

**Understorey dynamics following
partial logging in *Eucalyptus*
delegatensis forests on the Central
Plateau, Tasmania**

Andrew K. Gibbons B.Sc.

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E. delegatensis grassy forest (730 m asl) at Table Mountain, (top) unlogged control forest, (bottom) 7 years after logging.

Declaration

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material published or written by another person except where due acknowledgement is made in the text of the thesis.



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Abstract

Partial logging in high-altitude *E. delegatensis* forests involves the retention of approximately 50 % of original forest basal area, and was implemented to overcome the problem of “growth check” in regenerating eucalypts following clearfelling. It is increasingly being carried out in these forests in an effort to provide income to landowners while still allowing regeneration of the overstorey eucalypts.

This thesis looks at the effects of partial logging on understorey floristics and structure in both, the short (~2 years), and the long (15-20 years) term. Analysis of a floristic, structural and environmental dataset using multivariate and ANOVA techniques found that two understorey types, grassy and shrubby, were present, and that short term trends included reduced cover of all lifeform groups, reduced understorey height, species richness and structural complexity, and increased bare ground cover and soil disturbance. Four of these trends, increased grass and forb cover, decreased shrub cover and structural complexity, were still apparent 5-8 years after logging, and two, reduced shrub cover and habitat complexity, 16-21 years after logging, particularly in shrubby forest. These changes were attributed to the reduced cover of the overstorey and subsequent changes in the light/temperature/moisture regimes of the forest floor microclimate.

Effects of plantation establishment in wetter areas of this forest type were similar to those of partial logging, but of a greater magnitude and duration.

Ecological processes structuring the understorey were examined by, first, looking at changes in species cover/abundance under individual overstorey eucalypts and in forest gaps in unlogged forest, and, second, with a laboratory shading/disturbance experiment. It was found that canopies of overstorey eucalypts were causing distinct patterns in understorey distribution. Species richness and cover increased moving from trunk to canopy edge to forest gap and from unshaded to shaded sector of forest gaps primarily due to the inhibitory effects of high litter and shade under trees, and cold induced photoinhibition in high light areas of gaps. Chlorophyll fluorescence measurements confirmed the requirement of shade for, the shrub *Lomatia tinctoria*, and the sedge *Lomandra longifolia*, and the ability of grasses to out compete these species in full sun, mimicking the patterns observed logged forest.

Results are discussed in relation to the theory of ecological resilience and it is suggested that increasing divergence of understorey will occur with each logging and/or plantation rotation and may lead to shifts in forest/grassland boundaries.

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The work presented in this thesis initially arose as a topic for a master's degree looking at the effects of intensive forest management on flora and fauna in Tasmania's production forests. Early in the study the project was revised to its present form examining the flora in partially logged *E. delegatensis* forests. Many thanks to Clare McArthur, Mike Battaglia, Kirsten le Mar, Nicholas Coop and Jurgen Bauhus whose discussions in the early part of this study helped crystallise it into its present form.

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1. Introduction

1.1 *E. delegatensis* R.T. Baker forests of the Central Plateau, Tasmania

Eucalyptus delegatensis is a widespread dominant of montane forests at altitudes over 600m, occupying 317,104 hectares (Forestry Tasmania 2001) with more than half of *E. delegatensis* forests in Tasmania occurring on the Central Plateau. The Tasmanian subspecies (*Eucalyptus delegatensis* subsp. *tasmaniensis*) is physiologically and morphologically different from the mainland form of *E. delegatensis*. It has fibrous bark that extends up to the base of the branches in the crown, is more fire resistant as an adult, and can persist as a suppressed seedling in dry sclerophyll understoreies for up to 30 years (Forestry Tasmania 2001, Bowman & Kirkpatrick 1986a, b).

E. delegatensis forests on the plateau typically occur on free draining, relatively fertile soils derived from dolerite with a high surface rock cover, and within rainfall ranges from 700 mm per annum in the south-east to greater than 2000 mm in the north-west (Bowman & Kirkpatrick 1986b, Bowman 1986). Fire is an important element in the structure and regeneration of these forests with most recruitment occurring on freshly burnt seedbed. The seedlings then continue to grow if the canopy of the forest has been sufficiently disrupted to reduce competition, or they become suppressed seedlings that may be subsequently released by a later disturbance of the canopy (Forestry Tasmania 2001, Bowman & Kirkpatrick 1986a).

Moisture supply and time since last fire control the understorey type in these forests producing a grassy understorey under the driest conditions, through to a rainforest understorey under the wettest conditions (Forestry Tasmania 2001, Williams & Potts

1996, Bowman 1986, Bowman & Kirkpatrick 1984). Community structure varies from tall open forest in dry sclerophyll-wet sclerophyll ecotones, to low open woodland in subalpine sites. These forests also include a number of other eucalypt species, either as codominants with *E. delegatensis*, or as patches scattered throughout the forest and associated with small-scale changes in drainage/soil depth/exposure/surface rock cover. The principle species found on sites in this study included: *E. delegatensis*; *E. dalrympleana*; *E. amygdalina*; *E. pauciflora*; *E. rodwayi*; *E. gunnii* and *E. coccifera*.

This study took place in the south-east quadrant of the Central Plateau in five areas, four of which had rainfalls of less than 1000mm per annum, and fall into the dry sclerophyll forest and woodland (of Duncan 1988). Two understorey types were present on these sites corresponding to the grassy and shrubby groups of Duncan & Brown (1985). The grassy type forest is most common on the drier eastern surface of the plateau at altitude of 730-820m, but it also occupies sheltered sites on the lower plateau surface (altitude 915-1065m). The predominant species of these grassy understoreys are *Poa gunnii*, *Leucopogon hookeri*, *Pultenaea* spp. and *Lomandra longifolia*. The shrubby type forest occurs at an altitudinal range of 500-900+ m where it is strongly associated with a high surface cover of dolerite (Duncan & Brown. 1985). The shrubby understorey is dominated by the shrubs *Cyathodes parvifolia*, and *Olearia viscosa*. The fifth area, at Tarraleah, has a higher mean annual rainfall of 1200mm and, consequently, there is a wet sclerophyll understorey dominated by *Pomaderris apetala*, *Dicksonia antarctica* and *Bedfordia salicina*.

1.2 Silvicultural systems in dry *E. delegatensis* forest

The development of an export woodchip market in 1971 and the consequent increased demand for pulpwood resulted in an increase in forestry in high altitude *E. delegatensis* forest (> 600 m a. s. l.). As a result, clearfelling replaced the practice of selective logging with the aim of producing vigorous high quality stands. During the 1970's clearfelling of dry forest increased to a rate of 4000 to 5000 hectares per annum (Forestry Commission 1994). The silvicultural practice of clearfelling involved removing all trees from a coupe, followed by a slash burn and aerial sowing, with the aim of producing vigorous high quality stands (Keenan 1986). By the end of the decade, it had become apparent that regeneration using this silvicultural system was not always successful in these high altitude (> 600m) forests, with regeneration subject to 'high altitude growth check' (Keenan & Candy 1983).

