of the simulated data sets are represented by an envelope (e.g. Figure 8.8). Aggregation in the observed data is shown by departure above the simulation limits and regularity by departure below the simulation limits. The size of aggregations, or the minimum distance between trees in a regular distribution, can be read from the points of departure compared to the distance scale along the x-axis (Figure 8.8).

8.3 RESULTS

8.3.1 The sapling pool height and size age relationship.

Table 8.2 indicates that height is generally a good estimator for age at those sites with a significant pool of saplings. It is also evident from the kurtosis coefficient that the ages of saplings have a frequency distribution that suggests recruitment occurs over a variable but extended period of time. Figure 8.2 supports this contention and also indicates the high correlation between stem diameter at ground level and stem age in saplings ($r=0.94$; $n=12$; $P < 0.001$). Typically, the skewness coefficient (Table 8.2) indicates long upper tails in the age distribution of saplings. Such a distribution suggests that some attrition of the sapling pool occurs, probably due to density dependent thinning and other competitive interactions. The thinning process will have consequences for the pattern of the population as it matures.

The presence or absence of seedlings and/or saplings indicates whether or not regeneration is continuing. In the absence of such a pool, the range of ages (size-classes) indicates the relative length of the earlier recruitment phase. It must be remembered, however, that the environment (temperature, moisture and light) and competitive interactions between plants control the growth rate and this will confound relationships between sites. Thus, the data must be interpreted conservatively in the absence of actual ages. The limited age data from the Celery Top Islands, ie sites 32-35OR (Figures 8.1 and 8.2) indicate that there is considerable variability in the ages of mature trees at these two sites and so the interpretation of an extended recruitment phase is correct and withstands the confounding influences. Although the relationship between dbh and age is significant ($P < 0.001$) in both samples (Figure 8.2), the strength of the relationship has weakened in comparison to saplings. Nevertheless, Figure 8.3 illustrates the similarity in the shape of the distributions based on both size and age in these stands, thus confirming the size of stems as a surrogate for age.

8.3.2 Establishment success by microsite

Table 8.3 summarizes the data from 50 sites into percent frequencies according to a simplified group of microsites. If a seedling occurs in moss on a log, or on a log in a gap, it was counted for each microsite separately. Moss and litter on the ground support 50% of seedling germination and represent greater than 75% of available surface area. The remaining 50% of seedlings occur on elevated sites and in gaps which, in total, cover less

Table 8.2. The relationship between height and age (determined from node counts) for saplings at 25 sites. S is a coefficient of skewness in the age distribution at each site. Positive values indicate that the upper tail of the distribution curve is longer than the lower tail while negative values indicate that the lower tail is longer. K is a kurtosis coefficient. Zero equals a normal distribution while values > 0 indicate a steep curve and values < 0 indicate a flat curve.

**Sapling Height/Age Correlations
and Age Distribution**

Site	r	n	P	S	K
9MF	.79	25	<.05	-0.35	-0.57
13ALF	.96	4	<.05	-0.86	1.74
13BLF	.78	77	<.05	-0.03	-0.30
18NE	.85	22	<.05	0.09	-1.20
20NE	.94	13	<.05	0.98	-0.56
24FP	.66	18	<.05	0.52	1.09
27NB	.69	10	<.05	0.47	-0.48
28FP	.74	18	<.05	-0.23	-0.67
29PB	.97	4	<.05	1.64	2.56
30PB	.82	18	<.05	-0.45	-1.25
33OR	.58	7	<.05	0.15	-1.93
34OR	.77	30	<.05	0.14	-1.23
35OR	.67	14	<.05	0.03	-1.39
36OR	.70	104	<.05	0.90	1.08
38HM	.76	31	<.05	0.47	-0.55
40BI	.78	68	<.05	0.92	-0.59
41BI	.80	17	<.05	0.24	-0.28
42BI	.82	21	<.05	-0.48	-1.36
43DH	.94	24	<.05	0.47	-0.48
45AR	.94	24	<.05	-0.08	-0.81
46AR	.82	16	<.05	1.54	1.82
47HT	.77	43	<.05	1.80	4.32
48HT	.72	37	<.05	0.96	0.13
49PV	.81	26	<.05	0.37	-0.65
50PV	.78	12	<.05	0.05	-0.91

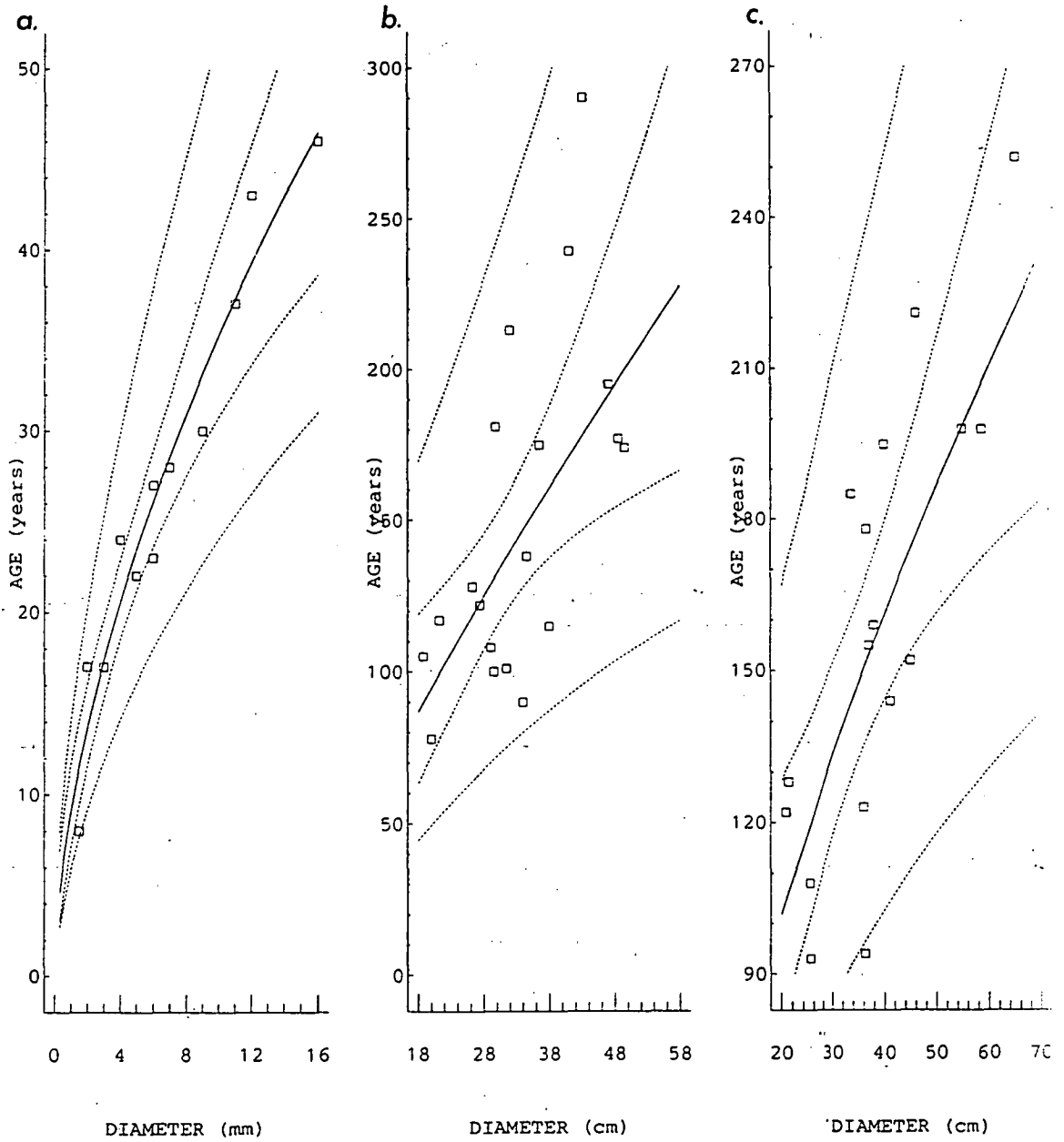


Figure 8.2. Multiplicative linear regressions of age on diameter for 3 samples of *P. aspleniifolius*, a. saplings, b and c mature trees. The inner broken lines represent 95% confidence limits and the outer, the limits of prediction. Slope $P < 0.01$; a. $n=12$, $df\ 11$, $f\ 86.77$, $r^2 = 0.88$; b. $n=19$, $df\ 18$, $f\ 16.6$, $r^2 = 0.48$; c. $n=16$, $df\ 15$, $f\ 17.9$, $r^2 = 0.54$

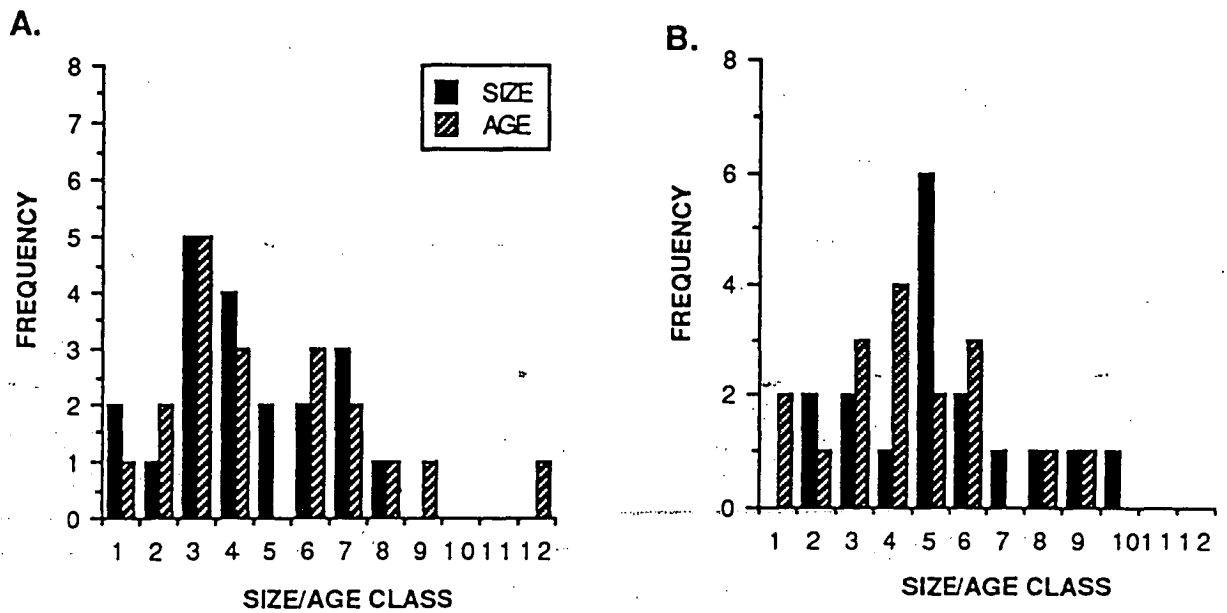


Figure 8.3. A comparison of the distribution of ages (years) and sizes (cm) from two samples of *Phyllocladus aspleniifolius*. The class sizes are determined by the average growth rates of the trees, 20 years per 5 cm dbh.

than 20% of the surface area of the site. The analysis of these data indicate that the expected number of seedlings, compared to the observed number for each microsite, is significantly different from a Chi-square distribution. The data clearly indicate that the elevated and gap microsites are more successful seedling nurseries than moss and litter on the ground. However, the percentage change from the number of seedlings compared to the number of saplings for each particular microsite indicates that mossy logs, stump mounds and moss and litter on the ground display more successful recruitment of seedlings to the sapling pool than gaps and buttresses (Table 8.3). The lower rate of recruitment from the seedling stage in gaps may be attributed to competition from other regenerating species, while on buttresses it may be the effect of low light, because buttresses are immediately below large canopies.

It should be remembered that even though gaps and buttresses are less successful at recruitment from the seedling pool than moss and litter on the ground their superiority as seedling nurseries results in them being more successful microsites overall. Therefore, in forests where microsites other than ground moss and litter are available recruitment from the seedling pool is likely to be more successful.

The analysis of sapling growth rates (height) from two selected sites with significant numbers of saplings elevated microsites and at ground level, confirms that saplings on the elevated sites grew faster than those at ground level (Table 8.4) (df. 1,38, F ratio 10.218, $P < 0.01$). These growth rates and the diameter growth rates of saplings in mixed forest at the Celery Top Islands (Figure 8.2) reveal extremely low annual increments but in doing so indicate the ability of the small size-classes to persist.

8.3.3 Population structures and dispersion patterns

8.3.3.1 Size class distributions

The size-class distributions for all sites grouped by population type are illustrated in Figure 8.4. In an attempt to synthesize the data in these figures, the peaks and gaps in the distributions have been graphed on cumulative frequency histograms for all sites (Figure 8.5) and on relative frequency histograms for each group of sites (Figure 8.6). Peaks and gaps are size classes with relatively more or less individuals than those classes on either side. It should be emphasised here that the data express the frequencies at which peaks and gaps occur and not the absolute amounts in each size class. Almost all size classes show peaks and gaps and both are skewed toward the smaller classes. Peaks are most common for seedlings, saplings and diameters less than 5 cm dbh. A peak also

occurs at 15-20 cm and a second mode of peaks occurs in the 25-40 cm classes. Larger size classes may be undersampled as a result of limits to the tree size attainable on high altitude and poorly drained sites. However, the peaks in classes 65-75 cm and 80-85 cm suggest that only a few trees of this size occur even on the sites that do support them. Gap frequencies are greatest for seedlings, and 5-10 cm and 20-25 cm classes. These data suggest a dichotomy between sites with peaks in the small size-classes and those with no small class sizes. The second group of peaks between 25 and 40 cm is alternate with gaps in the small size-classes.

Table 8.3. Frequency of the occurrence of seedlings (SDL) and saplings (SAP) according to germination microsite across all sites. The moss/litter microsite was assigned to saplings because it was not clear which of the two sites the individual germinated on due to the considerable time since germination. Germinates in moss or litter on one of the elevated microsities are recorded by site only to avoid double counting. The percentage cover attributed to each microsite (column 2) was used to determine the expected number of germinates on each microsite (column 3) as the appropriate percentage of the total number of germinates observed.

Microsite	Cover	Seedlings		Chi-sq.	Saplings	
		Obs. (n)	Exp.		Obs. (n)	% Change
Mossy Logs	5	210	78	225	258	23
Stump Mound	5	113	78	16	149	32
Buttress	5	94	78	4	93	-1
Canopy Gaps	5	360	78	1025	364	1
Moss (grnd.)	34	217	528	183	-	-
Litter (grnd.)	41	559	636	9	-	-
Moss/Litter	-	-	-	-	1005	30
Unoccupiable	5	0	78	78	0	0

Chi-square = 1540.58 , d.f. 6.
Significance level = <.001

Microsite	Seedlings		Saplings		Annual Growth (cm) (n) (se)		
	Freq. %	Obs. (n)	Freq. %	Obs. (n)			
Moss (elev.)	38	605	-	-			
Litter (elev.)	1	14	-	-			
Bare (elev.)	11	158	-	-			
Total elevated	50	777	46	864	3.5	(18)	(.50)
Total ground	50	776	54	1005	1.8	(21)	(.15)

Table 8.4. Growth rates from two forests of saplings less than 1 m tall on elevated and non-elevated germination microsites compared in a one-way analysis of variance. (n) - number of individuals measured. Rate (cm) - mean vertical growth rate per year and (se) - standard area.

Position	(n)	Rate(cm)	(se)
Elevated	18	3.45	.50
Ground	21	1.85	.15

F = 10.218 d.f.1,38 P < .01			

The distributions of size-class peaks and gaps for each population type are illustrated in Figure 8.6. These data summarize the population structures of the various forest types, and indicate a variety in the distributions of both peaks and gaps within the range of size-classes present among the groups of sites.