High altitude growth check describes a condition where seedlings and small saplings grow very slowly, or not at all. The condition is most often associated with clearfelling, which results in increased exposure to frost and desiccating winds and proliferation of grass. It was originally thought to result from an interaction of factors including frost, browsing, grass competition, nutritional imbalances, and insect attack. Recent research, however, suggests that growth check is primarily due to thermal inhibition of tree seedlings over a grassy ground cover (Ball *et al.* 2002, 1997). The actual onset of the condition is unpredictable, with the same area producing failed regeneration in some years but rapid early growth of regeneration in others. Identification of this problem and the amenability of *E. delegatensis* to a range of silvicultural regimes, led to the adoption of selective or partial logging systems during the 1980s (Forestry Tasmania 2001, Battaglia & Wilson 1990).

Several silvicultural systems fit under the broad term of partial logging as used in this study including: seed tree retention; advanced growth retention; potential sawlog retention; selective logging; and shelterwood (Forestry Tasmania 2001, Neyland 2000, Orr 1994, Bowman 1986).

The following brief description of each system is taken from Forestry Tasmania (2001):

1.2.1 Seed tree retention

Applied to open forests where a continuing seed source will maximise regeneration. Seven to 12 well-spaced trees per hectare are retained.

1.2.2 Advanced growth retention

Applied to uneven-aged forests that contain groups of advanced growth suitable for retention. All mature trees are harvested other than young stems that have potential for further value increment.

1.2.3 Potential sawlog retention

Applied to forests containing poles at or slightly below minimum sawlog size. Logging should retain a minimum of 100 stems per ha over 25 cm DBH (diameter at breast height).

1.2.4 Selective logging

Applied to open, multi-aged stands with an adequate stocking of sawlogs. Only selected merchantable trees are logged, retaining all other growth.

1.2.5 Shelterwood

Applied to high altitude open forests on cold sites that contain little advanced sapling growth. Trees with good crowns are retained at 12 – 14 m² of basal area on wet sites and 9 – 12 m² on dry sites. The overstorey is removed when the regeneration is greater than 1.5 m mean height.

The shelterwood system, unlike other partial logging systems, is considered to result in distinct units of even-aged regeneration (Bowman 1986), in practice, however, the variable structure of the forests mean that extensive areas suitable for uniform shelterwood retention are rare. The naturally occurring variable stands are harvested using a combination of advance growth retention, shelterwood and potential sawlog retention methods. The result is a mosaic containing groups of various age classes and structures within the one stand (Forestry Tasmania 2001, Forestry Commission 1994).

1.3 Advantages and disadvantages of partial logging

In addition to the protection from extremes of temperature and high wind, partial logging systems provide a number of economic and ecological advantages over clearfelling, particularly in dry forests (Orr 1994, McCormick & Cunningham 1989).

These are:

- Well-formed smaller trees can be left to grow into sawlogs that are more valuable than pulpwood.
- Increased regularity of income with harvesting returns being more frequent.

- Retained trees provide a source of seed, making regeneration establishment more reliable, particularly on difficult sites, reducing the cost of regeneration.
- Retained trees provide a form of fire insurance in the form of crown-stored seed.
- The treatment has lower environmental and visual impact than does clearfelling.
- The seed shed from retained trees helps protect the genetic diversity of each forest stand.

Partial logging systems, however, require greater planning and supervision, and need considerable care to be taken by contractors. Major problems include poor quality of retained trees, erratic spacing, and unacceptably high damage of retained trees (Neyland 2000). The target for retained basal area when partial logging these forests is approximately $12 \text{ m}^2 \text{ ha}^{-1}$ for dry (700-1000 mm yr⁻¹) sites above 600 m (Battaglia and Wilson 1990). In reality, however, this figure is often much lower particularly in the grassy type forest.

1.4 Plantations

Plantation establishment on the Central Plateau is largely restricted to wetter areas with higher productivity. Two such plantations are found near Tarraleah in this study on ex native forest and ex pasture sites (Fig. 2.1). Current prescriptions for plantation site selection include: a maximum altitude of 700m; annual rainfall in excess of 800mm; slope of less than 14 degrees; and fertile soil of at least 70 cm depth (Forestry Tasmania 1999, Orr 1994). Plantations are expensive to establish and are very management intensive when compared to partial logging regimes. Stages in their development

include: logging; residue removal; cultivation; weed control; planting; browsing control; fertilising; fire protection; thinning; and pruning (Orr 1994).

1.5 Extent of partial logging and plantation regimes

The high altitude forests of the Central Plateau are an important timber resource, with 155,000 ha available for wood production. Of this 60% (92,900 ha) is privately owned, with the remaining 62,200 ha State-owned (Ellis 1995). In 1995 650,000 tonnes of wood were cut annually on the Plateau and it was envisaged that an expansion of forestry on private land would occur in the next 10-15 years. It is expected that 380,000 tonnes of wood will be cut per annum in the early years of this century and that the ratio of sawlog to pulpwood will increase from 1:10 in 1990 to 1:2.5 by the middle of this century (Ellis 1995).

The south-eastern quadrant of the Central Plateau, where the five study areas are located is part of the Derwent Forest District and managed by Forestry Tasmania (Fig. 2.1). The area of partially logged State Forest in this District in 2001/2002 was 2902 ha as compared to 1743 ha per year for 1990-92 for all areas of crown dry eucalypt forest (Forestry Tasmania 2002). While the areas of partial logging for 2001/2002 are taken from State Forest, large areas of which occur outside the plateau, the figures do not include private land where the majority of partial logging on the plateau is taking place.

1.6 Importance of Study

1.6.1 Impact of logging

Tasmanian State Government policy for privately owned rural land is to ensure sustainable long-term use of the land and vegetation for agriculture and forestry.

Management objectives in the Derwent District Forest Management Plan include protection of rare and threatened plant species and plant communities of botanical significance and maintenance of the extent and diversity of habitat to maintain viable populations of plant species (Neyland 2000, Forestry Tasmania 1999, Orr 1994).

While there have been numerous studies on the ecology and silvicultural prescriptions for *E. delegatensis* forests (see Forestry Tasmania 2001, Ellis 1995, Forestry Commission 1994, Orr 1994, Battaglia & Wilson 1990, McCormick & Cunningham 1989, Bowman 1986, Bowman & Kirkpatrick 1986a, b, c, Keenan 1986, Bowman & Kirkpatrick 1984, Keenan & Candy 1983, Ellis *et al.* 1980,) little research has been carried out on the effects of logging on understorey in Australian forests and none in high altitude *E. delegatensis* forest (see Chapters 3 & 4 for review of research on effects of logging).

1.6.2 Ecological processes

An understanding of the ecological processes including disturbance regimes and their consequences for species niches, vegetation patterns and other ecosystem functions in these forests is essential for ecologically sustainable forest management practices (Lindenmayer 1999, Peacock 1997). It has been suggested that in order to achieve sustainability logging-induced disturbance needs to mimic the effects of natural disturbances like wildfire (Lindenmayer & McCarthy 2002). Long-term monitoring will be essential for testing this congruence between logging disturbance and wildfire disturbance (Lindenmayer & McCarthy 2002, Peacock 1997). This is particularly important given the general lack of monitoring of the impact of most management practices on eucalypt ecosystems (Williams & Woinarski 1997). While forest harvesting

will continue while monitoring studies are being developed, one way to implement monitoring programs in managed forests is to overlay carefully designed monitoring experiments on existing human disturbance regimes (Lindenmayer 1999, Walters & Holling 1990). This was the approach adopted for this thesis where forest harvesting was treated as a quasi-experiment (Dunning *et al.* 1995) and data collected on the response of understorey species and forest microclimate to partial logging.

It has been shown that composition of forest understorey species are controlled by overstorey trees that filter light, moderate the understorey air and soil temperature, and directly compete for soil water and nutrients, as evidenced by the response of individual species to increasing availability of these resources (Riegel *et al.* 1995). Understorey changes in logged forest, therefore, will be the result of the direct effects associated with the logging operation plus subsequent changes in the micro-environment of the forest floor, regulated by changes in overstorey cover, soil disturbance, slash volume and light penetration (Peacock 1994).

E. delegatensis forests are of particular interest as they occur within the climatic range of subalpine grasslands. Shifts in the range of environmental factors following deforestation may be sufficient to alter conditions at the regeneration site so that secondary succession occurs along a different path. Trees may be inhibited from invading the site by occupation of other species, particularly *Poa* spp., and conditions may become increasingly unfavourable for eucalypts (Forestry Tasmania 2001, Keenan & Candy 1983).

Considering the extent of land involved, the lack of research, the scant knowledge of ecosystem function and biodiversity, the importance of the understorey type on

regeneration, and the need to protect the biodiversity objectives mentioned above, it is clearly a priority research need that the effects of partial logging in *E. delegatensis* forests on understorey flora be understood.

1.7 Layout and aims of study

A systematic layout of the thesis is presented in Fig. 1.1. The site descriptions of the five general areas of the Central Plateau used for data collection, and common methods of experimental design, data collection and data analysis are set out in Chapter 2. The first aim of the study was to assess changes, if any, in understorey floristics and structure resulting from partial logging in high altitude *E. delegatensis* forests. Chapter 3 examines data from the four areas of dry sclerophyll forest, with coupes logged at different times. Multivariate techniques were used to detect patterns in the understorey vegetation that could be attributed to logging. Chapter 4 examines the floristic and structural data from these four areas in more detail, using a space-for time and a BACI (before-after-control-impact) experimental design. The two aims of this chapter were to find out if short-term impacts of logging were still apparent in the longer term, and if the impact of partial logging varied in different understorey types.

The results of these two chapters raised questions about the effect of individual overstorey eucalypts on the distribution of understorey species beneath them. Chapter 5 examined this ‘halo’ effect and specifically asked: do individual overstorey eucalypts produce a halo effect in understorey species composition and distribution? How does the tree halo effect, if any, compare with the understorey patterns in adjacent forest gaps? Which biophysical factors associated with individual trees are causing the observed

understorey patterns? and, could cold-induced photoinhibition be contributing to understorey patterns in these forests?

An important part of ecology is the linking of pattern to process (Williams & Eamus 1997). This was undertaken to a limited extent, in Chapter 4 and 5, and is expanded on in Chapter 6 with the implementation of an auto-ecological study on three common understorey species found in highland grassy *E. delegatensis* forests. Chapter 6 describes an experiment on the effect of a shading/disturbance gradient on above ground biomass in pure and mixed stands of these species. Specific aims were to find out the response of biomass to an increasing gradient of shading, the response of biomass to an increasing gradient of disturbance, and the response of biomass to the shading/disturbance gradients in mixed stands where interspecies competition was also present.

Chapter 7 compares and contrasts the impact of plantation establishment on understorey floristics and structure with the impact of partial logging in native forest.

The concluding Chapter 8 discusses key ecological points that arose during the course of this study and considers the results in light of theories on ecological resilience, and community convergence and/or divergence.