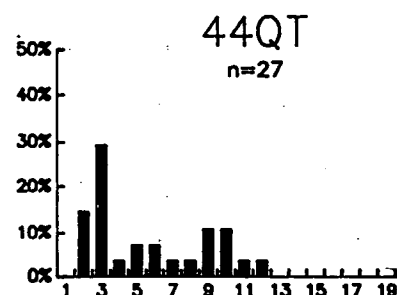
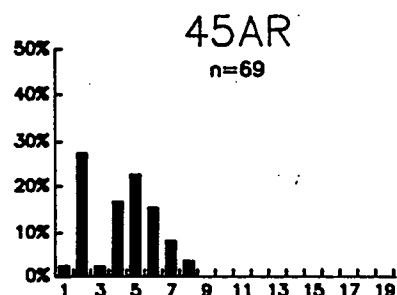
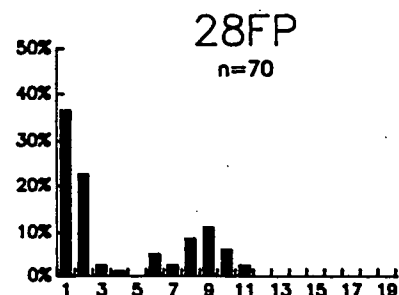
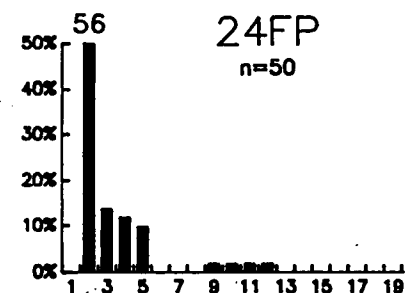
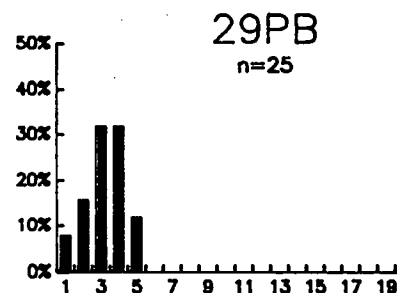
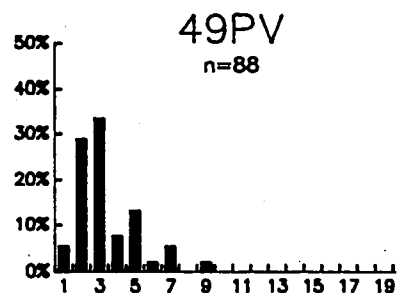
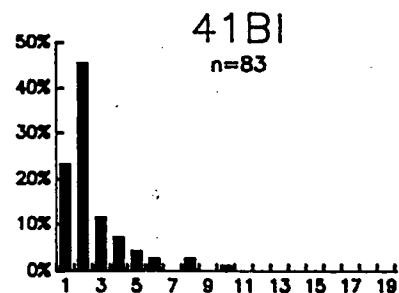
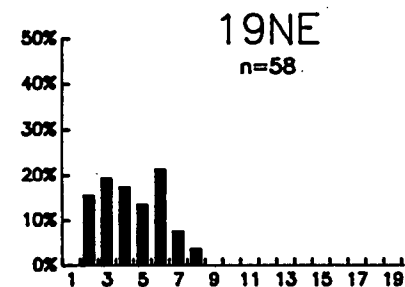
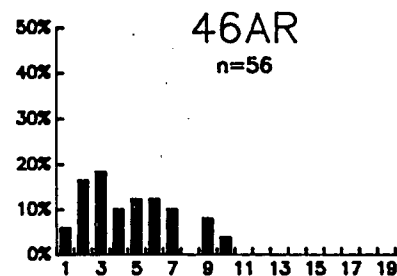
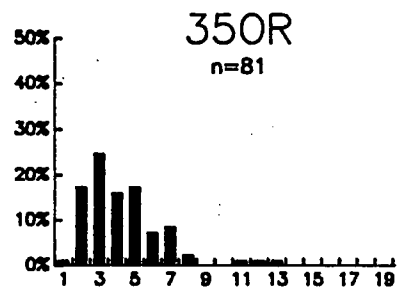
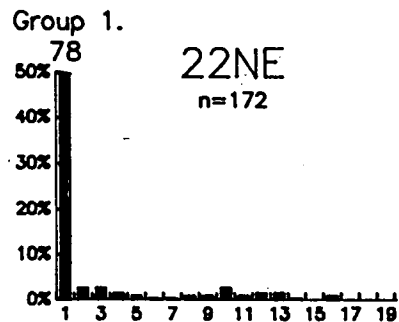
8.3.3.2 Gap phase and bimodal size class structures

Gap phase regeneration has been observed at a number of sites (Figure 8.4, sites 19NE, 24FP, 49PV, 29PB, 45AR, 35OR, 28FP, 22NE). These sites display two types of frequency distribution. The first appears similar to a continuous recruitment curve (a reverse J-curve) but is spatially and temporally dependent upon gaps. The gaps are likely to begin to form when the community reaches a considerable age. In the situation described by these curves, gaps are likely to have been part of the environment for a long period, hence the variety of size-classes between different gaps.

The second type of frequency distribution associated with gaps is bimodal for example, sites 45AR, 28FP, 24FP (Figure 8.4a). The bimodal size distribution may represent recent gap phase regeneration. The distribution may be attributed to an extended period of forest development followed by a period with no regeneration. In this period of relative stability in species composition and abundance, no gaps or other favoured microsites are available. Although these forests probably indicate the relatively recent development of gaps the community may still be of considerable age. The dominant canopy species have a large range of potential ages, including *Nothofagus* c. 5-600 years, *Phyllocladus* c. 1000 years and *Athrotaxis* greater than 1000 years (Ogden 1978ab). Due to this variation, the age of a community when gaps form due to tree senescence (the beginning of the gap phase) may vary from one community to another.

Figure 8.4. Percent frequency distribution of size classes for 49 belt transects. Group 1. gap phase and bimodal distributions; Group 2. mixed forests; Group 3. continuous regeneration in non-forest communities and implicate rainforest; Group 4. hilltops; Group 5. secondary *Nothofagus* forests; Group 6. *Nothofagus* forests with irregular size classes of *P. aspleniifolius*.; Group 7. Unique stand on Maria Island; Group 8. islands.

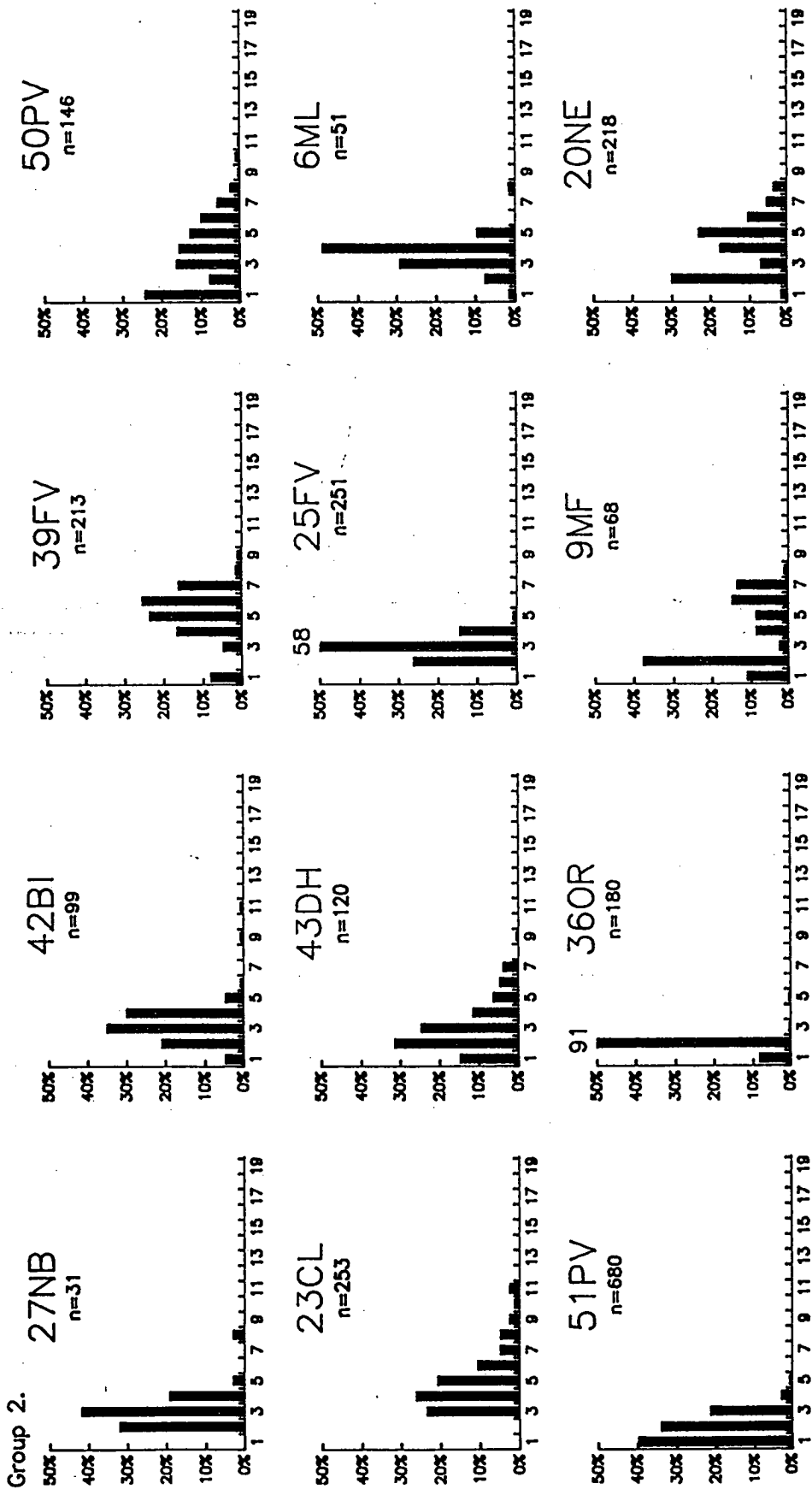
FREQUENCY (%)



LEGEND
class: diameter range (cm)

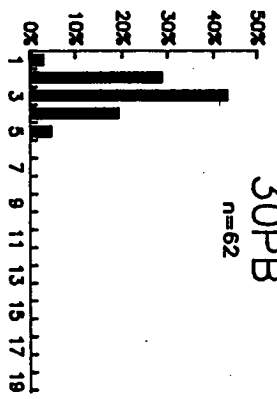
1: seedling	2: sapling	3: < 5	4: 5-9
5: 10-14	6: 15-19	7: 20-24	8: 25-29
9: 30-34	10: 35-39	11: 40-44	12: 45-49
13: 50-54	14: 55-59	15: 60-64	16: 65-69
17: 70-74	18: 75-79	19: 80-84	

SIZE CLASS

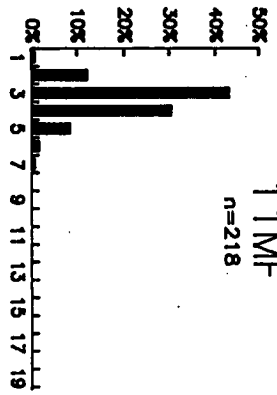


Group 3.

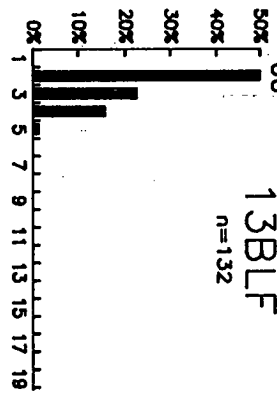
30PB
n=62



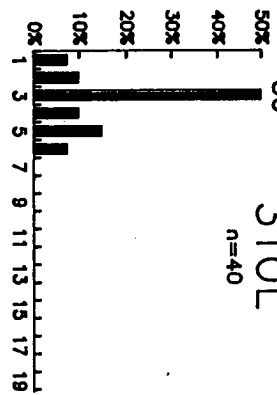
11MF
n=218



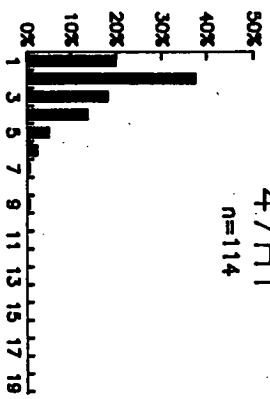
13BLF
n=132



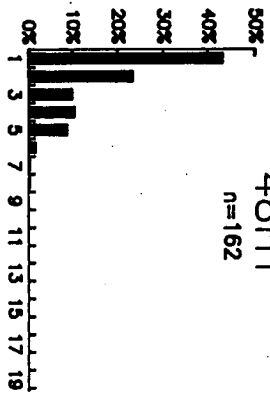
50
31OL
n=40



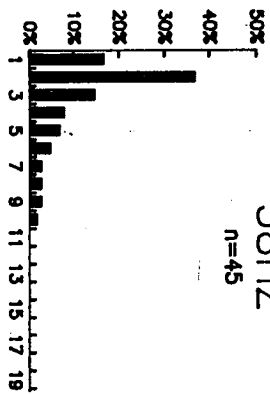
47HT
n=114



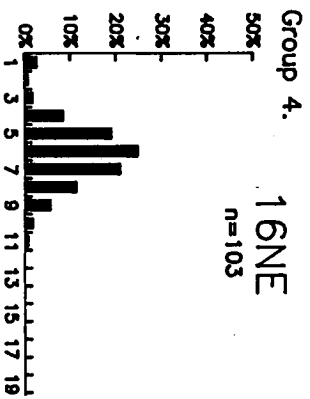
48HT
n=162



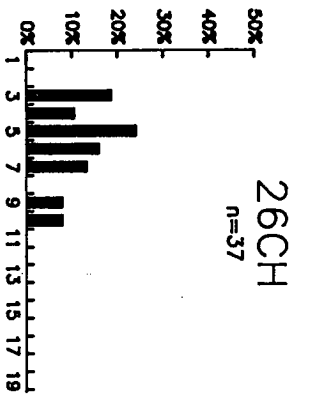
38HZ
n=45



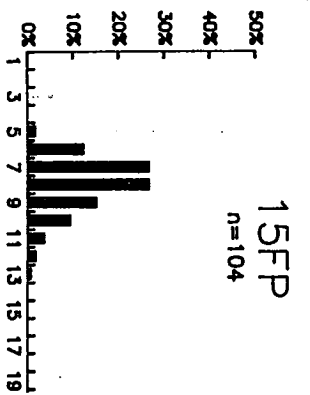
16NE
n=103



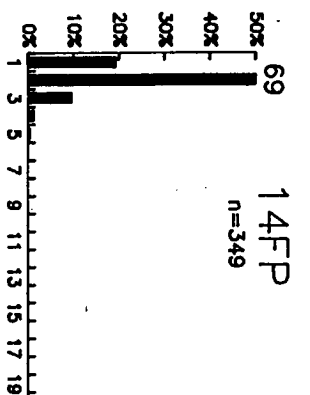
26CH
n=37



15FP
n=104

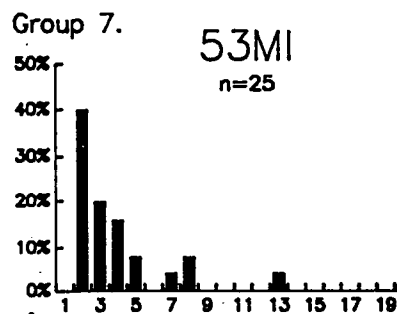
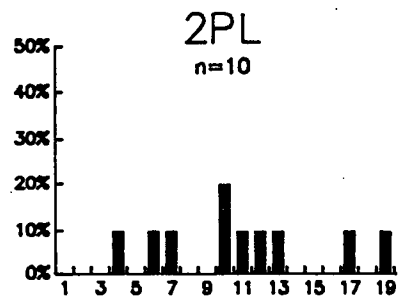
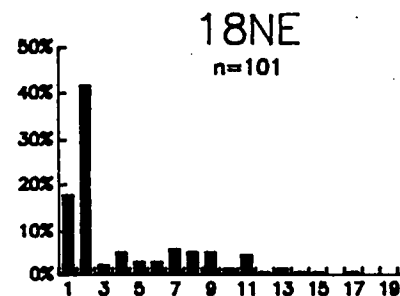
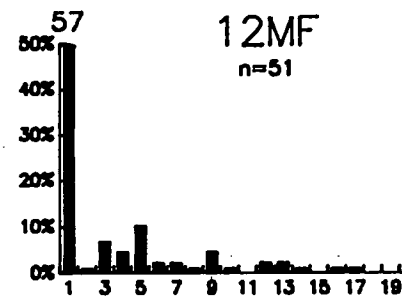
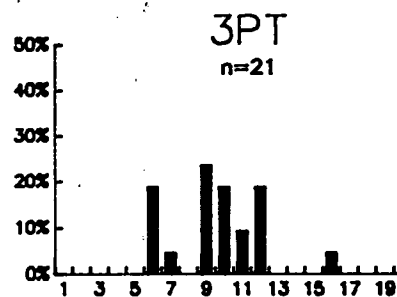
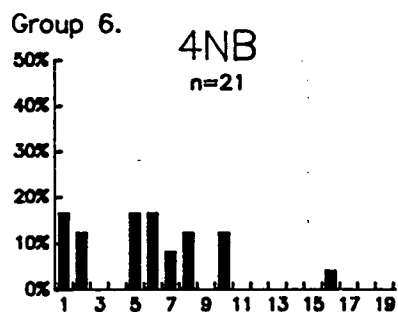
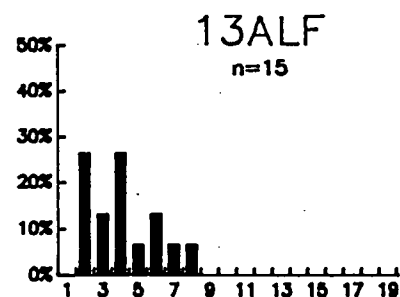
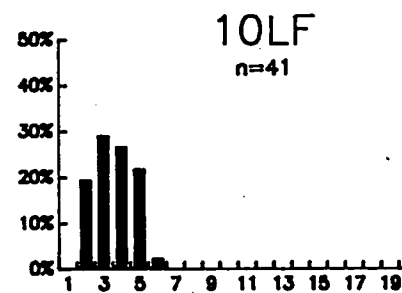
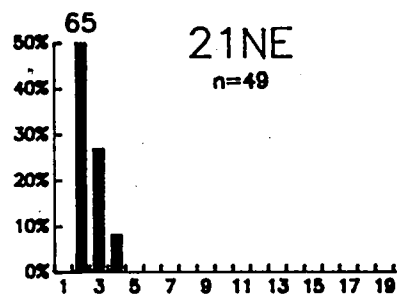
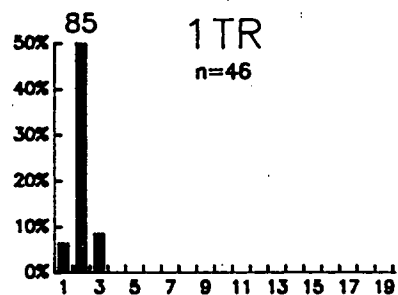
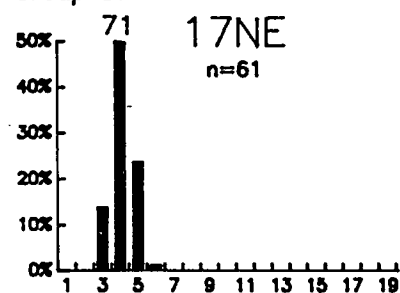


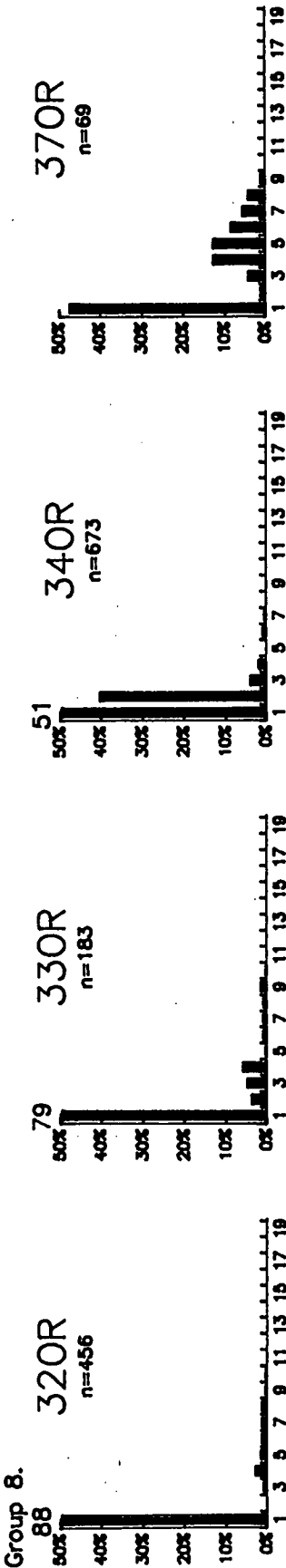
14FP
n=349



Group 4.