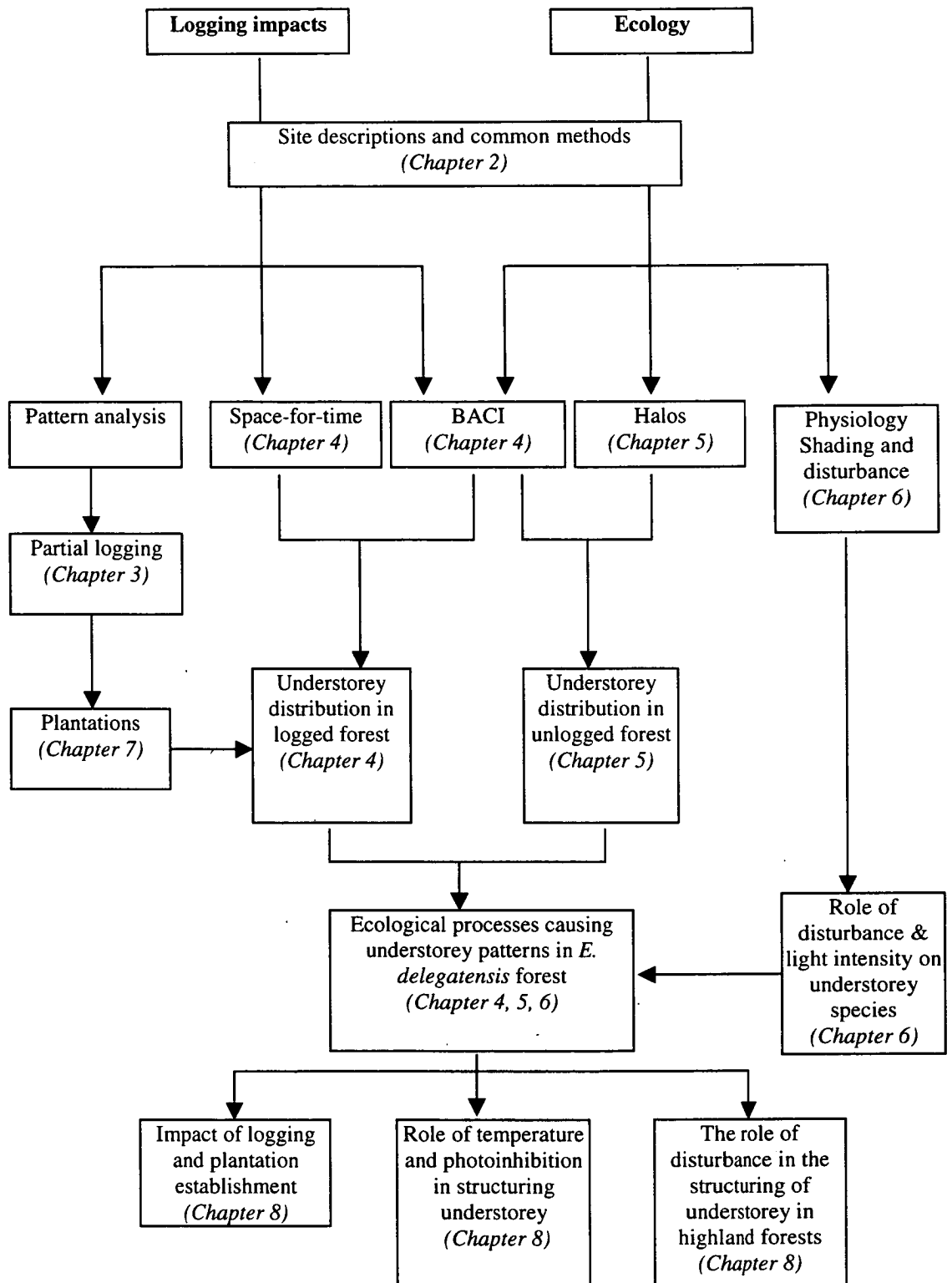


Figure 1.1 Flow diagram showing the layout of thesis by chapter.

2. Sites and methods

The data for the majority of experiments in this thesis were collected in the same five areas, using many of the same methods of data collection and data analysis. In particular, the techniques of multivariate analysis were identical for Chapters 3, 4, 5 and 7. This chapter describes the common sites and methods of the thesis. Specific methods of survey design and data analyses will be found in the relevant chapters.

2.1 Site descriptions

The study was conducted in five general areas dominated by *E. delegatensis* forest on the south-eastern Central Plateau of Tasmania: area 1 at Table Mountain; area 2 at Glenmark; area 3 at Clarence Lagoon; area 4 at Mt. Franklin; and area 5 at Tarraleah (Fig. 2.1, Table 2.1). Areas 1-4 were dry sclerophyll forest, whereas area 5 at Tarraleah (the plantation site) was wet sclerophyll forest. Two understorey types are present in the dry sclerophyll forest, grassy at Table Mountain and Mt Franklin, and shrubby at Table Mountain, Glenmark and Clarence Lagoon (Duncan & Brown 1985).

Collectively, these areas encompass a range of understorey types from the southern Central Plateau, but do not include the high altitude, high rainfall, grassy and rainforest understoreys of the northern Central Plateau and high altitude *E. delegatensis* of northeast Tasmania.

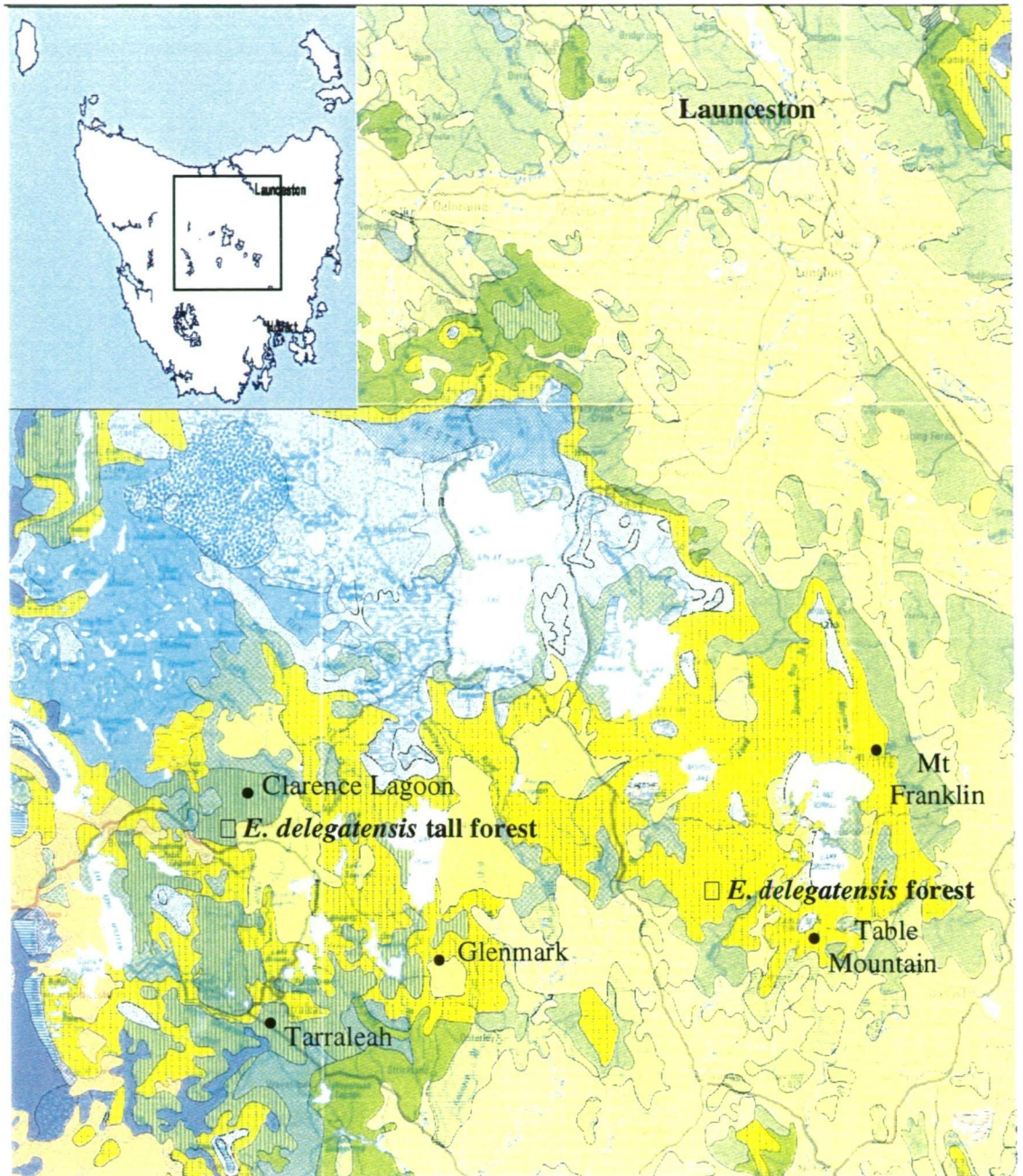


Figure 2.1 Central Plateau of Tasmania showing the five study areas where data were collected for this thesis and extent of *E. delegatensis*. Map modified from Kirkpatrick & Dickinson (1984).