Group 5.





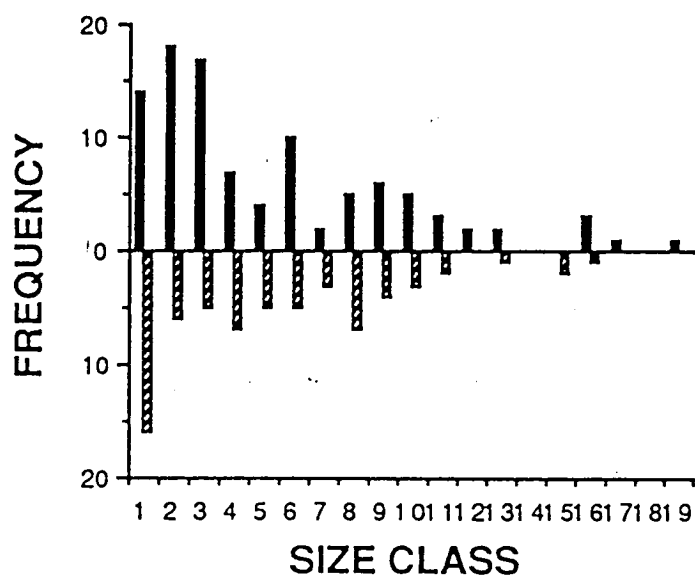


Figure 8.5. A frequency histogram of the number of peaks (above x axis) and the number of gaps (below x axis) in the size class distributions of 50 transects. (see text for explanation of peaks and gaps).

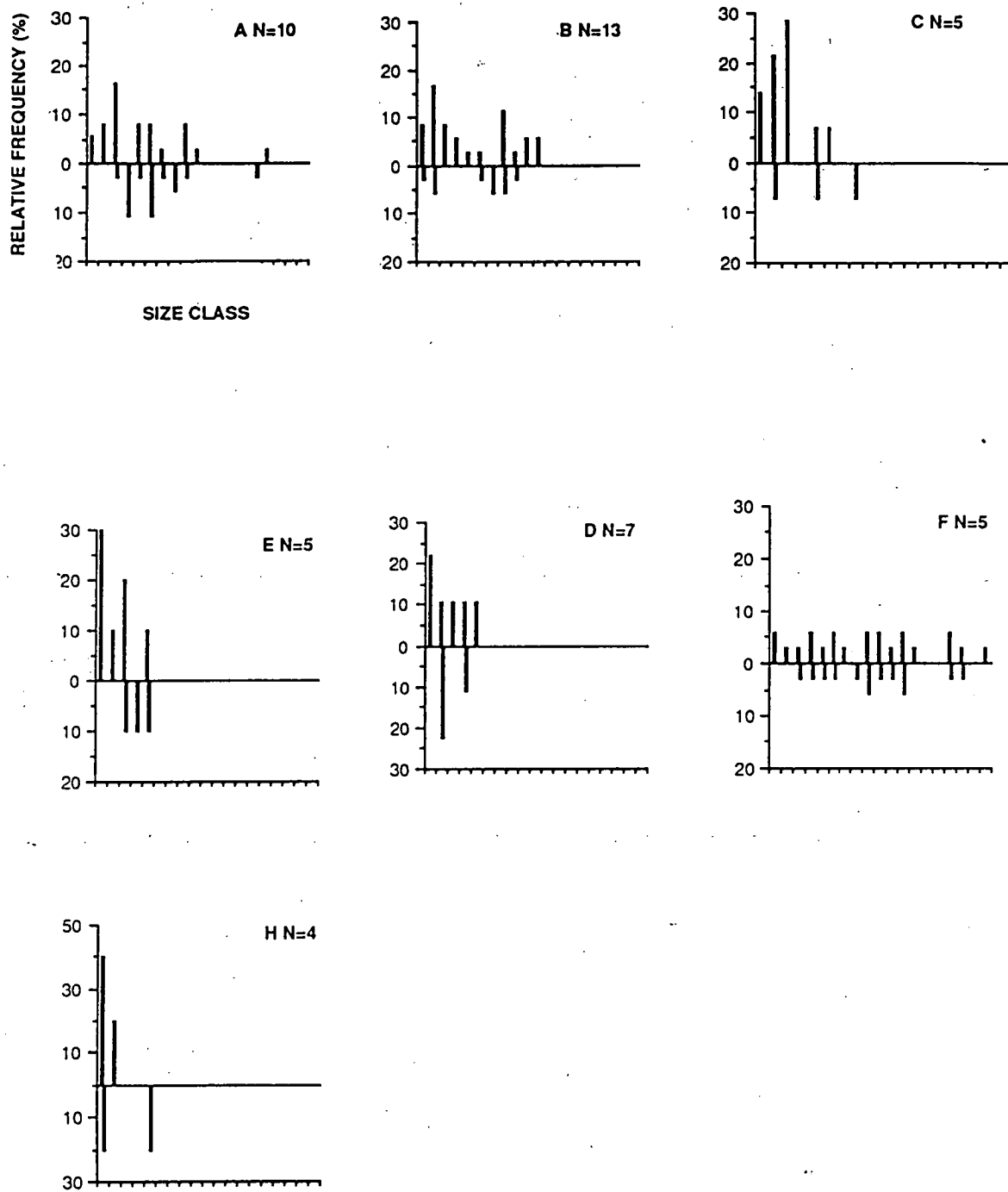


Figure 8.6. Relative frequency histograms of the number of peaks (above x axis) and gaps (below x axis) in the size class distributions of each group of sites depicted in Figure 8.4.

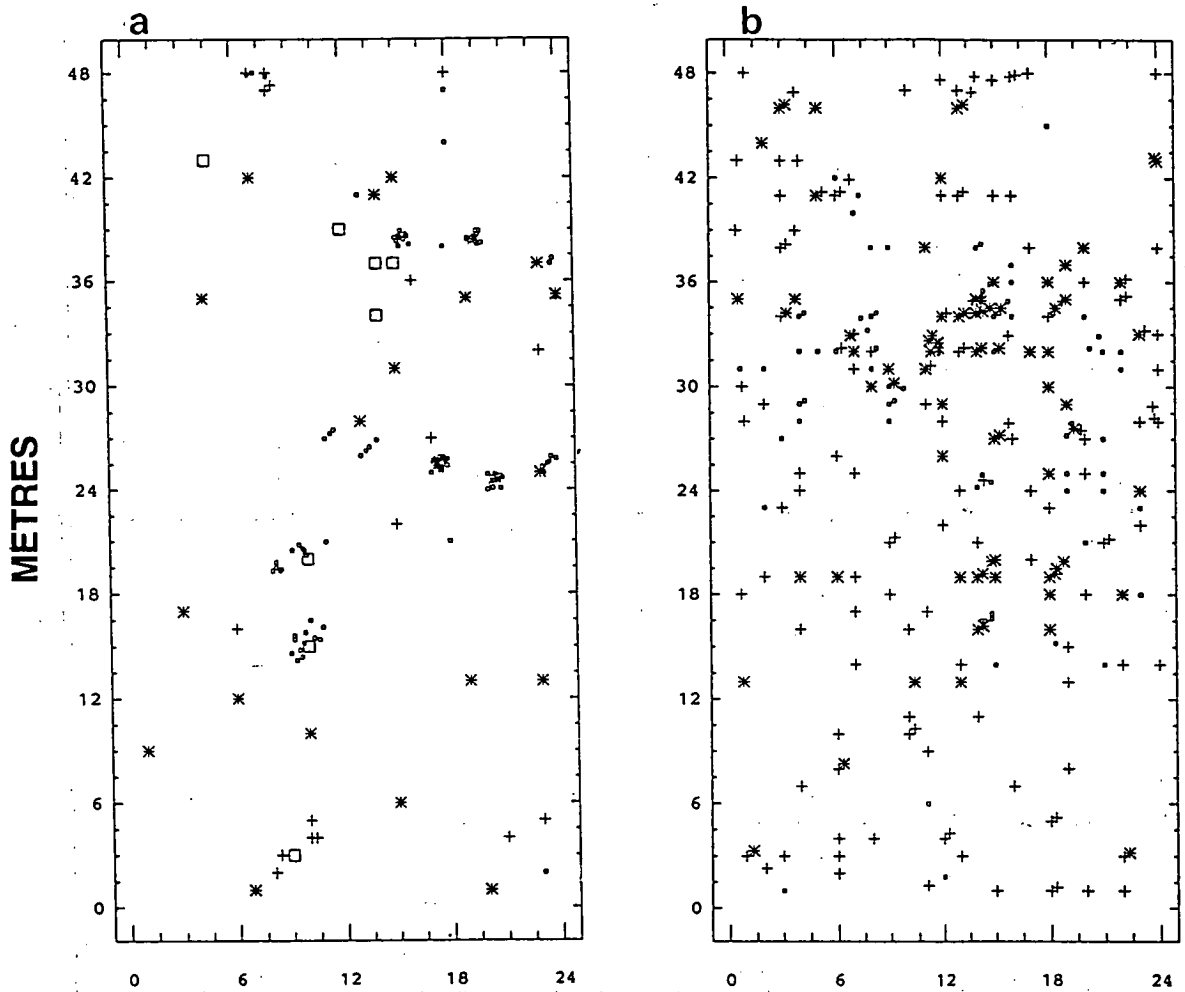


Figure 8.7. Mapped distributions of all individuals along five belt transects. a. Q22NE: seedlings \square , saplings +, old growth *, dead \square ; b. Q23CL: trees < 5 cm dbh. \square , 5-10 cm dbh. +, > 10 cm dbh. *; c. Q11MF: all trees \square ; d. Q48HT: seedlings and saplings \square , mature trees +; dead *; e. Q12MF: seedlings and saplings \square , mature trees +.

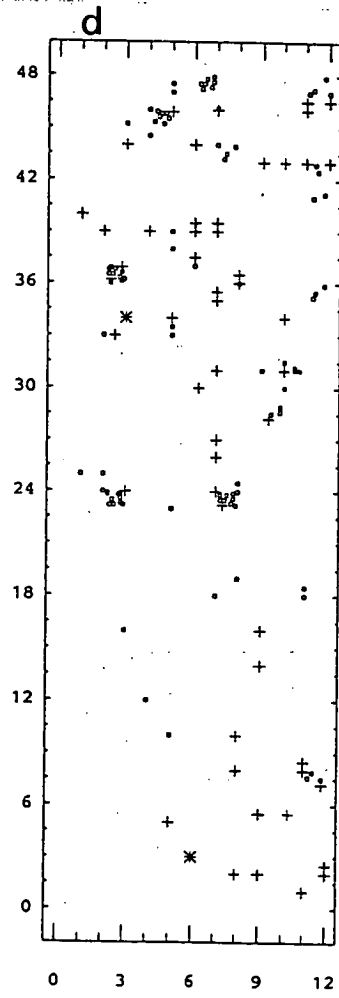
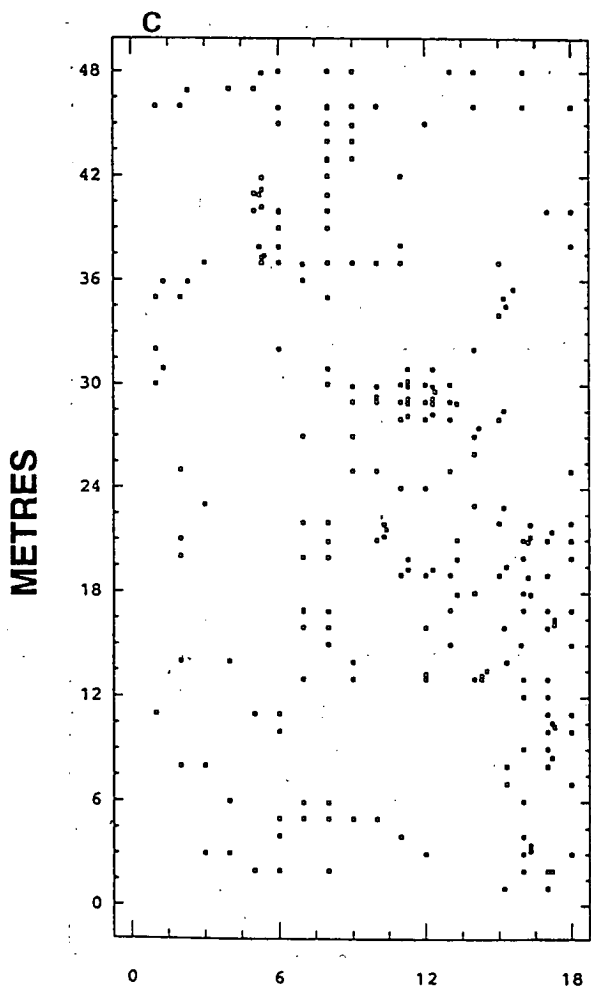


Figure 8.7 (cont'd)

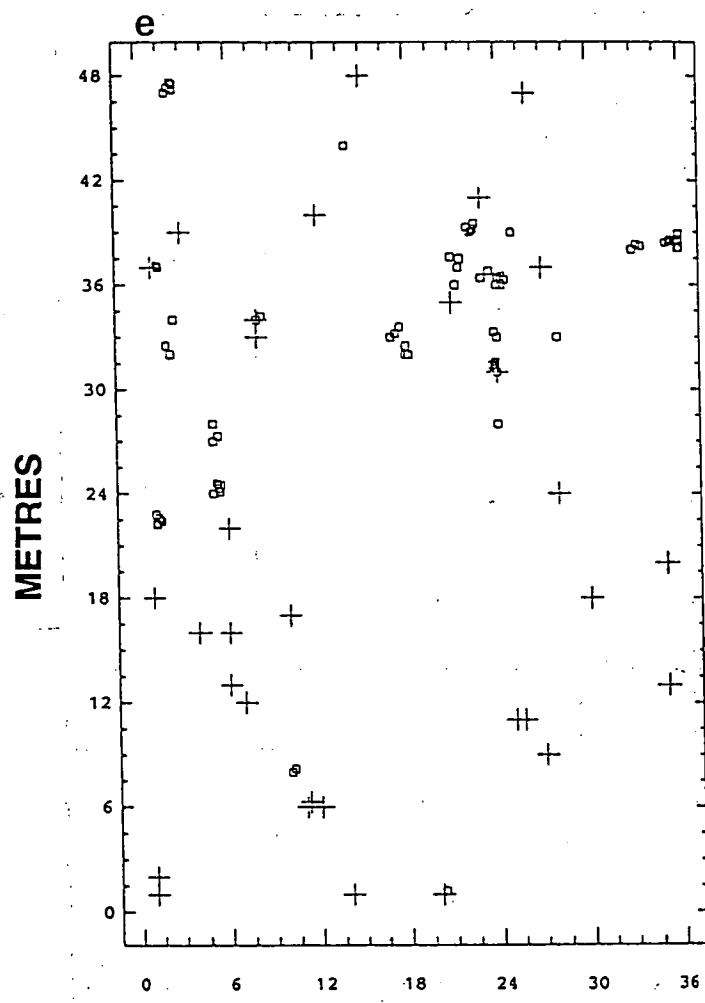


Figure 8.7 (cont'd)

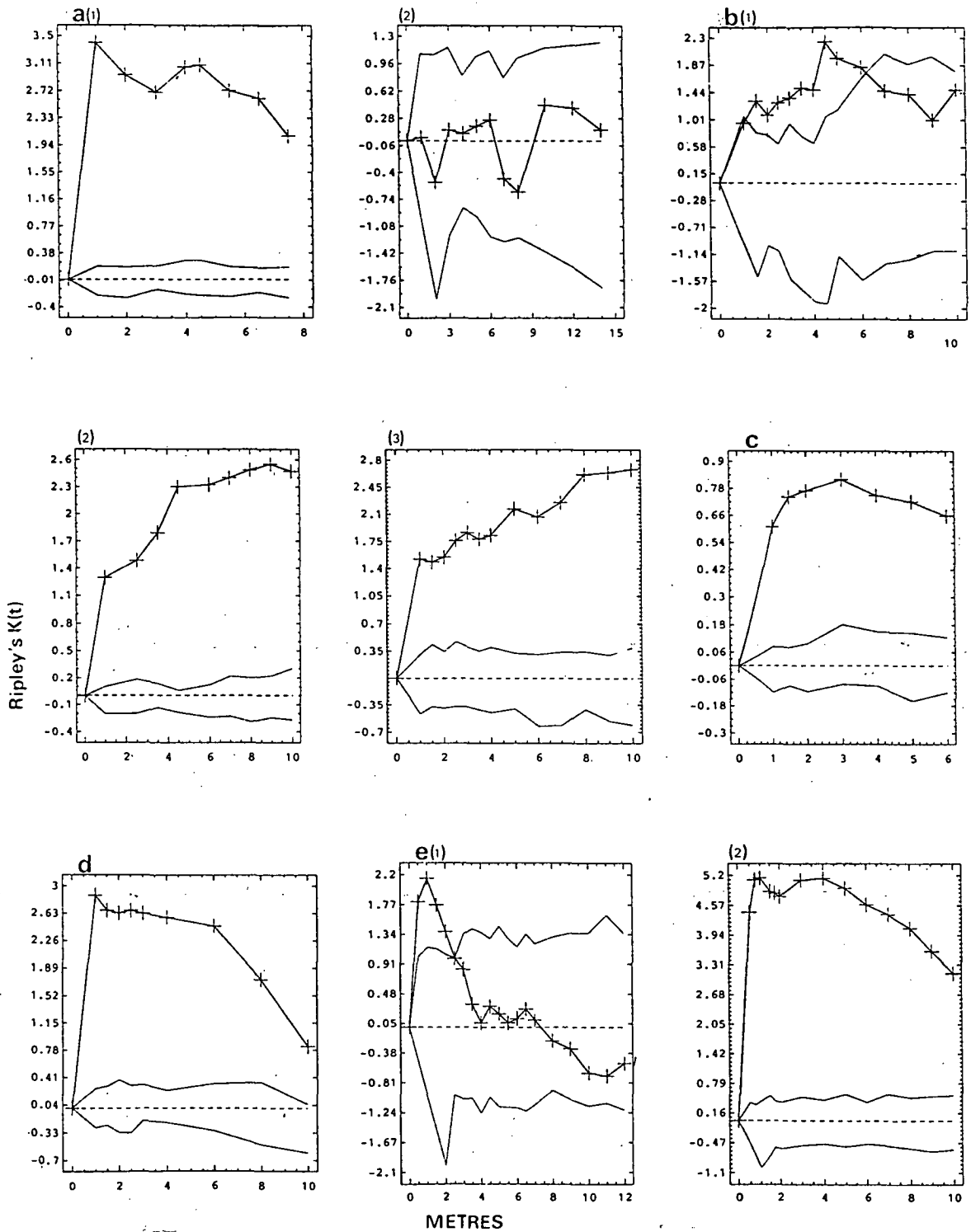


Figure 8.8. Ripley's $K(t)$ function and 49 simulations of randomized spatial patterns for five transects. a. Q22NE (1) seedlings and saplings, (2) old growth; b. Q23CI (1) trees <5 cm dbh. (2) trees >5 <10 cm dbh. (3) trees >10 cm dbh.; c. Q11MF all trees; d. Q48HT all tree; e. Q12MF:(1) mature trees, (2) seedlings and saplings.