Table 2.1 Site information for logged coupes, plantations and matched controls for the five areas surveyed in the space-for-time study. Basal area data are mean \pm SEM (n).

| General areas | Coupe year logged | Rainfall (mm yr ⁻¹) | Altitude (m) | Basal area in coupe (m ² ha ⁻¹) | Basal area in control (m ² ha ⁻¹) |
|---|-------------------------------------|---------------------------------|--------------|--|--|
| Table Mountain 42°18'S, 147°09'E | 1991 | 743 | 785 | 9 \pm 2(6) | 18 \pm 1(6) |
| | 1992 | | 777 | 8 \pm 1(6) | 27 \pm 1(6) |
| | 1996 | | 792 | 5 \pm 1(6) | 30 \pm 2(6) |
| | 1998 | | 892 | 6 \pm 1(6) | 18 \pm 1(6) |
| | 1999/00 | | 730 | 9 \pm 1.0(24) | 28 \pm 1.3(24) |
| Glenmark 42°15'S, 146°40'E | 1993/94 | 834 | 796 | 11 \pm 1(6) | 32 \pm 4(5) |
| | 1995 | | 841 | 16 \pm 3(5) | |
| Mt Franklin 42°06' S, 147°13' E | 1977/78 | 741 | 1010 | 14 \pm 2(6) | 30 \pm 2(6) |
| Clarence Lagoon 42°08' S, 146°25' E | 1983 | 939 | 800 | 13 \pm 2(6) | 32 \pm 1(6) |
| | 1987 (relog of 83 coupe) | | | 7 \pm 1(6) | |
| Tarraleah plantations 42°18'S, 146°27'E | 1979 <i>E. delegatensis</i> row | 1175 | 609 | 27 \pm 3.4(12) | 27 \pm 2.6(6) |
| | 1979 <i>E. delegatensis</i> windrow | | 609 | 17 \pm 2.3(6) | 27 \pm 2.6(6) |
| | 1995 <i>E. nitens</i> | | 588 | 7 \pm 0.5(6) | 28 \pm 1.8(6) |

The soils in all areas are predominantly derived from Jurassic dolerite, although there is a mixed substrate of dolerite and metamorphosed sandstone, that both outcrop over the site of the grassy forest at Table Mountain. Surface rock cover varies between 0-85 percent, with the shrubby type understorey associated with a higher proportion of rock cover.

Four separate experiments were carried out across the five areas with data collected at various times: 1) pattern analysis at all five areas (Chapter 3-native dry sclerophyll forest-October 1998-February 1999, Chapter 7-Tarraleah plantations-February 1999-

April 1999); 2) space-for-time study at Table Mountain, Glenmark, Clarence Lagoon and Mt Franklin (Chapter 4- October 1998-February 1999); 3) BACI study (Chapter 4- October 1999, March-April 2000, April-May 2001); and 4) halo study (Chapter 5- October 1999), both in grassy forest at Table Mountain. The first three examined impacts of partial logging and plantation establishment, the fourth examined understorey patterns in unlogged forest

The grassy forest (Duncan & Brown 1985) at Table Mountain has a mixed overstorey of *E. delegatensis*, *E. pauciflora*, *E. dalrympleana*, *E. amygdalina* and *E. rodwayi* and a predominantly sclerophyllous, species rich understorey dominated by the shrubs *Leucopogon hookeri* and *Lomatia tinctoria*, the sedge *Lomandra longifolia*, and the grasses *Poa gunnii* and *P. rodwayi*.

2.2 Methods

2.2.1 Data collection

Quadrat based floristic and environmental data collection was carried out for all surveys. Two different quadrat sizes were employed: 20 m x 20 m quadrats were used for the pattern analysis surveys of Chapters 3 and 7, and the space-for-time survey of Chapter 4; 2 m x 2 m quadrats were used for the BACI and halo surveys of Chapters 4 and 5, respectively.

2.2.1.1 Floristic data

Floristic data were collected as follows. All vascular plant species growing in or projecting over each quadrat were recorded and assigned a visually assessed cover-abundance value based on a modified Braun-Blanquet scale (Swayn *et al.* 1993, Mueck & Peacock 1992,) as follows:

- r solitary species
- +
- 1 cover less than 5%, few individuals
- 2 cover less than 5%, any number of individuals
- 3 cover 5-25%, or very numerous
- 4 cover 25-50%, any number of individuals
- 5 cover 50-75%, any number of individuals
- 6 cover 75-100%, any number of individuals

Nomenclature of species followed Greuter *et al.* (2000), Buchanan (1999) and Curtis and Morris (1994, 1979, 1975). In the BACI and halo studies all orchid species, with the exception of *Pterostylis* spp., were grouped together as Orchidaceae, and a number of commonly occurring grass genera with low cover, including *Austrostipa* spp., *Austrodanthonia* spp., *Deyeuxia* spp., and the exotic *Vulpia* spp., were grouped together as Poaceae spp. prior to analyses.

2.2.1.2 Structural and environmental data

22 structural and environmental variables were also collected from each quadrat, both 20 m x 20 m and 2 m x 2 m (Table 2.2). Evenness (J), Shannon Diversity Index (H'), weed, grass and total cover were then derived from the floristic data for each quadrat.

Percentage scores were derived from the Braun-Blanquet cover/abundance scores

recorded for each species using a mid-point percentage value as follows: r = 0.1%; + = 1%; 1 = 4%; 2 = 15%; 3 = 37.5%; 4 = 62.5%; 5 = 87.5%.

The Shannon-Weiner Diversity Index (H') (Kent & Coker 1999) was calculated for each quadrat from the formula:

$$H' = - \sum_{i=1}^s p_i \ln p_i$$

p_i = the abundance of the i th species expressed as a proportion of total cover

\ln = logarithm base e

The evenness (J) (Kent & Coker 1999) was calculated for each quadrat as:

$$J = H' / \ln s$$

Where s = the species richness or number of species

The Shannon diversity index expresses the diversity of a sample or quadrat with a single number combining species richness with relative abundance. Values of the index usually lay between 1.5 and 3.5, with the higher the value the more diverse the quadrat.

Once H' is known the equitability or evenness (J) can be calculated. The higher the value of J , the more even the species are in their distribution within the quadrat (Kent and Coker 1999).

Mean annual rainfall for each area was taken from records of the closest weather station (Bureau of Meteorology).