Figure 8.9. A 12 year old sapling of *P. aspleniifolius* growing on the buttress of an over mature *Nothofagus cunninghamii*.

Seedlings and saplings in the gap-phase forests are clearly concentrated in gaps, for example sample 22NE (Table 8.5, Figures 8.4 and 8.7). The aggregation is at various scales comparable to the size of gaps, but some of the variation in the sizes of aggregations is also due to heterogeneity within the gaps. Heterogeneity within gaps is controlled by microsite suitability. Logs and stump-mounds within gaps, and buttresses at the margins of gaps are often the focus for regeneration (Figure 8.9).

In the absence of gaps, there are some sites where bimodal distribution is also evident (Figure 8.4, 44QT, 46AR). At sites 44QT and 46AR there appears to have been occasional recruitment to the sapling stage but only low levels of recruitment to larger size-classes. A weak aggregation of stems is not significantly different from complete spatial randomness ($P = 0.58$, Table 8.5), and no association with particular microsites is evident.

8.3.3.3 Mixed Forests

Eucalyptus delegatensis and *E. nitida* forests

These forest types are dominated by eucalypts with *P. aspleniifolius* sub-dominant. They are apparently fire-maintained disclimaxes. Non fire adapted species, such as *P. aspleniifolius*, must recolonise the site by dispersal or else survive the fire, either vegetatively or as soil-stored seed. Other rainforest dominants are often poorly represented. Many stands in the north-east (Ellis 1984) and in the central north-west of the state are anthropogenic and less than 200 years old.

The frequencies in size-classes in these stands are skewed toward the smaller sizes (Figure 8.4). Many of these stands are still regenerating and they provide evidence for extended recruitment phases spanning at least 100 years (present age of *Leptospermum* sp. on site).

Bimodal size-class distributions in the absence of gaps, are associated with communities that are recruiting *P. aspleniifolius* in a second phase of regeneration (sites 9MF and 20NE, Figure 8.4b). The second phase, represented by the smallest size-classes, may be a response to the development of suitable microsites for regeneration (e.g. logs or mosses) sometime after the initial recruitment phase had finished or in response to the opening of the maturing eucalypt canopy. These stands differ from the bimodal gap phase stands in pure rainforest in that the regeneration microsite is different and the regeneration is part of population growth rather than its maintenance. It is likely that the initial phase finished when competition from the low shrub and fern layer precluded further regeneration. Evidence of this at site 9MF includes a relatively tall and dense ground

cover amongst which *P. aspleniifolius* seedlings are restricted to logs, mossy rocks and buttresses. The distribution of the second phase of regeneration is therefore influenced by the distribution of these sites rather than reflecting the distribution of seed.

In some cases (Figure 8.4, 51PV and 36OR), the largest (oldest) trees are not sexually mature, which ensures that immigration is the only source of seed; if seed is not stored in the soil. In older stands (Figure 8.4b), mature trees add to the seed available for regeneration. However, dead stems in the smaller size-classes are often indicative that stem density is greater than carrying capacity and hence that recruitment declines as the carrying capacity is reached.

At all stands, spatial aggregation of the smaller size-classes is evident throughout the forest (Table 8.5, Figures 8.7b and 8.8b), while a similar analysis of the larger size-classes indicates a larger scale of pattern and a weaker aggregation. It is likely that this pattern of clustering has evolved as a result of immigrant seed being deposited by birds from perches in the emergent eucalypts and later from perches in older *Phyllocladus*. As the community matures, seed produced at the site adds to the regeneration and the infilling of smaller unoccupied patches produces the change in the scale of pattern.

8.3.3.4 Continuous Regeneration

a. Non forest communities

At the boundary between moorland and forests that contain *P. aspleniifolius*, an invasion of the former by *P. aspleniifolius* is common (Figure 8.4). Copses may develop as isolates in moorland and tend to be dominated by one or two tree species from genera such as *Eucalyptus*, *Leptospermum* or *Banksia*. Mixed ages of *Phyllocladus* are typical of the copses and the dispersion pattern of *Phyllocladus* is aggregated in association with the dominant trees.

At site 11MF (Table 8.5, and Figures 8.7 and 8.8), the aggregated pattern is clearly illustrated. The inter-copse region is sparse heath and *Sphagnum* with a high light regime and abundant *P. aspleniifolius* seed (pers. obs.), but regeneration is absent. The relatively high light environments of these forests at ground level, and the persistence in the use of favoured microsites, suggests that these sites have some quality other than higher light intensity that permits survival and recruitment of seedlings. Micro-relief and its influence on drainage may explain the distribution of copses.

b. Implicate rainforest

At sites which have a reverse J-curve size-class distribution (Figure 8.4, sites 47HT, 38HZ, 48HT), the species composition is diverse and the forest is low with no discernible strata except for a sparse emergent canopy (implicate rainforest, Jarman *et al.* 1984). These sites have mature *Phyllocladus*, and standing and fallen dead trees. Gaps are small and ineffective due to the relatively small stature of the forest and the dense lower strata which often hold the fallen trees well above the ground. The shape of the size-class distribution indicates that the regeneration is continuous. Small moss-covered logs and procumbent live limbs, stump mounds and *Sphagnum* mounds are often foci for regeneration. Adult female trees are associated with clusters of regeneration.

An example of the dispersion of *Phyllocladus* in these forests at site 48HT indicates that the regeneration of *P. aspleniifolius* is clustered around adult *P. aspleniifolius* (Figures 8.7 and 8.8). No regeneration of *P. aspleniifolius* is present under other emergent species which presumably could also act as perch trees. The *Phyllocladus* adults are dispersed in a random pattern (Table 8.5) but may be associated with logs and stump mounds. The exclusive association of *Phyllocladus* seedlings with *Phyllocladus* adults suggests that the regeneration is from locally produced seed dropped from the female tree at the centre of the regeneration cluster. However, the influence of perches and birds is evident as *Phyllocladus* sometimes grows as an epiphyte, particularly on taller *Athrotaxis selaginoides*.

Table 8.5. Probability for seven quadrats that the hypothesis of complete spatial randomness would be rejected when true. The seven sites were chosen as representative of the classes in Figure 8.4.

Site	Regeneration	Mature
	P	P
Q22NE	0.02	0.30
Q44QT	-	0.58
Q23CI	0.02	0.02
Q11MF	0.02	0.02
Q48HT	0.02	0.44
Q15FP	-	0.86
Q10LF	-	0.90

8.3.3.5 Hilltops and Islands.

Consistent features in populations of *P. aspleniifolius* on hilltops are their domination of the site and the similarity in the shape of their size-class frequency distributions which tend towards normality (Figure 8.4, sites 14FP, 15FP, 16NE, 26CH, 32OR, 37OR). Young

populations on hilltops (e.g. site 14FP) reflect an extended recruitment phase maintained by continuous seed immigration from remote parent trees. The density change with age, from as high as 11 633 per ha at site 14FP (maximum size 15 cm dbh) to 1 155 per ha at site 16NE (maximum 40 cm dbh) and 866 per ha at site 15FP (maximum 50 cm dbh.), indicates that there may be greater than 90% attrition during population growth.

On hilltops, where other rainforest dominants are poorly represented, and where there is a lack of emergent perch trees, *Phyllocladus* does not appear to be associated with particular microsites. Table 8.5 indicates that the effect of this is a random distribution of *Phyllocladus* stems which may be the result of reduced competition from other species.

Communities on small islands are geographically similar to communities that are distinctly located on hilltops. After catastrophic disturbance and in the absence of a seed pool, a species must disperse to the island or hilltop from a remote population to be part of the regrowth forest. At the Celery Top Islands (Figure 8.4, sites 32OR, 37OR), *P. aspleniifolius* displays a size-class structure that is similar to the hilltop populations of other areas. The perimeters of the islands are vulnerable to storm damage. *Phyllocladus* is regenerating vigorously around the perimeters.

The similarity in the frequency distribution between the hilltop sites, the island sites, and the eucalypt sites is probably because all are the result of remote seed sources and do not experience significant competition from other rainforest dominants.

8.3.3.6 Secondary *Nothofagus* dominated rainforests.

Eucalyptus spp. are absent from these forests but they may or may not support secondary species such as *Leptospermum* spp. These stands form the boundary between rainforest and more regularly burnt communities such as sclerophyll forests or moorlands (see Jackson (1968) and Mount (1979) for a discussion of the effect of fire frequency in Tasmanian vegetation). The size-class structure is often confined to a relatively small range (Figure 8.4) suggesting that the regeneration period is limited to the immediate post-disturbance period and may reflect strong competition from *Nothofagus cunninghamii*.

Other *Nothofagus*-dominated secondary forests support *Phyllocladus* with an irregular size-class structure (Figure 8.4). Similar sizes tend to be aggregated on the barely recognizable remnants of large stumps (Table 8.5, Figures 8.4 and 8.7). Recently occupied stump mounds are not in obvious canopy gaps. The oldest *Phyllocladus* have

reoccupied stump mounds during the early part of the succession (Figure 8.10). Therefore, the stump mounds do not appear to indicate current or old gap phase recruitment but instead have become favourable regeneration microsites at irregular time intervals.

8.3.4 The population structure and its relationship with floristics and structure.

Figure 8.11 illustrates the density of seedlings and saplings in relation to the relative dominance of *P. aspleniifolius* in the same forest. The 23 sites represent mature rainforests in which recruitment is in the form of population maintenance. The selection is intended to remove the bias toward high seedling numbers on sites that are regenerating after large scale disturbances. The lack of order may be due to differences in the structure of forests that support high percentages of *P. aspleniifolius*, for example implicate forest compared to the hilltop pole stands. This relationship is further explored in Figure 8.12 in which the densities of four size-classes, all less than 10 cm (dbh) for the same selection of sites are compared to the basal area and the density of sizes greater than 10 cm dbh. The sites are arranged in order of decreasing total density of small size-classes (left to right). It can be seen that there is a tendency for sites with the least number of stems less than 10 cm dbh to have higher basal areas of *P. aspleniifolius* represented by a relatively low number of stems. In other words, there is least regeneration in forests with a high basal area of relatively large *P. aspleniifolius*, however this relationship is not absolute, being tempered by a number of sites that support little regeneration in forests with low numbers and basal area of *P. aspleniifolius*. Such inconsistencies continue in the relationship between regeneration mode and floristics.

The first two axes of the MDS (Figure 8.13) indicate the floristic variation is continuous. Although many of these sites are quite distinct physically, the relatively depauperate nature of the Tasmanian rainforest estate results in the generally high floristic similarity (low eigenvalues). This problem is heightened by the bias introduced by the restriction of sampling to the communities in which *P. aspleniifolius* is important. There is, however, separation of some of the assigned groups along the floristic axis, groups 4, 5 and 6 being floristically similar while groups 1, 2, 3 and 8 are separated.

Different regeneration modes in similar floristic groups may be controlled by minor structural variation instigated by the presence or absence of a single species. Small understorey tree species such as *Trochocarpa gunnii*, *Archeria* spp. and the fern *Blechnum wattsi* may produce a conspicuous forest structure by producing a dense, often closed,

stratum. Such closed strata may preclude regeneration of *P. aspleniifolius* from forests in which they occur.



Figure 8.10. An aggregation of mature *P. aspleniifolius* growing on the remains of an old stump mound.

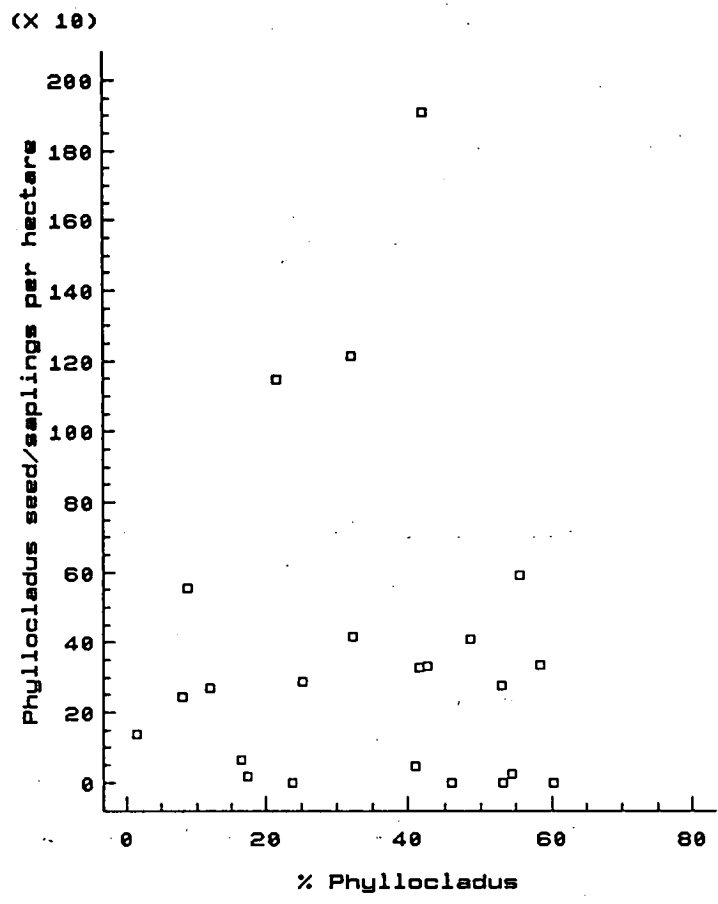
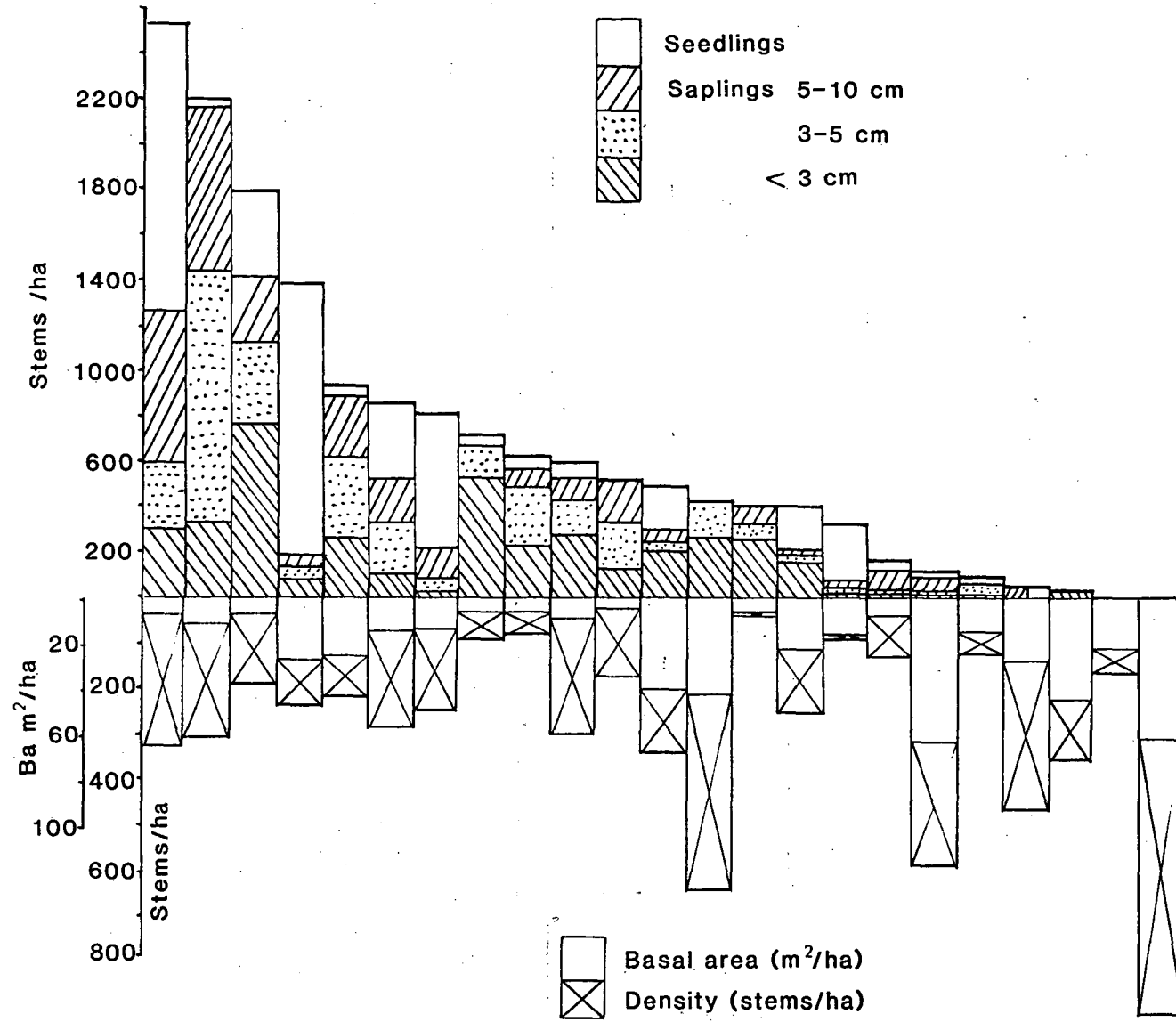


Figure 8.11. Scatter plot for 23 mature sites of the density of seedlings and saplings < 3cm dbh versus the relative dominance of *Phyllocladus aspleniifolius* as a percentage of stems in the dominant canopy.

Figure 8.12. A comparison of 23 mature sites of the number of seedlings and saplings < 3cm, 3-5cm and 5-10cm dbh, in relation to total *Phyllocladus aspleniifolius* basal area ($\text{m}^2 \text{ha}^{-1}$) and density of stems greater than 10cm dbh. Sites are arranged from left to right in order of decreasing total density of stems < 10cm dbh.



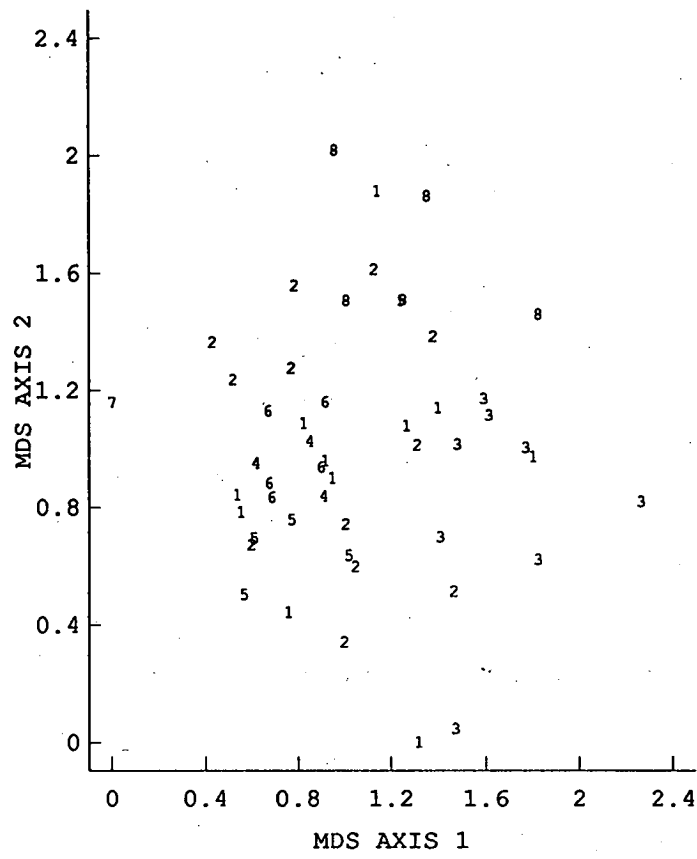


Figure 8.13. Ordination plot of the first two axes from the Multidimensional Scaling procedure of floristic data from 50 sites. Numbers 1-8 correspond to the groups in Figure 8.4.

8.4 Discussion

Given the relationships between sapling height and age, and tree-size and age (Table 8.2, Figure 8.2), the interpretations of size-class distributions (Figure 8.4) are likely to be ecologically meaningful. The sensitivity of *P. aspleniifolius* to fire (Kirkpatrick 1977) suggests that it is unlikely that the influence on size distributions produced by suppression and thinning (Figure 8.4d) would be hiding a cohort structure. Such a complication has been described for fire tolerant taxa by Ogden and Powell (1979). For a fire sensitive taxon, Duncan and Stewart (1992) have demonstrated the hazards when transects cross imperceptible age class boundaries. In these situations, the site history and spatial distribution of size-classes, is important for the interpretation of the size-class distribution.

Phyllocladus aspleniifolius clearly displays greater germination success and recruitment to the sapling pool in association with elevated microsites and in canopy gaps (Table 8.3). Reasons for differential microsite success have often been related to light regimes (Whittaker and Levin 1977, Clayton-Greene 1977). In New Zealand, Clayton-Greene (1977) found that in established vegetation, seedlings, small saplings and poles of the native conifer *Libocedrus bidwillii* are usually found growing on decaying logs and other elevated sites. He measured higher growth rates on elevated sites compared to individuals on the ground. A similar superiority in growth rate of *Phyllocladus* saplings on elevated sites was also found in the present study (Table 8.4). Clayton-Greene recorded equal vigour on open or exposed sites and concluded that *L. bidwillii* may not be as competitive as associated species and that logs reduce root competition and receive more light. However, this conclusion begs the question, why do not the more competitive species occupy the same logs and other elevated sites? Wilson (1988) demonstrated that the microsite had little influence over the short term survival of seed in the rainforests of Queensland. If this were the case in Tasmanian rainforest, then niche separation is likely to involve qualitative attributes of the microsite. These may include, for example, fungal pathogens, the seed bed nutrient status, seed and seedling water relations, and protection from predation (Whittaker and Levin 1977).

The growth rate of *P. aspleniifolius* seedlings is very slow (Figure 8.2). Hence they are vulnerable to removal by the scratching of foraging animals (pers. obs.). Logs, buttresses and old stump mounds may offer protection from such foraging. This may have become increasingly important in Tasmanian wet sclerophyll forests since the introduction of lyrebirds. These birds have been reported to be capable of turning over the forest floor every 1-2 years, while grazing by both introduced and native animals was observed to be

heavy on *Athrotaxis cupressoides* in Tasmania (Cullen and Kirkpatrick 1988). Cameron (1963) also commented on the effect of introduced animals on New Zealand's podocarp forests and more recently Veblen and Stewart (1982) demonstrated their impact. In the present study, animal scratching was noted by the author to be concentrated in tree-fall gaps. Such activity increases the likelihood of the removal of slow-growing seedlings from the gaps. In conjunction with the already considerable pressure of competition from other regenerating species (Read and Hill 1988), seedling removal may explain the relatively poor recruitment rate from the seedling pool to sapling pool in gaps (Table 8.3). While Read and Hill (1988) demonstrate that light intensity is at least correlated with the recruitment of *Phyllocladus* in Tasmania, the qualities and availability of microsites and agents such as damping off and seedling removal cannot be disregarded.

The spatial arrangement and the temporal availability of suitable microsites allows regeneration to occur at different stages of forest development. Therefore, the availability of microsites through time is likely to be a major determinant of the population's age structure in any particular forest. In the classification of regeneration types in this study, a number of sites (Figure 8.4a,b and f) have been interpreted as bimodal or irregular and attributed to younger cohorts responding to gradually opening canopies or the temporally staggered availability of suitable microsites for regeneration. Wardle (1963b) and Clayton-Greene (1977) observed bimodality in the age distributions of *Dacrydium cupressinum* and Matai (Podocarpaceae) beneath opening hardwood canopies in New Zealand.

Pulses of regeneration due to other causes have been recorded for other endemic Tasmanian conifers (Ogden 1985, Gibson 1986). Ogden (1985) argued that *Athrotaxis cupressoides* reflected climatic fluctuations by having regeneration restricted to times with favourable combinations of climatic conditions but persisting between favourable times by virtue of its longevity. For *Phyllocladus*, the absence of seedlings at a number of sites in the presence of a sapling pool (Figure 8.4) may indicate an indirect effect of climate via its correlation with the phenomenon of mast seeding years. There is a large variation in *Phyllocladus* seed production from year to year and between sites which is reflected in the amount of germination from year to year (see chapter 6). There is, therefore, the possibility that the mast seeding habit could result in missed opportunities to occupy suitable microsites if seed is in low supply.

In New Zealand, a number of authors have reported the importance of birds and perch trees in the distribution of podocarps, for example, dead trees in gaps (Beveridge 1973), invasion of secondary *Leptospermum* forest and into copses in heaths at the margins of

forests containing podocarps (Pook 1978). The importance of birds and perches has also been noted in Tasmania (F. Podger pers. comm.). Horn (1974) described copses of even ages scattered in a multi-aged matrix, as not only being determined by safe site frequency but also dispersal characteristics. In the present study, the pattern of *Phyllocladus* appears to reflect the distribution of suitable microsites (Figure 8.7a and c), the spatial distribution of immigrant seed, and the spatial distribution of perches (Figure 8.7b), plus or minus seed produced by mature trees on the site (Figure 8.7d). These factors may interact to some degree at single sites. The result is the evolution of a pattern as the position and number of perches changes as the forest develops and as the *Phyllocladus* themselves become perches and/or seed producers.

Little is known about the disturbance cycles of Tasmanian rainforests. Our present knowledge has, therefore, been limited to the description of the development phase of the forest and to a lesser extent to gap-phase maintenance. Regeneration of species in the absence of exogenic disturbance is dependent upon internal community processes. Often, these processes are correlated with increasing community age and the associated crown senescence but are also related to the structure and floristics of a community. Figure 8.12 illustrates the variability in regeneration success with respect to the importance of *P. aspleniifolius* in mature communities undergoing maintenance regeneration. However, the relationship may be confounded by the strong negative influence over regeneration of the presence of single species which form a closed stratum at or near the ground (ferns) or in the shrub layer (*Trochocarpa gunnii*, *Monotoca glauca* or *Anodopetalum biglandulosum*). The modes of regeneration have been distinguished in terms of pattern (Figure 8.7), microsite and typical population structure (Figure 8.6). Relationships between the modes of regeneration and the structure and floristics of the forests are apparent (Figure 8.13), but by no means are they clear and simple associations. The variability suggests that the continuum of floristics and structure has produced a complex and multi-dimensional variation in the opportunities for regeneration of *P. aspleniifolius*.

Phyllocladus regenerates in gaps in old forests where *Phyllocladus* and *Nothofagus cunninghamii* are co-dominant (Figures 4a and 7a) but fails in *Nothofagus*-dominated forests (callidendrous, Jarman *et al.* 1984) (Read and Hill 1988). Read and Hill (1988) suggest that this is because the light level is too low and that under these conditions *P. aspleniifolius* is excluded by faster growing species. I have personally observed regeneration of *Phyllocladus* in callidendrous forests adjacent to *P. aspleniifolius* dominated forests in which canopy disintegration is advanced and in which there is little competition from understorey species. This observation supports the contention of Read

and Hill (1988), but suggests that *Phyllocladus* and other species might enter these communities as the *Nothofagus* canopy begins to disintegrate.

Read and Hill (1985) suggest that, in the absence of catastrophic disturbance, the dynamics of the implicate rainforests are uncertain because little is known about the ecology of the understorey species or their potential effect on the regeneration of canopy species (see chapter 7). The present study, and Calais and Kirkpatrick (1983), have demonstrated that in these forests *Phyllocladus* regenerates in the absence of gaps and exogenic disturbance (Figures 4c and 7d).

The future of hilltop stands (Figure 8.4d) is uncertain as it is not clear whether such stands are a fire-maintained disclimax or have a more complex ecological basis. No appropriate environmental factors such as light intensity and quality or substrate qualities were measured at hilltop sites. However, four hypotheses may reasonably explain the domination of hilltops by *P. aspleniifolius*. The first may be inherent low soil fertility; a condition generally considered to favour the dominance of *Phyllocladus* (Read and Hill 1988, see Chapter 4), which is exacerbated by down-hill and down-profile leaching of nutrients in areas of high rainfall. Grime (1979) argues that the predominant distribution of a plant on low fertility sites is not merely due to competitive exclusion from more fertile sites but that it is the ability of the plant to conserve the resources and resist the hazards of infertile sites that accounts for the distribution on them.

The second hypothesis involves side-lighting through canopies, an opportunity which is restricted to steep slopes and hilltops (Grubb 1977b). Increased light may improve the success of regeneration.

The third involves the need for uphill movement of seed to recolonise these sites after disturbance by fire. *P. aspleniifolius* has a clear advantage by being effectively bird dispersed. Early access to the site implies potential dominance (Watt 1947).

The fourth involves fungal pathogens; Pook (1978) cited this cause for a similar phenomenon in *P. trichomanoides* in New Zealand, in which the pathogens were not favoured by the relatively dry substrates of ridges.

Beveridge (1973) considered five New Zealand podocarps and identified at least five situations in which podocarp regeneration occurs. These are sparse regeneration in dense forest; frequent regeneration beneath a gradually opening hardwood canopy; a complex cyclic regeneration in gaps; as fire-induced secondary forest and at the ecotone

between forest and heath vegetation. Beveridge also noted the association of podocarp seedlings with perch trees in gaps, on stumps and along dry ridge-tops. Also in New Zealand, Pook (1978) reports abundant regeneration of *Phyllocladus trichomanoides* in *Leptospermum* scrub and on hill tops and ridges where *Agathis australis* is also prevalent.

The results of the present study indicate a set of situations similar to those described by Beveridge and Pook also apply to the regeneration of *Phyllocladus* in Tasmania. However, it is contended that *P. aspleniifolius* alone demonstrates all of the regeneration modes described for the New Zealand podocarps as a whole. This may reflect the breadth of the niche available to *P. aspleniifolius* as a result of the depauperate tree flora and more specifically to the relative lack of well-dispersed podocarp taxa. New Zealand supports at least 17 trees and shrubs in the family Podocarpaceae; whereas Tasmania has five, three of which are almost entirely restricted to the alpine and the fourth, *Lagarostrobos franklinii*, displays a close association with streams and rivers (Gibson and Brown 1991a).

Pook (1978) suggests that in competition with *Agathis australis*, *P. trichomanoides* may be restricted to the early stages of community development. Furthermore, Pook argues that the abundance of *P. trichomanoides* in secondary forests and its poor representation in primary forests supports the contention that it is well adapted to the early stages of forest succession but of short duration in the long-term development of mature forests. Read and Hill (1988) point out that at sites which are only a few hundred years old, the forest has not completed one generation, and in such forests a large proportion of *P. aspleniifolius* is likely to have originated after catastrophic disturbance and will eventually fail to recruit further as the canopy closes. Wardle (1963a) suggests that in the absence of exogenic disturbance populations of podocarps degenerate and eventually become locally extinct. In New Zealand, some consideration has been given to this proposal but no conclusive evidence has been uncovered (Baylis and Mark 1963, Cameron 1963). No evidence of local extinction or observations of degenerating populations have arisen from the present study. Although the theoretical possibility is acknowledged the author believes endogenous non-catastrophic and stochastic events of various scales would provide opportunities for *P. aspleniifolius* to maintain representation in the community, albeit at a reduced density. Furthermore, long-lived tree species, such as *P. aspleniifolius*, may only require very occasional recruitment to maintain a population, or, at least, representation in a forest (Read and Hill 1988, Ogden 1985, Stewart and Rose 1989).

8.5 Conclusion

The size-class distributions of *P. aspleniifolius* in Tasmania's forests indicate that populations in different community types recruit individuals over a range of time frames. It is clear that the opportunities for, and patterns of, regeneration are associated with a variety of microsites. The type and availability of a microsite, and the distribution of seed in a community is related to the floristics and structure of the community. Emergent trees act as a focus for immigrant seed, while the distribution of effective gaps, logs, stump-mounds, moss and litter, and parent trees, in both space and in time, represent opportunities for regeneration which produce a variety of population structures and dispersion patterns. The opportunistic nature of regeneration in this species is supported by its high vagility; an attribute which permits coexistence with other species that are limited to a particular mode of regeneration.

Chapter 9. General Discussion

Distributions

The distribution and phytosociology of *P. aspleniifolius* and *A. biglandulosum* coincide over much of their range. Differences between their distributions are, however, apparent at particular intervals along rainfall and fertility gradients. There is some evidence to suggest that *P. aspleniifolius* is more drought resistant than *A. biglandulosum*. *P. aspleniifolius* occurs in drier areas than *A. biglandulosum*. However, *A. biglandulosum* does not reduce stomatal conductance more than *P. aspleniifolius* on summer days, although its stomatal density and lack of stomatal protection is more typical of a mesic anatomy than that of *P. aspleniifolius*. Inhibition of photosynthesis may be expected where water shortage is prolonged. Alternatively, the occurrence of *P. aspleniifolius* in drier areas than *A. biglandulosum*, often also in the absence of *Nothofagus cunninghamii*, could be attributed to historic displacement, or the exclusion of *A. biglandulosum* by intense fire with poor vagility preventing its reinvasion.

P. aspleniifolius displays a typical stress tolerant nutrient physiology, being relatively insensitive to the concentration of nutrients, while *A. biglandulosum* shows a preference for acidic substrates. The different responses suggest that habitat differentiation might be expected but phytosociological and distributional data suggest that it is barely evident. Where they coexist differences in resource gain should be expressed in their relative performance, yet both appear to perform best on similar sites. These results, and the extraordinary range of communities in which *P. aspleniifolius* and *A. biglandulosum* coexist over a range of habitats, suggests that differentiation in the use of the nutrient resource does not play a primary role in determining the distribution of these two species. One exception is where they are excluded from rainforest on Tertiary basalts.