Vegetation structure was assessed using a habitat complexity score derived for each quadrat based on five features: (1) percentage canopy cover; (2) shrub cover; (3) ground vegetation cover; (4) amount of litter fallen logs and rocks; and (5) a soil moisture rating

(Newsome & Catling 1979). Each feature was rated on a scale 0-3 and the scores for the five features were totalled to give an overall score out of 15. A score of 5 or lower denoted a forest with few understorey shrubs and sparse ground cover. A score of 9 or more indicated a forest with a thick understorey and thick ground and/or litter cover.

Table 2.2 Description of environmental variables collected in each 20 m x 20 m quadrat in the pattern analysis and space-for-time surveys, and in each 2 m x 2 m quadrat in the BACI/Halo study, and variables derived from collected data. *All* refers to all four surveys (pattern analysis, space-for-time, BACI and Halo).

| Variable | Study | Description |
|----------------------|---|---|
| rainfall | Pattern analysis & Space-for-time | Annual mean precipitation (Bureau of Meteorology records from weather station nearest to site) |
| altitude | Pattern analysis & Space-for-time | Altitude in metres from 1: 25000 topographic sheet |
| aspect | All | Orientation of slope of site in degrees |
| slope | All | Slope of site in degrees |
| no. of veg. layers | All | Number of distinct vegetation layers |
| max tree ht. | All | Height in metres of tallest overstorey tree |
| max. understorey ht. | All | Height in metres of tallest understorey tree or shrub |
| euc classes | All | Number of eucalypt age/size classes |
| acacia cover | Pattern analysis & Space-for-time | Percentage cover of all <i>Acacia</i> species |
| grass cover | All | Percentage cover of all grasses |
| no. euc sp | All | Number of eucalypt species |
| basal area | All | Basal area ($\text{m}^2 \text{ha}^{-1}$) of overstorey eucalypt species taken from centre of quadrat with a factor x1 wedge |
| richness | All | Number of species |
| total cover | All | Total percentage cover of all vegetation |
| J | Pattern analysis & Space-for-time, derived data | Equitability or evenness index (Kent and Coker 1994) |
| H' | Pattern analysis & Space-for-time, derived data | Shannon Diversity Index (Kent and Coker 1994) |
| habitat complexity | Pattern analysis & Space-for-time | Score out of 15 based on structural attributes of the vegetation. |
| weed cover | All | Percentage cover of all introduced species |
| litter | All | Percentage cover of all litter, fallen logs and woody debris |
| rock | All | Percentage cover of all exposed rock |
| bare ground | All | Percentage cover of all bare ground |
| type | Pattern analysis & BACI | Rating of 1 or 2 where 1 = quadrat before logging and 2 = quadrat after logging |
| time | BACI | Time of sampling with 1 = prelog, 2 = postlog 1, 3 = postlog 2. |
| control | BACI | Rating for control quadrats with 1 = other quadrat, 2 = control quadrat. |
| aspect 1 | BACI | Scale where N, E, S, W quadrats are labels 1 – 4 respectively for both trees and gaps |
| soil disturbance | BACI | Rating from 1 to 3 where 1 = none/low, 2 = moderate, 3 = high |
| grazing | BACI | Rating from 1 to 3 where 1 = none/low, 2 = moderate, 3 = high |
| geology | BACI | Rock substrate where 1 = dolerite, 2 = sandstone |

As all studies examined patterns in the understorey, the floristic data from overstorey eucalypts were not included in floristic analyses; however, four environmental variables providing measures of the overstorey eucalypts were retained.

2.2.2 Data analysis

Multivariate techniques of ordination, classification and vector fitting were used in three of the studies: the pattern analysis, the BACI survey, and the Halo survey. These techniques were carried out in the software package PATN (Belbin 1994a, b).

Quantitative data (cover scores) were used for all multivariate analysis rather than presence-absence data. This allowed analysis of species-in-site data by classification and ordination to assess whether logging and/or plantation establishment were influencing the variation in the species composition and pattern of each site. The total data matrices were 91 quadrats by 140 species for the pattern analysis and 182 quadrats by 85 species for the BACI and halo survey.

2.2.2.1. Ordination

Site ordination was by semi- strong- hybrid multidimensional scaling (SSH) based on a Bray-Curtis dissimilarity coefficient (Belbin 1994a, b). Species (inverse) ordination was by semi-strong hybrid multidimensional scaling (SSH) based on a Two-Step dissimilarity coefficient (Austin & Belbin 1987). Floristic data was unstandardised in the pattern analysis survey as this gave the clearest separation of groups in the ordination space. Floristic data for the BACI/Halo survey, however, were site standardized (i.e. x_{ik} -

minimum i / range i , where x_{ik} is the data value for the i th quadrat and k th species of the data matrix, i is the whole of the i th quadrat) prior to analysis. This has the effect of placing all species within a quadrat on the scale zero to one, giving equal weight to all sites (i.e. species rich plots don't dominate the ordination) and is the recommended standardisation procedure prior to the use of the Bray-Curtis association measure (Belbin 1994a, b). This standardisation of species to equal maxima has been shown to improve both linear and rank correlations with ecological distance (Faith *et al* 1987). This refers to the separation of quadrats along underlying ecological factors (e.g. rainfall, time since logging, etc) that influence the variation of site floristics. The combination of the Bray-Curtis index and data standardization with SSH is, therefore, ideal for use in a study like this where the aim is to recognize trends in floristic variation related to underlying ecological factors (Mueck & Peacock 1992).

Eight ordinations were carried out for the pattern analysis survey of Chapter 3 & 7: one of all site controls (41 quadrats); one of the entire data set (91 quadrats); two for Table Mountain; and one each for Glenmark, Clarence Lagoon, Mt. Franklin and Tarraleah. One ordination was carried out for the BACI study of Chapter 4 and four for the halo study of Chapter 5.

The number of dimensions that any ordination was taken too depended on the stress values obtained and how clear an interpretation could be made from the groupings. For the most efficient trade-off between stress and consistency of solutions from 10 random starts, the site controls (stress = 0.16), the entire data set (stress = 0.21), the two Table Mountain analyses (stress = 0.17), Clarence Lagoon (stress = 0.17) and Tarraleah plantations (stress = 0.17) required three dimensions. Glenmark (stress = 0.22) and Mt. Franklin (stress = 0.17) required two dimensions for an adequate representation of their

variation. The BACI ordination (stress = 0.16) required four dimensions, the four halo study ordinations (stress = 0.16, 0.15, 0.12 and 0.14) required five, five, four and four dimensions, respectively. Where ordinations were carried out to higher dimensions, often only those permutations of the axes best displaying the trends in the data are presented.