Secondary influences including fire, and the availability of opportunities for regeneration, explain some of the differences in distribution. For example, *P. aspleniifolius* occurs on basalts in the absence of *A. biglandulosum*, and most other poorly dispersed wet forest taxa, as a result of the removal of callidendrous rainforest by Aboriginal fires (Jones 1969, Ellis 1984). *A. biglandulosum* occurs on basalts along creeklines amid callidendrous rainforest from which *P. aspleniifolius* is competitively excluded (Read and Hill 1988). A creekline habitat is often taken to indicate high water needs. However, correlation does not equate to causation. Callidendrous rainforest occurs on sites with adequate rainfall for the growth of *A. biglandulosum*. Its presence in this habitat may be due to the prevalence of physical disturbances such as failing creek banks and tree-falls. Other wet forest taxa which respond to

physical disturbance survive in related environments in Tasmania. For example, *Acacia melanoxylon*, which regenerates prolifically after forest fires, also does well along riverside levees which are prone to strong flood currents. The absence of *P. aspleniifolius* from this environment may be due to the return period of floods being less than the time for *P. aspleniifolius* to reach sexual maturity and competitive exclusion of immigrant propagules by the rapidly growing *A. melanoxylon*.

In the present study, the vagility of *P. aspleniifolius* is clearly and repeatedly demonstrated to be of the utmost importance to its distribution at small and large spatial and temporal scales. Vagility has been emphasised in the distribution and composition of post glacial forests in Tasmania (Macphail 1980) and New Zealand (McGlone 1985). Some current distributions of Tasmanian endemic taxa are also suggested to be in climatic disequilibrium due to various degrees of vagility (Kirkpatrick and Brown 1984). In the absence of other generalist Podocarpaceae, *P. aspleniifolius* was able to dominate the post glacial reafforestation of Tasmanian wet forest, with the less vagile *A. biglandulosum* associating with it after a considerable time (Macphail 1980). However, the climatic and distributional correlation demonstrated in chapter three suggests the range of *A. biglandulosum* is now in climatic disequilibrium. This is likely to be as a result of extinction, caused by the Pleistocene glacial times, from the now climatically suitable habitat island in the north-east of Tasmania.

Cause of coexistence

The results of the growth trial in chapter four, in which high and low nutrient and pH treatments were imposed, indicate that *P. aspleniifolius* and *A. biglandulosum* are not trophic equivalents with regard to nutrients, although this does not preclude the possibility of competition. They do not stratify the light resource. Hence, they may often be in direct competition for light. The demonstrated "stress tolerant" nutrient physiology of *P. aspleniifolius* and *A. biglandulosum* is not a direct causal factor for their prominence in forests on infertile sites. The conditions in the implicate forests mirror those that are considered to promote species richness indirectly by the slow expression of site dominance (Shmida and Ellner 1984). They include low fertility, vacant microsites suitable for regeneration and long-lived species. In this environment, species may not be required to interact in the early life-stages, and may thereby avoid competition. Grime (1979) suggests that in similar situations many of the species are likely to be poor competitors, with slow growth rates and a tolerance of low resource levels. They rely for their persistence on the decline in vigour of potentially more vigorous competitors, which dominate fertile substrates. In essence, the infertile sites provide a temporal refuge from competitive exclusion. The

probability of endogenous and exogenous disturbance providing opportunities for *P. aspleniifolius* and *A. biglandulosum* to regenerate within their long life spans is also high.

In Tasmania, Jackson (1968) suggested that in the absence of fire, nutrient levels would rise and succession would slowly continue, eventually supporting a *Nothofagus cunninghamii* dominated forest of simple floristics. Jackson's hypothesis reflects the direction predicted on infertile substrates by Grime (1979) and Tilman (1982) and Shmida and Ellner (1984). But Jackson suggests slow enrichment of soils rather than the slow expression of competitive advantage will bring about simplification of the community.

A number of communities in this study, including many implicate forests, are less than a complete generation old, indicated by the presence of eucalypts and/or other secondary Myrtaceae. Relatively even-sized stands of *P. aspleniifolius*, or *Nothofagus cunninghamii* cannot be assumed to be regrowth in response to exogenic disturbance, as synchronous mortality and cohort replacement has been demonstrated for a number of species (Ogden *et al.* 1987). In older communities and communities on fertile substrates, the maintenance of populations is favoured by differentiation in the regeneration niche. Differences are reflected in the spatial and temporal separation of regeneration and its relationship to community processes.

It is difficult to determine which differences between species are important for coexistence in systems where stochastic events are likely to be important, and where environmental constancy and species equilibrium are not likely to be realities. Furthermore, the breadth of floristic association between the two species has presented diverse regeneration opportunities which may be specific products of one community or another. Despite this complexity, the contrasts in life history characteristics and the regeneration niche are manifest in ways that are consistent and are likely to contribute to the coexistence of *P. aspleniifolius* and *A. biglandulosum*.

Fundamental differences in the phenological niche of *P. aspleniifolius* and *A. biglandulosum*, including dissimilar pollination and dissimilar dispersal mechanisms, clearly exclude competition at this early and critical life stage. Comparison of phenological strategies does not indicate any inherent advantage to either species. The effect of seed predation, poor seed dispersal and rare seedling establishment does, however, leave *A. biglandulosum* at an apparent disadvantage in relation to the chances of sexually produced propagules being present at the time of an opportunity for regeneration.

Although the different pollination and dispersal mechanisms of these two species prevent competition for vectors, the evolution of the flower and its attendant directed pollination theoretically provides *A. biglandulosum* with an advantage over the dioecious, wind-pollinated *P. aspleniifolius*. However, unlike diverse tropical forests, the depauperate forests of temperate zones have only small distances between conspecifics, distances over which, it is argued, there is no apparent disadvantage for wind pollinated taxa (Regal 1979). The conspicuous red cone and fleshy aril of *P. aspleniifolius* compared to the inconspicuous and dehiscent green fruit of *A. biglandulosum*, highlight a strategic division in dispersal mechanism with spatial consequences for regeneration.

Temporal variation in sexual reproduction is also evident. Both species appear to be impeded in their ability to produce regular seed crops. The mast seeding pattern, such as displayed by *P. aspleniifolius*, is argued to be a means of avoiding the loss of much of the seed crop to predators (Janzen 1971). *A. biglandulosum* is probably a more consistent producer, but suffers large losses to a predatory moth and to birds.

The effect of masting is exacerbated by poor seed viability in non-mast years (Nilsson and Wastljung 1987). Masting in *P. aspleniifolius* was reflected in the abundance of germination two years after the mast. If that pattern is consistent, then the density of viable seed present when an opportunity for regeneration arises is reduced in intervening years. Assuming that the amount of predation of the seeds of *A. biglandulosum* also varies from year to year, the balance in competition for space could fluctuate, sometimes being tipped in favour of *A. biglandulosum*. This notion of changing favours in competition was recognised by Hutchinson (1961) who describes safe years as well as safe sites as affecting the coexistence of species in competition for space.

Interspecific competition during regeneration from seed is mainly relevant after catastrophic events have killed the incumbent trees. In other circumstances, the most important difference between the regeneration strategies of *P. aspleniifolius* and *A. biglandulosum* is the role of vegetative reproduction and proliferation.

Where physical disturbance to an existing population is encountered, the vegetative response of *A. biglandulosum* is most successful. This is evident along creeklines and in tree-fall gaps. Its prolific space-filling ability, and subsequent reinforcement by layering and suckering, is an opportunistic means of holding, and extending, its possession of the site.

In contrast, the high vagility of the obligate seed regenerator, *P. aspleniifolius*, allows it to take up regeneration opportunities well away from the parent tree. The uneven distribution of seed, and the distribution and range of suitable microsites provide a probabilistic basis for its dispersion through the community.

Differentiation of strategies between dispersers to space and holders of space has been widely recognised as promoting coexistence between trophic equivalents and between species of different competitive abilities (Levin 1976, Whittaker and Goodman 1979, Pickett 1980, Schmida and Ellner 1984). The particular microsite associations and consequent aggregation of *P. aspleniifolius* seedlings, and ensuing adults, also serves to separate the species at the all-important regeneration stage when competition is usually most apparent (Watt 1947).

In the gap-phase, which both species exploit, chance has been demonstrated to play a vital role in the persistence of *A. biglandulosum*. To retain site possession *A. biglandulosum* needs to have established on the site prior to the formation of a gap if it is to reinforce its possession of the site in the event of tree-fall. *P. aspleniifolius*, on the other hand, has widely dispersed seed, with some aggregations being correlated with perch trees. Consequently seed should be present in gaps, more often than would be expected due to chance, because the perches are often the dominant trees which produce gaps when they fall. Where *A. biglandulosum* is established *P. aspleniifolius* is unable to win the site as an extremely slow growing germinant competing against relatively fast vegetative regeneration and proliferation.

Given its site-holding potential, the absence of widespread dominance by *A. biglandulosum* presents a problem. Its relatively short life-span compared to dominant species may be the key. It is not certain whether *A. biglandulosum* can hold a site for longer than a single generation. In Chile, Veblen (1982) found that *Chusquea* bamboo proliferates in an environment similar to *A. biglandulosum*. He noted differences in its density and dispersion depending upon the structure of the forest. Where shade tolerant species formed a subdominant canopy, bamboos were scattered in light wells and were partly dependent upon gaps for persistence. But, where the shade tolerant species were absent, an even and high percentage cover was evident. As demonstrated in this research, the architecture and abundance of *A. biglandulosum* varies with forest structure, and patchiness in cover creates different chances of *A. biglandulosum* occupying a tree-fall gap. Where a dense patch of *A. biglandulosum* develop in response to tree-fall it may eventually relinquish possession of the site to the forest dominants if no further disturbance to the patch occurs within its life-span. Hence, the patchiness of its distribution through the forest would be maintained.

For bamboo species and *Weinmannia racemosa* Veblen (1982) and Wardle (1966) indicate inhibition of the establishment of seedlings of other species due to the light reduction and characteristics of litter produced by these proliferators. Webb (1953) indicated the possibility of *A. biglandulosum* producing an acid high aluminium humus which could inhibit growth of other plants. The data gained in the present research, however, are equivocal. Both reduced light levels and litter density would be expected to ameliorate as the stand thins out. In New Zealand, podocarp species emerge through dense stands of *Weinmannia racemosa* after density dependent thinning (Wardle 1966, Stewart and Veblen 1982). This is a late entry for what is often considered to be a colonising group. Similarly, seedlings of other species may re-enter the *A. biglandulosum* thicket at this point, eventually dominating and outliving *A. biglandulosum*. The continuance of the dynamic process would support a "shifting steady state" of discrete areas at different developmental stages *sensu* Bormann and Lickens (1979). This situation describes a cyclic succession in which the community as a whole maintains a stable structure and floristic composition, the distribution of species being dependent upon suitable opportunities in response to stochastic disturbance events at all scales *sensu* Pickett (1980).

Although neither *P. aspleniifolius* nor *A. biglandulosum* was suppressed by the other in pot trials, the faster growth rate and taller habit of *P. aspleniifolius* and the vegetative resprouting of *A. biglandulosum* are likely to result in differential success in the field. The outcome is probably dependent upon the type of microsite, seed availability, and degree and type of disturbance. One situation where this scenario may be acted out is in stands where *P. aspleniifolius* is dominant over *A. biglandulosum* scrub with only a few scattered associated species. The relatively even size structure of *P. aspleniifolius* in these forests indicates a post catastrophic genesis. Their aggregation is associated with elevated microsites. It is this relationship that is likely to explain both the association of *P. aspleniifolius* with a vigorous and high cover of *A. biglandulosum* as well as the dominance of *P. aspleniifolius* rather than *N. cunninghamii*; the *N. cunninghamii* being largely excluded by the *A. biglandulosum* scrub in the absence of suitable microsites for establishment.

Following a catastrophic disturbance by fire in thamnic rainforest, *A. biglandulosum* recovers as clusters of fire-induced coppice with the same dispersion as the former stand. In contrast, the full range of microsites would be available to *P. aspleniifolius*, and consequently a relatively even-aged and regularly dispersed stand will develop from immigrant seed and seed surviving in safe sites, such as in peat and in stump mounds. Subsequent mortality may be greater between favoured microsites, thus leading to a clumping of individuals on these safe sites. In the absence of further catastrophic disturbance the aggregation would be maintained by tree replacement

being confined to favoured microsites. Thus the differing patterns of dispersion between two species promotes coexistence by reducing competitive interaction.

Interestingly, microsite specificity of *P. aspleniifolius* is most apparent in the less diverse thamnian communities on moderately to highly fertile substrates, where competition from vigorous competitors is expected to be most intense (*sensu* Grime 1979). The broader range of microsites occupied by *P. aspleniifolius* on infertile substrates may reflect the limitations imposed by resource shortages and the subsequent alleviation, or at least postponement, of direct competition via the factors influencing slow dynamics.

Conclusion

P. aspleniifolius and *A. biglandulosum* do not compete for pollinators or dispersal vectors. The contrasts at this early stage of reproduction are reflected in their spatial and temporal patterns of regeneration. In particular, the dependence upon seeds for regeneration of *P. aspleniifolius* and its high vagility, compared to site holding capability and low vagility of *A. biglandulosum* has been shown to be important in promoting coexistence

Phenological, and physiological attributes of these species combine with community processes to conform with the notion of the non-equilibrium coexistence of plants (Pickett 1980). Various scales of disturbance have proved to be important to the coexistence of *P. aspleniifolius* and *A. biglandulosum*. Fallen trees are implicated in the production of at least three regeneration microsites utilized by *P. aspleniifolius*; gaps, logs and stump mounds. Tree-fall is also a stimulus to the regeneration of *A. biglandulosum*. It is the tree-fall gap that is the site of greatest potential competition between *P. aspleniifolius* and *A. biglandulosum*. Prior occupation and differential dispersal of seed determines the outcome in this event. The small scale opportunities, particularly the availability of suitable regeneration microsites, were identified as important for population maintenance. Catastrophic disturbances produce extensive renewal for populations. Patch dynamics at various scales are an important factor in species richness contributing substantially to the 'non-equilibrium' coexistence in many communities (Whittaker and Levin 1977, Pickett 1980, Caswell 1982).

The prominence of the association between *P. aspleniifolius* and *A. biglandulosum* on infertile sites was correlated with relative insensitivity to nutrient levels compared to *Nothofagus cunninghamii*. The slow dynamics of competitive exclusion have been evoked to explain their persistence on such sites.

The opportunity for widespread coexistence across a range of communities along extended intervals of various environmental gradients has been provided by Tertiary and Pleistocene environmental fluctuations. The extinction of many potential competitors has allowed expansion of the realized niches of the resilient remnant species.

Different opportunities presented by different communities have produced various spatial and demographic relationships between the two species. Some regeneration opportunities are community specific, and consequently, the greater the number of communities in which a species exists the greater the diversity of regeneration opportunities may be. It is this diversity of opportunities combined with the contrasting aspects of the autecologies of *P. aspleniifolius* and *A. biglandulosum* that provide the basis to their coexistence.

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Appendix 1.

The floristic composition of rainforest and wet eucalypt forest communities in which *Phyllocladus aspleniifolius* and *Anodopetalum biglandulosum* are characteristic.

Rainforest (Jarman et al. 1984, 1991)

Thamnic 1.1

Dominant species: *Nothofagus cunninghamii*, *Eucryphia lucida*, *Phyllocladus aspleniifolius*, *Atherosperma moschatum*

Other species: *Anodopetalum biglandulosum*, *Anopterus glandulosus*, *Cenarrhenes nitida*, *Tasmannia lanceolata*, *Trochocarpa gunnii*

Structure: Open forest

T1.2

Dominant species: *Nothofagus cunninghamii*, *Eucryphia lucida*, *Phyllocladus aspleniifolius*

Other species: *Anodopetalum biglandulosum*, *Richea pandanifolia*, *Orites diversifolia*, *Anopterus glandulosus*, *Cenarrhenes nitida*, *Tasmannia lanceolata*, *Trochocarpa gunnii*

Structure: Open forest

T1.3

Dominant species: *Athrotaxis selaginoides*

Other species: *Anodopetalum biglandulosum*, *Anopterus glandulosus*, *Cenarrhenes nitida*, *Tasmannia lanceolata*, *Trochocarpa gunnii*

Structure: Closed forest

T1.4

Dominant species: *Lagarostrobos franklinii*, *Nothofagus cunninghamii*

Other species: *Anodopetalum biglandulosum*, *Anopterus glandulosus*, *Cenarrhenes nitida*, *Tasmannia lanceolata*, *Trochocarpa gunnii*

Structure: Open forest

T3.1

Dominant species: *Nothofagus cunninghamii*, *Eucryphia lucida*, *Phyllocladus aspleniifolius*, *Atherosperma moschatum*

Other species: *Anopterus glandulosus*, *Microsorium diversifolium*, *Rumohra adiantiformis*, *Blechnum wattsii*, *Cenarrhenes nitida*, *Monotoca glauca*, *Trochocarpa gunnii*, *Cyathodes juniperina*, *Aristotelia peduncularis*, *Trochocarpa cunninghamii*, *Hymenophyllum australe*, *H. rarum*, *Grammitis billardieri*

Structure: Closed forest

T4.1

Dominant species: *Nothofagus cunninghamii*, *Eucryphia lucida*, *Atherosperma moschatum*, *Phyllocladus aspleniifolius*

Other species: *Archeria eriocarpa*, *Anopterus glandulosus*, *Anodopetalum biglandulosum*, *Trochocarpa gunnii*, *Cenarrhenes nitida*, *Acianthus* sp., *Uncinia tenella*, *Blechnum wattsii*, *Hymenophyllum rarum*, *Grammitis billardieri*

Structure: Closed forest

T6.1

Dominant species: *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*, *Eucryphia lucida*

Other species: *Trochocarpa cunninghamii*, *Trochocarpa gunnii*, *Atherosperma moschatum*, *Cenarrhenes nitida*, *Telopea truncata*, *Tasmannia lanceolata*, *Drymophila cyanocarpa*

Structure: Closed forest

T7.1

Dominant species: *Phyllocladus aspleniifolius*, *Nothofagus cunninghamii*

Other species: *Eucryphia lucida*, *Phebalium squameum*, *Leptospermum* spp., *Cenarrhenes nitida*, *Monotoca glauca*, *Cyathodes juniperina*, *Trochocarpa cunninghamii*, *Blechnum watsii*, *Dianella tasmanica*, *Grammitis billardieri*, *G. magellanica*, *Hymenophyllum rarum*, *H. marginatum*

Structure: Open forest

T8.1

Dominant species: *Phyllocladus aspleniifolius*, *Nothofagus cunninghamii*, *Eucryphia lucida*

Other species: *Cenarrhenes nitida*, *Anopterus glandulosus*, *Cyathodes juniperina*, *Trochocarpa gunnii*, *T. cunninghamii*, *Prionotes cerinthoides*, *Blechnum watsii*

Structure: Closed forest

Implicate 1.1

Dominant species: *Phyllocladus aspleniifolius*, *Nothofagus cunninghamii*, *Eucryphia lucida*, *E. milliganii*, *Leptospermum* spp.

Other species: *Agastachys odorata*, *Atherosperma moschatum*, *Cenarrhenes nitida*, *Anopterus glandulosus*, *Anodopetalum biglandulosum*, *Archeria eriocarpa*, *A. hirtella*, *Trochocarpa gunnii*, *Olearia persoonioides*, *Richea pandanifolia*, *Monotoca submutica*, *Coprosma nitida*, *Cyathodes juniperina*, *Trochocarpa cunninghamii*, *Aristotelia peduncularis*, *Pseudopanax gunnii*, *Tetracarpaea tasmanica*, *Prionotes cerinthoides*, *Gahnia grandis*, *Blechnum watsii*, *Grammitis billardieri*, *Hymenophyllum rarum*, *H. marginatum*

Structure: Open forest

I1.3

Dominant species: *Athrotaxis selaginoides*, *Richea pandanifolia*, *Phyllocladus aspleniifolius*

Other species: *Agastachys odorata*, *Olearia persoonioides*, *Monotoca submutica*, *Coprosma nitida*, *Cyathodes juniperina*, *Trochocarpa cunninghamii*, *Prionotes cerinthoides*, *Blechnum watsii*, *Grammitis billardieri*, *Hymenophyllum peltatum*

Structure: Open forest

I2.1

Dominant species: *Athrotaxis selaginoides*, *Diselma archeri*, *Phyllocladus aspleniifolius*, *Richea pandanifolia*, *Nothofagus gunnii*

Other species: *Agastachys odorata*, *Anopterus glandulosus*, *Archeria hirtella*, *A. eriocarpa*, *A. serpyllifolia*, *Cenarrhenes nitida*, *Coprosma nitida*, *Cyathodes juniperina*, *Tasmannia lanceolata*, *Olearia persoonioides*, *Telopea truncata*, *Richea pandanifolia*, *Tetracarpaea tasmanica*, *Trochocarpa gunnii*, *Trochocarpa cunninghamii*, *Uncinia tenella*, *Uncinia compacta*, *Blandfordia punicea*, *Astelia alpina*, *Gahnia grandis*, *Blechnum watsii*, *Grammitis billardieri*, *Hymenophyllum rarum*, *Apteroptis* sp.

Structure: Low forest

I3.1

Dominant species: *Leptospermum lanigerum*, *Phyllocladus aspleniifolius*, *Nothofagus cunninghamii*, *Eucryphia lucida*

Other species: *Atherosperma moschatum*, *Anodopetalum biglandulosum*, *Anopterus glandulosus*, *Tasmannia lanceolata*, *Aristotelia peduncularis*, *Pimelea drupacea*, *Coprosma nitida*, *Trochocarpa cunninghamii*, *Blechnum watsii*, *Grammitis billardieri*, *Hymenophyllum rarum*, *H. australe*, *Hydrocotyle javanica*, *H. pterocarpa*, *Callitriche brachycarpa*

Structure: Open forest

I4.1

Dominant species: *Phyllocladus aspleniifolius*, *Nothofagus cunninghamii*, *Eucryphia lucida*

Other species: *Anodopetalum biglandulosum*, *Trochocarpa cunninghamii*, *Trochocarpa gunnii*, *Prionotes cerinthoides*, *Cenarrhenes nitida*, *Anopterus glandulosus*, *Drymophila cyanocarpa*, *Grammitis billardieri*, *Blechnum watsii*

Structure: Open forest

Callidendrous/thamnic T2

Dominant species: *Nothofagus cunninghamii*, *Atherosperma moschatum*

Other species: *Anodopetalum biglandulosum*, *Polystichum proliferum*,

Structure: Open forest

CT3

Dominant species: *Phyllocladus aspleniifolius*, *Nothofagus cunninghamii*

Other species: *Hymenophyllum peltatum*, *H. rarum*, *Grammitis billardieri*, *Acianthus viridus*

Structure: Closed forest

CT4

Dominant species: *Phyllocladus aspleniifolius*

Other species: *Cenarrhenes nitida*, *Telopea truncata*, *Pittosporum bicolor*, *Oxalis magellenica*,

Structure: Closed forest

Wet eucalypt forests (Kirkpatrick et al. 1988)

1.

Dominant species: *Eucalyptus brookerana*, *Phyllocladus aspleniifolius*, *Acacia melanoxylon*, *Nothofagus cunninghamii*, *Atherosperma moschatum*, *Eucryphia lucida*

Other species: *Anodopetalum biglandulosum*, *Monotoca glauca*, *Trochocarpa cunninghamii*, *Melaleuca squarrosa*, *Cyathodes juniperina*, *Anopterus glandulosus*, *Cenarrhenes nitida*, *Phebalium squameum*, *Blechnum watsii*, *Hymenophyllum rarum*, *H. cupressiforme*, *Gahnia grandis*

Structure: Tall open forest

2.

Dominant species: *Eucalyptus coccifera*, *E. delegatensis*, *E. subcrenulata*, *Phyllocladus aspleniifolius*

Other species: *Tasmannia lanceolata*, *Telopea truncata*, *Coprosma nitida*, *Pultenaea juniperina*, *Hakea lissosperma*, *Leptospermum lanigerum*, *Cyathodes parvifolia*, *Pittosporum bicolor*, *Polystichum proliferum*, *Poa labillardieri*, *Geranium potentilloides*, *Viola hederacea*

Structure: Open forest

3.

Dominant species: *Eucalyptus coccifera*, *E. delegatensis*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*, *E. subcrenulata*, *Atherosperma moschatum*, *E. gunnii*

Other species: *Telopea truncata*, *Leptospermum lanigerum*, *Trochocarpa cunninghamii*, *Bauera rubioides*, *Monotoca aff. linifolia*, *Coprosma nitida*, *Gaultheria hispida*, *Hakea lissosperma*, *Tasmannia lanceolata*, *Cyathodes juniperina*, *Tetratheca tasmanica*, *Orites revoluta*, *Polystichum proliferum*, *Gahnia grandis*

Structure: Open forest

4.

Dominant species: *Eucalyptus coccifera*, *E. subcrenulata*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*

Other species: *Atherosperma moschatum*, *Anodopetalum biglandulosum*, *Trochocarpa cunninghamii*, *Cyathodes glauca*, *Cyathodes parvifolia*, *Cenarrhenes nitida*, *Leptospermum lanigerum*, *Coprosma nitida*, *Orites diversifolia*, *Richea pandanifolia*, *Olearia persoonioides*, *Telopea truncata*, *Tasmannia lanceolata*, *Gaultheria hispida*,

Prionotes cerinthoides, *Aristotelia peduncularis*, *Eucryphia milligani*, *Pittosporum bicolor*, *Blechnum watsii*, *Grammitis billardieri*, *Polystichum proliferum*, *Gahnia grandis*

Structure: Open forest

5.

Dominant species: *Eucalyptus delegatensis*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*

Other species: *Acacia dealbata*, *Atherosperma moschatum*, *Dicksonia antarctica*, *Histiopteris incisa*, *Blechnum watsii*, *Polystichum proliferum*, *Gahnia grandis*

Structure: Tall open forest

6.

Dominant species: *Eucalyptus delegatensis*, *Phyllocladus aspleniifolius*, *Nothofagus cunninghamii*, *Eucryphia lucida*

Other species: *Atherosperma moschatum*, *Anodopetalum biglandulosum*, *Cenarrhenes nitida*, *Trochocarpa cunninghamii*, *Blechnum watsii*, *Grammitis billardieri*, *Hymenophyllum peltatum*, *Gahnia grandis*

Structure: Tall open forest

7.

Dominant species: *Eucalyptus delegatensis*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*, *Eucryphia lucida*, *Eucalyptus obliqua*

Other species: *Atherosperma moschatum*, *Anodopetalum biglandulosum*, *Monotoca glauca*, *Telopea truncata*, *Cenarrhenes nitida*, *Aristotelia peduncularis*, *Cyathodes juniperina*, *Anopterus glandulosus*, *Phebalium squameum*, *Pittosporum bicolor*, *Trochocarpa cunninghamii*, *Cyathodes glauca*, *Trochocarpa gunnii*, *Blechnum watsii*, *Grammitis billardieri*, *Hymenophyllum rarum*, *Drymophila cyanocarpa*

Structure: Tall open forest

8.

Dominant species: *Eucalyptus delegatensis*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*

Other species: *Telopea truncata*, *Coprosma nitida*, *Cyathodes parvifolia*, *Tasmannia lanceolata*, *Pittosporum bicolor*, *Polystichum proliferum*, *Libertia pulchella*, *Drymophila cyanocarpa*

Structure: Tall open forest

9.

Dominant species: *Eucalyptus delegatensis*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*

Other species: *Cyathodes parvifolia*, *Telopea truncata*, *Pultenaea juniperina*, *Tasmannia lanceolata*, *Coprosma nitida*, *Leptospermum lanigerum*, *Polystichum proliferum*, *Poa labillardieri*, *Hydrocotyle sibthorpioides*, *Geranium potentilloides*, *Viola hederacea*, *Oxalis lactea*

Structure: Open forest

10.

Dominant species: *Eucalyptus delegatensis*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*

Other species: *Telopea truncata*, *Hakea lissosperma*, *Pultenaea juniperina*, *Monotoca glauca*, *Leptospermum lanigerum*, *Cyathodes parvifolia*, *Bauera rubioides*, *Phebalium squameum*, *Gahnia grandis*

Structure: Open forest

11.

Dominant species: *Eucalyptus delegatensis*, *E. coccifera*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*, *Eucalyptus subcrenulata*

Other species: *Hakea lissosperma*, *Coprosma nitida*, *Pittosporum bicolor*, *Oxylobium ellipticum*, *aultheria hispida*, *Telopea truncata*, *Orites revoluta*, *Tasmannia lanceolata*, *Monotoca aff. linifolia*, *Cyathodes juniperina*, *Trochocarpa thymifolia*, *Leptospermum lanigerum*, *Olearia phlogopappa*, *Olearia pinifolia*, *Rubus gunnianus*, *Gnaphalium umbricola*

Structure: Open forest

12.

Dominant species: *Eucalyptus gunnii*, *Phyllocladus aspleniifolius*, *Nothofagus cunninghamii*, *Eucalyptus coccifera*, *E. delegatensis*, *Athrotaxis selaginoides*

Other species: *Telopea truncata*, *Trochocarpa cunninghamii*, *Orites revoluta*, *Coprosma nitida*, *Gaultheria hispida*, *Cyathodes parvifolia*, *Leptospermum lanigerum*, *Polystichum proliferum*, *Blechnum penna-marina*, *Lycopodium fastigiatum*

Structure: Open forest/Mixed forest

13.

Dominant species: *Eucalyptus gunnii*, *E. delegatensis*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*, *Eucalyptus rodwayi*, *E. subcrenolata*, *E. coccifera*

Other species: *Telopea truncata*, *Leptospermum lanigerum*, *Monotoca aff. linifolia*, *Cyathodes juniperina*, *Coprosma nitida*, *Monotoca glauca*, *Pittosporum bicolor*, *Pultenaea juniperina*, *Tasmannia lanceolata*, *Hakea lissosperma*, *Lissanthe montana*, *Lomatia polymorpha*, *Hibbertia procumbens*, *Blechnum nudum*, *Lycopodium fastigiatum*, *Gahnia grandis*, *Drymophila cyanocarpa*, *Rubus gunnianus*, *Stylidium graminifolium*, *Viola hederacea*

Structure: Open forest

14.

Dominant species: *Eucalyptus nitida*, *Phyllocladus aspleniifolius*, *Nothofagus cunninghamii*, *Eucryphia lucida*

Other species: *Anodopetalum biglandulosum*, *Cenarrhenes nitida*, *Phebalium squameum*, *Cyathodes juniperina*, *Leptospermum glaucescens*, *Anopterus glandulosus*, *Monotoca glauca*, *Trochocarpa cunninghamii*, *T. gunnii*, *Tasmannia lanceolata*, *Melaleuca squarrosa*, *Aristotelia peduncularis*, *Blechnum wattsi*, *Gleichenia microphylla*, *Grammitis billardieri*, *Hymenophyllum rarum*, *Gahnia grandis*, *Drymophila cyanocarpa*

Structure: Open forest

15.

Dominant species: *Eucalyptus nitida*, *Phyllocladus aspleniifolius*, *Nothofagus cunninghamii*

Other species: *Atherosperma moschatum*, *Monotoca glauca*, *Phebalium squameum*, *Pomaderris apetala*, *Anopterus glandulosus*, *Cenarrhenes nitida*, *Leptospermum scoparium*, *Blechnum wattsi*, *Pteridium esculentum*, *Dicksonia antarctica*, *Gleichenia microphylla*, *Gahnia grandis*

Structure: Tall open forest/Mixed forest

16.

Dominant species: *Eucalyptus obliqua*, *Nothofagus cunninghamii*, *Anodopetalum biglandulosum*, *Atherosperma moschatum*, *Eucryphia lucida*, *Acacia melanoxylon*, *Phyllocladus aspleniifolius*

Other species: *Anopterus glandulosus*, *Coprosma quadrifida*, *Pomaderris apetala*, *Dicksonia antarctica*, *Microsorium diversifolium*, *Blechnum wattsi*, *Rumohra adiantiformis*, *Grammitis billardieri*, *Hymenophyllum rarum*, *Histiopteris incisa*, *Hymenophyllum flabellatum*, *Polystichum proliferum*, *Blechnum nudum*

Structure: Mixed forest

17.

Dominant species: *Eucalyptus obliqua*, *Nothofagus cunninghamii*, *Eucryphia lucida*, *Atherosperma moschatum*, *Phyllocladus aspleniifolius*, *Anodopetalum biglandulosum*

Other species: *Anopterus glandulosus*, *Cenarrhenes nitida*, *Trochocarpa cunninghamii*, *Monotoca glauca*, *Blechnum watsii*, *Grammitis billardieri*, *Dicksonia antarctica*, *Gahnia grandis*

Structure: Mixed forest

18.

Dominant species: *Eucalyptus obliqua*, *Eucryphia lucida*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*, *Acacia melanoxylon*

Other species: *Cyathodes juniperina*, *Monotoca glauca*, *Phebalium squameum*, *Telopea truncata*, *Anodopetalum biglandulosum*, *Cenarrhenes nitida*, *Leptospermum nitidum*, *Orites diversifolia*, *Tasmannia lanceolata*, *Trochocarpa cunninghamii*, *Agastachys odorata*, *Trochocarpa gunnii*, *Blechnum watsii*, *Pteridium esculentum*, *Blechnum nudum*, *Gahnia grandis*, *Gleichenia microphylla*, *Billardiera longiflora*

Structure: Mixed forest

19.

Dominant species: *Eucalyptus obliqua*, *Eucryphia lucida*, *Lagarostrobos franklinii*, *Nothofagus cunninghamii*, *Acacia melanoxylon*

Other species: *Anopterus glandulosus*, *Orites diversifolia*, *Coprosma quadrifida*, *Tasmannia lanceolata*, *Acacia verticillata*, *Anodopetalum biglandulosum*, *Leptospermum riparium*, *Monotoca glauca*, *Pomaderris apetala*, *Phebalium squameum*, *Blechnum nudum*, *Blechnum watsii*, *Sticherus tener*, *Hymenophyllum rarum*, *Grammitis billardieri*, *Gahnia grandis*, *Viola hederacea*, *Deyeuxia gunniana*

Structure: Mixed forest

20.

Dominant species: *Eucalyptus regnans*, *Atherosperma moschatum*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*

Other species: *Phebalium squameum*, *Pittosporum bicolor*, *Dicksonia antarctica*, *Grammitis billardieri*, *Hymenophyllum peltatum*, *Hymenophyllum rarum*, *Polystichum proliferum*, *Histiopteris incisa*

Structure: Mixed forest

21.

Dominant species: *Eucalyptus subcrenulata*, *E. coccifera*, *E. delegatensis*, *Phyllocladus aspleniifolius*, *Nothofagus cunninghamii*

Other species: *Telopea truncata*, *Tasmannia lanceolata*, *Trochocarpa thymifolia*, *Pittosporum bicolor*, *Hakea lissosperma*, *Lissanthe montana*, *Coprosma nitida*, *Polystichum proliferum*, *Rubus gunnianus*

Structure: Mixed forest

22.

Dominant species: *Eucalyptus delegatensis*, *E. subcrenulata*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*

Other species: *Telopea truncata*, *Leptospermum lanigerum*, *Cyathodes parvifolia*, *Pultenaea juniperina*, *Tasmannia lanceolata*, *Polystichum proliferum*

Structure: Mixed forest

23.