2.2.2.2 Vector Fitting

The analytical technique of vector fitting was used to interpret the 22 environmental, structural and management variables (Table 2.2). The technique finds the vector (rotated axis) in the ordination space where the scores of the samples on this vector are maximally correlated with the values of the particular variable (Fensham *et al.* 2000, Kantvilas & Minchin 1989, Bowman & Minchin 1987, Dargie 1984). The significance of the maximum correlation values was tested using a Monte-Carlo approach. There were 1000 random permutations, with the values of the variable randomly placed among the quadrats. Correlations obtained for the randomised data were sorted together with the value calculated from the observed values of the variable. Probabilities were calculated as the proportion of the 1000 correlations that were greater than or equal to the value obtained from the actual data. Only those vectors with probabilities > 0.01 were considered significant. Vector diagrams are plotted to display the direction of the trend of each significant fitted vector in the ordination space.

2.2.2.3 Classifications

The classifications for both site and species data were carried out by a hierarchical polythetic agglomerative clustering procedure using the UPGMA flexible ($\beta = -0.1$) sorting strategy. Two-way tables showing both quadrat and species groups were then produced for each forest/site type in PATN (Belbin 1991). The site groups created by classification were statistically tested with the ANOSIM algorithm in PATN. ANOSIM was developed as a means of determining if a series of replicate samples were more similar to each other than they were to another set of samples. The method is essentially ANOVA in nature in that a comparison of 'within-group' and 'between-group' is determined. The differences from ANOVA are twofold. First, a Monte-Carlo type randomisation is performed and second the raw data is a symmetric association matrix between all pairs.

The statistic is:

$$\frac{\text{Average between group dissimilarity}}{\text{Average within group dissimilarity}}$$

The randomisation component was performed on the allocation of replicates (in this case quadrats) to samples (classification defined groups). This means that quadrats were randomly allocated to a set of pre-defined groups. The test is to find out in what proportion of cases the randomly generated statistics equalled or exceeded the statistics of the real data. Ideally, the final test-statistic will be $\ll 0.05$, particularly if choices for

data coding, standardization, association measure and classification are 'wise' (Belbin 1994a, b).

Seven ANOSIM analyses were run: 1) the five control groups; 2) Table Mountain 'grassy' forest data; 3) Table Mountain 'shrubby' forest data; 4) Glenmark; 5) Clarence Lagoon; 6) Mt. Franklin and 7) Tarraleah plantations. Analysis 1 tested for significant difference between the five control quadrat groups, analyses 2-6 tested for significant difference between logged quadrats and control quadrats; analysis 7 was used to test for significant differences between three groups, one group of control quadrats and one group for each of the two plantations.

3. A pattern analysis of vegetation change after partial logging in *E. delegatensis* R.T. Baker forests of the Central Plateau, Tasmania.

3.1 Introduction

Partial logging is a term used to describe harvesting treatments such as: selective logging; partial cutting; shelterwood; advanced growth retention; potential sawlog retention, and thinning and overstorey removal (Forestry Tasmania 2001). These silvicultural practices result in the removal of a proportion of the overstorey canopy and an increase in light levels on the ground, soil disturbance by heavy ground-based machinery, and the destruction or damage to a large proportion of the understorey trees and shrubs during the harvesting operation. Studies on the impact of different logging treatments have concentrated on the regeneration and development of the eucalypt overstorey in *E. delegatensis* forests (Battaglia & Wilson 1990, Bowman & Kirkpatrick 1986a, b, c, Nunez & Bowman 1986, Ellis *et al.* 1980) but have given little consideration to the impact on other biota, although Taylor and Haseler (1995) have examined the effects of partial logging on bird assemblages.

The effects of logging, both clearfelling and partial logging, on the understorey of other types of eucalypt forests suggest that logging leads to an increase in the cover of forbs (Bauhus *et al.* 2001, Peacock 1994, Dickinson & Kirkpatrick 1987, Kutt *et al.*

unpublished), increased biomass of ground ferns (Peacock 1994), particularly with fertilizer application (Bauhus *et al.* 2001, Connell & Raison 1996), and increased weed cover (Ough 2001, Peacock 1994, Dickinson & Kirkpatrick 1987). These studies all reported minimal changes in species richness and diversity, and no loss of native species following logging.

Unsurprisingly, logging has profound effects on the structure of a forest reducing the proportion and spatial distribution of old and large trees, the abundance of standing dead wood, logs and woody debris, and the range of ages of trees and the density of understorey (Recher 1996). It has also been suggested that the reduced density of the understorey may disrupt the normal pattern of secondary succession on logged sites, both in wet sclerophyll forest in Tasmania (Peacock 1994), and in *Picea-Tsuga* forest in North America (Alaback & Herman 1988).

Reported changes in the floristics and structure of the understorey following logging disturbance in North America, Madagascar, (Messier & Mitchell 1994, Ganzhorn *et al.* 1990, Alaback & Herman 1988) and in Australia (Ough 2001, Dickinson & Kirkpatrick 1987, Loyn *et al.* 1983) emphasize the importance of local site factors. Some common responses, particularly at the lifeform level, can be expected, but the impact on particular species, and the intensity and duration of impact, may be community and site specific.

An exploratory data analysis using multivariate techniques of ordination, classification and vector fitting are used here to summarise the floristic data, display any plant community patterns and link displayed community patterns to a set of environmental variables collected at the same time as the floristic data.

These techniques are a group of methods for data reduction and exploration leading to hypothesis generation (Kent & Coker 1999). They are ideal for recovering the latent

structure in a data matrix (of quadrats by species) so that patterns in community structure can be related to underlying ecological factors (Dickinson *et al.* 2002, Whinam *et al.* 2001, Fensham *et al.* 2000, Hans *et al.* 1999, Kent & Coker 1999, Tong 1992, Faith & Norris 1989, Kantvilas & Minchin 1989, Minchin 1989, Bowman & Minchin 1987, Faith *et al.* 1987). Multivariate techniques have proved particularly useful in human induced pollution and disturbance studies (Clarke 1993, Warwick 1993, Mueck & Peacock 1992, Underwood & Peterson 1988).

This chapter addresses three main questions: 1) does partial logging change the understorey floristics and/or vegetation structure? 2) are floristic changes associated with time since logging, i.e. do older logged sites more closely resemble unlogged sites? and 3) do different highland forest understorey types differ in sensitivity to partial logging?

3.2 Methods

Area descriptions and the multivariate data analysis techniques of ordination, classification, vector fitting and ANOSIM were common to chapters 3, 4, 5 and 7, and are detailed in chapter 2.

3.2.1 Survey design

A total of seven control sites and nine logged coupes, of different ages and sizes (8-50 ha) were surveyed for the dry sclerophyll pattern analysis survey. Controls were unlogged sites, adjacent to logged coupes where possible, and matched in altitude, slope

and aspect as closely as possible. Surveyed sites from all areas included: four control sites and four logged coupes at Table Mountain; one control site and two logged coupes at Glenmark; one control site and two logged coupes at Clarence Lagoon; and, one control site and one logged coupe at Mt. Franklin. The Clarence Lagoon coupe was partially logged in 1983, then an overstorey removal operation was carried out in 1987 on half of the original coupe. Both halves of the coupe were surveyed in this study. Each logged coupe and its adjacent control were surveyed within a week to minimise any seasonal effects on species abundance.