Dominant species: *Eucalyptus subcrenulata*, *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius*, *Atherosperma moschatum*

Other species: *Trochocarpa cunninghamii*, *Cyathodes glauca*, *Olearia persoonioides*, *Richea pandanifolia*, *Tasmannia lanceolata*, *Telopea truncata*, *Cenarrhenes nitida*, *Aristotelia peduncularis*, *Gaultheria hispida*, *Coprosma nitida*, *Prionotes cerinthoides*, *Pittosporum bicolor*, *Leptospermum lanigerum*, *Blechnum watsii*, *Gahnia grandis*

Structure: Mixed forest

24.

Dominant species: *Eucalyptus subcrenulata*, *Phyllocladus aspleniifolius*, *Nothofagus cunninghamii*, *Atherosperma moschatum*, *Eucalyptus delegatensis*, *Eucryphia lucida*

Other species: *Cyathodes parvifolia*, *Trochocarpa cunninghamii*, *Grammitis billardieri*, *Blechnum wattsii*, *Gahnia grandis*

Structure: Mixed forest

Appendix 2.

Anodopetalum biglandulosum

Number of records 480

Variable: var1 var2 var3 var4 var5 var6 var7 var8 var9

Minimum	1	5.9	1.1	15.9	14.4	1.9	10.2	2.2	10.2
Maximum	973	12.2	5.9	21.8	19.9	9.4	15.6	9.7	15.6
Average	290.9	10.2	2.9	20.4	17.4	6.6	14.2	6.9	14.2
Std. Dev.	202.2	1.2	1.2	1	.8	1.3	1	1.3	1

Variable:var10 var11 var12 var13 var14 var15 var16 var17

Minimum	1026	104	49	13.5	300	174	300	174
Maximum	3236	343	161	37.5	966	560	966	560
Average	2000.	241.1	86.9	29.5	5659.3	3308.0	642.9	308.1
Std. Dev.	479	55.2	21.8	5.4	140	84	131	84

Phyllocladus aspleniifolius

Number of records 389

Variable: var1 var2 var3 var4 var5 var6 var7 var8 var9

Minimum	1	5.8	-1.4	16	14.3	1.8	10.2	2	8.5
Maximum	1011	12.2	5.9	23	20	9.4	16.6	10.9	16.6
Average	317	10.3	2.8	20.3	17.5	6.5	14.1	6.9	14.1
Std. Dev.	201	1.4	1.4	1.2	1	1.5	1.2	1.7	1.3

Variable: var10 var11 var12 var13 var14 var15 var16 var17

Minimum	1011	73	48	11.9	210	164	190	164
Maximum	3236	339	161	40.3	966	560	966	560
Average	1978	225.1	83	28.1	613.5	294.8	598.7	294.8
Std. Dev.	499	66.4	20.1	6.9	168.7	80.1	164.3	80.1

Appendix 2. Summary statistics for altitude and 16 climatic variables from the BIOCLIM data base;

var1 altitude (not in BIOCLIM)

var2 mean annual temperature

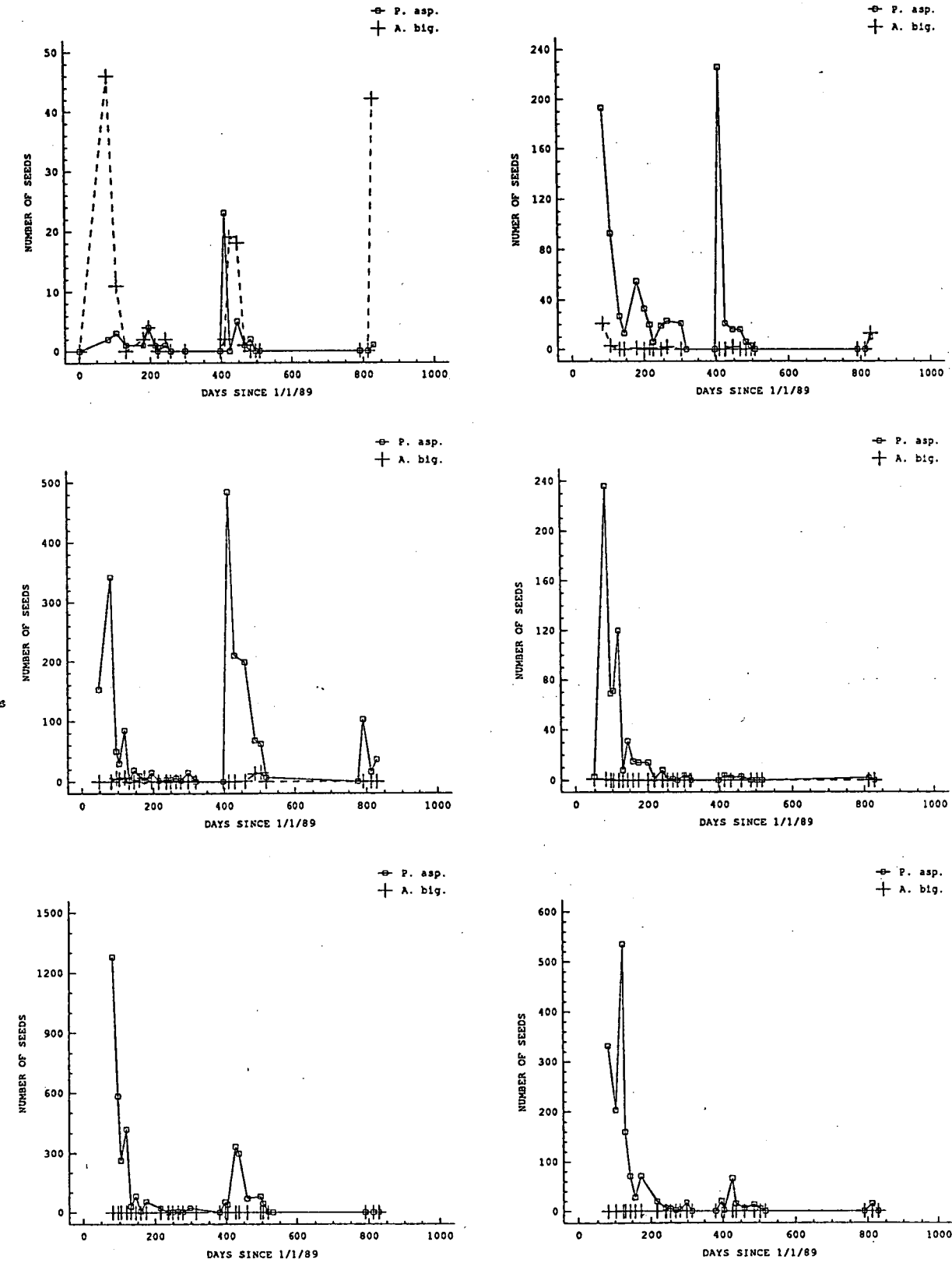
var3 minimum temperature of the coolest month

var4 annual temperature range
var5 maximum temperature of the warmest month
var6 mean temperature of the coolest quarter
var7 mean temperature of the warmest quarter
var8 mean temperature of the wettest quarter
var9 mean temperature of the driest quarter
var10 mean annual precipitation
var11 precipitation of the wettest month
var12 precipitation of the driest month
var13 coefficient of variation of monthly precipitation
var14 precipitation of the wettest quarter
var15 precipitation of the driest quarter
var16 precipitation of the coolest quarter
var17 precipitation of the warmest quarter

Recipe for the Nutrient Solution		
Nutrient	Molarity	Application rate per litre (full strength)
Ca (NO ₃) ₂	1.0	5 ml
MgSO ₄	1.0	2 ml
KH ₂ PO ₄	1.0	1 ml
KNO ₃	1.0	5 ml
Fe EDTA	1.0	1 ml
AlCl ₃	1.0	0.6 ml
Na ₂ MoO ₄	0.001	1 ml
H ₃ BO ₃	0.046	1 ml
MnCl ₂	0.009	1 ml
ZnCl ₂	0.0008	1 ml
CuCl ₂	0.0003	1 ml

Appendix 3 The recipe for the nutrient solution used in the present study, indicating molarity and the rate of application.

Appendix 4. The number of seeds collected from six traps over three years from 1989-1991.



SUCKER	-	Root sucker	BANKFAIL	-	Fallen due to collapsed stream bank	COVER210m	-	% cover 2 - 10m
STEMB	-	Stem bending	GAP	-	Tree fall gap	COVER10m	-	% cover above 10m
ROOTFAIL	-	Fallen due to broken root system	DOMHEIGHT	-	Height of dominant species	SUBCHEIGHT	-	Height of sub-canopy
PINNING	-	Held down by another tree	COVER2m	-	% cover below 2m			

TYPE	SITE	EASTING	NORTHING	ALTITUDE	SUCKER	STEMB	ROOTFAIL	PINNING	BANKFAIL	GAP	DOMHEIGHT	COVER2m	COVER210m	COVER10m	SUBCHEIGHT
1	1	4955	52082.	120	1	12	0	1	0	0	22	20	80	0	8
1	11	4733	52743.	700	1	0	0	1	0	0	30	20	80	0	4
1	12	4733	52744.	630	1	0	0	0	0	0	22	20	80	0	9
1	14	4498	52581.	580	1	11	0	0	0	0	15	10	90	0	0
1	19	3763	53501.	380	1	0	0	0	0	0	12	5	95	0	8
1	21	3846	53668.	600	1	0	0	0	0	0	16	10	80	10	6
1	40	4495	52860.	700	1	1	0	1	0	0	30	10	70	20	15
1	42	3861	53726.	400	1	1	0	1	0	0	25	5	15	80	0
1	44	4284	53449.	760	1	1	0	1	0	0	35	20	10	70	20
1	47	4489	52557.	480	0	13	0	0	0	0	22	90	10	0	0
2	15	4500	52578.	560	1	0	0	1	0	0	10	10	90	0	0
2	20	3773	53518.	520	1	1	0	1	0	0	13	20	80	0	9
2	29	3798	53317.	240	1	1	0	1	0	0	15	25	75	0	10
2	31	3802	53642.	600	1	13	11	1	0	0	8	40	60	0	0
2	34	4493	52573.	560	0	11	11	0	0	0	22	20	60	20	9
3	5	3596	54348.	440	1	11	0	0	0	0	35	40	40	20	14
3	10	4736	52744.	650	1	12	13	0	0	0	23	5	70	25	12
3	13	4737	52744.	580	1	11	0	0	0	0	25	0	80	20	16
3	17	4489	52557.	480	0	13	1	0	0	0	15	5	50	45	0
3	18	3560	53596.	220	0	1	0	1	11	0	22	10	50	40	17
3	23	3840	53739.	240	1	11	11	1	0	1	27	10	90	0	18

Appendix 5 Location and stand characteristics of 48 sites used in the analysis of architectural types of *A. biglandulosum* stands.

TYPE	SITE	EASTING	NORTHING	ALTITUDE	SUCKER	STEMB	ROOTFAIL	PINNING	BANKFAIL	GAP	DOMHEIGHT	COVER2m	COVER210m	COVER10m	SUBCHEIGHT
3	26	4236	53255.	560	1	13	11	1	0	0	19	5	25	70	17
3	27	3853	53131.	160	1	11	12	1	0	1	18	60	0	40	0
3	28	3805	53310.	320	1	0	1	1	0	0	16	0	100	0	0
3	32	3702	53786.	120	1	0	12	1	0	0	30	50	50	0	4
4	9	3595	54347.	460	0	12	11	1	0	0	25	45	35	20	0
4	16	4489	52557.	480	1	0	11	1	0	1	20	35	55	10	0
4	24	3834	53734.	240	1	12	0	1	0	1	38	25	60	15	20
4	30	3767	53517.	480	1	1	13	0	0	1	20	10	90	0	14
4	33	3702	53786.	120	1	0	0	1	0	1	32	50	50	0	0
4	37	4295	51975.	20	1	0	13	1	0	0	28	35	35	25	17
4	38	4315	51967.	10	1	0	0	1	0	1	15	5	80	15	0
4	41	5225	51988.	440	1	0	0	1	0	1	20	20	70	10	0
4	43	3710	53710.	400	1	1	1	1	0	1	26	5	80	15	0
5	3	3597	54348.	440	1	11	11	1	0	0	30	30	70	0	0
5	4	3596	54347.	440	1	0	11	0	1	0	20	20	80	0	10
5	22	3782	53793.	210	0	11	11	0	11	0	17	20	70	10	4
5	48	3782	53793.	240	0	1	11	1	0	0	25	20	80	0	0
6	2	3598	54348.	440	1	1	11	0	0	1	28	90	10	0	15
6	6	3597	54348.	440	1	13	0	1	0	1	20	30	70	0	0
6	7	3482	54536.	160	0	11	0	0	0	0	23	0	100	0	0
6	8	3269	54417.	180	1	12	0	0	0	0	12	10	90	0	0
6	45	3119	54394.	120	1	0	0	1	0	0	17	10	60	30	14
7	25	3863	53744.	400	1	0	0	0	0	0	42	0	20	80	15
7	35	4296	51974.	20	0	0	13	0	0	0	25	0	10	90	15
7	36	4296	51974.	10	1	1	12	0	0	0	18	0	60	40	0
7	39	4315	51967.	10	0	0	0	0	0	0	14	20	60	20	0
7	46	3119	54393.	120	0	0	1	1	0	0	45	10	20	70	14

Appendix 5 (cont'd)

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Appendix 6 A site by species matrix in which the order indicates floristic similarity. Cover classes: 1 rare; 2 <1%; 3 1-5%; 4 5-25%; 5 25-50%; 6 50-75%, 7 75-100%.

SITE	SLOPE	ASPECT	ALTITUDE	DOMINANT HEIGHT	DOMINANT COVER	SUB-DOM. HEIGHT	SUB-DOM. COVER	GROUND HEIGHT	GROUND COVER	C.T.P. HEIGHT	VIEW	DRAINAGE
1TR	2	90	240	8	4	5	4	0.1	4	3	1	2
2PL	4	36	440	2	4	3	6	0.1	0	25	1	2
3PT	2	150	180	25	4	10	5	1	3	22	1	2
4NB	8	120	180	14	4	5	5	1	2	14	1	2
6ML	6	210	390	45	4	15	4	1	4	12	2	2
9MF	10	160	860	40	4	25	4	1	5	12	3	2
10LF	2	335	440	30	4	14	4	0.1	4	14	3	2
11MF	2	170	650	8	4	2	5	1	4	7	3	3
12MF	13	160	650	40	3	25	5	5	5	22	2	2
13BLF	1	60	440	20	4	5	5	1	5	4	2	3
13ALF	1	60	440	24	5	10	4	1	4	20	2	2
14FP	2	581	600	7	4	5	4	1	3	5	2	2
15FP	20	230	650	20	5	4	5	1	3	19	2	2
16NE	2	330	800	17	5	5	3	1	6	17	3	2
17NE	3	160	800	17	4	13	5	0	0	13	3	2
18NE	2	240	800	21	5	4	4	0	0	21	2	2
19NE	0	360	780	22	5	5	3	0.1	6	22	2	2
20NE	4	310	830	15	4	4	4	0.1	5	13	2	3
21NE	4	330	830	13	5	4	3	0	0	5	2	2
22NE	5	330	830	25	5	8	4	0.1	6	25	2	2
23CL	4	15	700	40	3	15	5	0.1	7	20	2	2
24FP	15	130	600	20	3	7	4	0	0	20	1	2
26CH	27	115	820	16	6	8	5	0.1	3	16	2	2
25FV	3	180	600	40	4	10	7	0	0	10	2	2
27NB	1	270	120	45	4	10	5	1	2	13	2	2
28FP	5	300	600	20	5	6	6	1	3	17	<1	2
29PB	10	330	750	8	3	5	6	1	4	5	<1	2
30PB	0	360	720	7	3	1	4	1	7	5	2	3
31OL	40	45	760	6	5	4	5	1	4	4	<1	1
32OR	10	300	30	13	5	5	6	1	5	13	2	2
33OR	8	300	3	10	5	5	4	1	3	10	1	2
34OR	8	240	5	25	4	15	4	1	7	15	1	2
35OR	5	360	60	22	4	16	5	1	4	18	2	2
36OR	5	130	60	25	4	15	5	1	4	12	2	2
37OR	5	135	120	22	4	15	5	1	3	14	1	2
38HZ	1	30	760	25	3	12	4	2	6	16	2	3
39FV	8	240	750	40	4	15	6	2	3	18	2	2
41BI	4	150	440	30	3	15	4	1	6	15	2	2
42BI	32	190	360	35	4	10	5	0.1	5	12	2	2
43DH	30	130	520	45	4	18	5	1	6	18	2	2
44QT	12	330	320	24	4	18	6	1	4	16	2	2
45AR	8	160	520	14	5	8	6	2	4	14	2	2
46AR	18	120	640	13	5	7	5	1	4	13	1	2
47HT	12	210	600	7	4	3	5	1	3	8	1	2
48HT	4	60	600	12	4	4	5	1	5	7	1	2
49PV	2	210	950	18	4	7	6	1	2	8	2	2
50PV	5	240	940	30	4	18	6	1	3	18	2	2
51PV	8	210	940	30	5	15	6	2	7	15	1	2
52MI	30	40	610	15	4	4	4	1	4	12	2	1
53CP	2	30	1118	7	4	4	4	1	4	2	2	1

Appendix 7 Site characteristics. Cover classes as for Appendix 1. Dominant height = the height of the tallest stratum. Dominant cover = the cover class of the tallest stratum; Sub-dominant = the stratum below the dominant cover composed of species that do not normally reach the dominant canopy. Ground = the shrub and fern layer below the subdominant species. C.T.P. height = the of the tallest *Phyllocladus*; View = the visibility through the forest as multiples of the height of the tallest *Phyllocladus*. Drainage, 1 excess, 2 free, 3 impeded, this is a subjective estimate of the rate of drainage. Excess indicating that no surface water accumulates during rain periods and the site may be drought prone, free indicates that surface water does not accumulate and the site is not drought prone and impeded indicates surface water or water logging is a frequent or seasonal condition.