3.2.2 Data Collection

Six 20 m x 20 m quadrats were randomly situated within each of the logged coupes and each of the adjacent control sites. To achieve random placement of quadrats a set of random numbers determined a compass direction and a number of paces for each placement. Each quadrat was orientated such that two sides were parallel to the slope of the land.

At each corner within the 400 m² quadrat a 2 m x 2 m subplot was placed, giving a nested quadrat design that allowed different sized components of the vegetation to be surveyed (Kent and Coker 1999) (Fig 3.1). In this case the 400 m² quadrat was used to assess trees, dominant shrubs, grasses and ferns while the 4 m² quadrat was used to assess small ground forbs, smaller grasses and orchids. For these smaller species, percentage cover was estimated for the 20 m x 20 m quadrats by extrapolation.

Because of the range of different forest types sampled, the analysis for this chapter proceeded in four steps. Firstly, ordination and classification were carried out on only

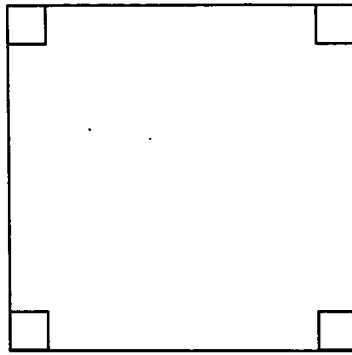


Figure 3.1 Configuration of 2 m x 2 m subplots nested within each 20 m x 20 m quadrat. Large quadrat used to assess trees, shrubs, grasses and ferns, small nested quadrats used to assess cover of small ground forbs.

the control quadrats to determine analogous forest types. Secondly, ecological correlates were determined for each forest type. Thirdly, effects of time since logging were assessed across all areas. Lastly, logging effects within similar forest types were assessed

3.3 Results

3.3.1 Analogous forest types and ecological correlates

The initial classification of the control quadrats differentiated six groups corresponding to: 1) grassy forest at Table Mountain-all 12 quadrats; 2) shrubby forest at Table Mountain-9 of 12 quadrats; 3) a mixed group of three quadrats of Table Mountain shrubby forest and two quadrats of Glenmark shrubby forest; 4) Glenmark shrubby forest –four of six quadrats; 5) Clarence Lagoon shrubby forest-all five quadrats; 6) grassy forest at Mt Franklin-all six quadrats (Fig 3.2). The three Table Mountain

shrubby forest quadrats of group 3 were on a south/south east aspect and were considered unrepresentative and so, despite their inclusion in the ordination of Figure 3.3 were discarded from all subsequent analyses. In the ordination the quadrats from 3) 'the mixed group' were given the same symbol as their original location (i.e. the three Table Mountain shrubby forest quadrats from the classification group 3 were placed back in group 2 with the majority of the Table Mountain shrubby forest quadrats, the two Glenmark shrubby forest quadrats were placed back in group 4 with the other Glenmark shrubby forest quadrats). This gave five site/forest understorey types that were spread along the environmental gradients of rainfall, altitude, rock and grass cover. *Rainfall*, *altitude*, and *rock cover* (correlation = 0.86, 0.81 and 0.78 respectively) were the strongest fitted variables in the ordination space (Fig. 3.3a, b).

Similarly, the ANOSIM analysis was run on the same five original location groups in Fig. 3.3a, b (grassy forest at Table Mountain and Mt Franklin, shrubby forest at Table Mountain, Glenmark and Clarence Lagoon) and was very significant ($P < 0.000$, best between group statistic = 1.053, real between group statistic 1.505, Table 3.1).

Table 3.1 Results of ANOSIM analysis on classification defined groups using 1000 random permutations in PATN.

| Site | No. of groups | Best between-group statistic | Real between-group statistic | Probability |
|-------------------|---------------|------------------------------|------------------------------|-------------|
| All controls | 5 | 1.053 | 1.505 | $P < 0.001$ |
| Table Mtn grassy | 2 | 1.145 | 1.188 | $P < 0.001$ |
| Table Mtn shrubby | 2 | 1.219 | 1.515 | $P < 0.001$ |
| Glenmark | 2 | 1.141 | 1.401 | $P < 0.001$ |
| Clarence Lagoon | 2 | 1.116 | 1.134 | $P < 0.001$ |
| Mt. Franklin | 2 | 1.201 | 1.754 | $P < 0.001$ |

There are two distinct forest understorey types at Table Mountain (clearly separated along axis 2 in Fig.3.3a): a forest type at altitude 730-780m comprised of more than one eucalypt species and understorey of predominantly: *Acacia dealbata*, *Leucopogon*

hookeri, *Lomatia tinctoria*, *Poa* spp. and *Lomandra longifolia*; and a higher altitude forest with *Cyathodes parvifolia* shrub dominated understorey. Glenmark has a shrubby type understorey of: *Acacia verniciflua*, *Cyathodes parvifolia*, *Notolea ligustrina*, *Olearia viscosa* and *Polystichum proliferum*. Clarence Lagoon, also a shrubby type understorey comprised of: *Bedfordia linearis*, *Notolea ligustrina*, *Pultenaea juniperina* and the lily *Diplarrena latifolia*, separated along axis 3 in Fig. 3.3b. Both Glenmark and Clarence Lagoon quadrats are positively associated with the vectors for increased *rock cover*, *rainfall* and *maximum tree height*. Mt. Franklin, a grassy type forest with characteristic species *Poa gunnii*, *Cyathodes parvifolia*, *Leucopogon hookeri* and *Lomatia tinctoria*, has quadrats that are clearly separated along axis 1 in Fig 3.3a, and positively associated with the vector for increased *altitude*.

The five area/forest types defined in Fig 3.3a, b can be split into two types of *E. delegatensis* forest defined by Duncan and Brown (1985): i.e. 'Grassy *E. delegatensis*' at Table Mountain and Mt Franklin; and 'Shrubby *E. delegatensis*' at Table Mountain, Clarence Lagoon and Glenmark, respectively. Each area in this study displayed site-specific species compositions along an increasing rainfall gradient from east to west. The trend across the plateau of increasing rainfall from east to west is clearly seen from the dry sites of Table Mountain and Mt Franklin to the wetter sites of Glenmark and Clarence Lagoon (Fig 3.3). These five area/forest types display a floristic variation that is continuous, rather than showing structuring into floristic groups. The continuous variation meant that each area was assessed separately in regard to the impact of logging.

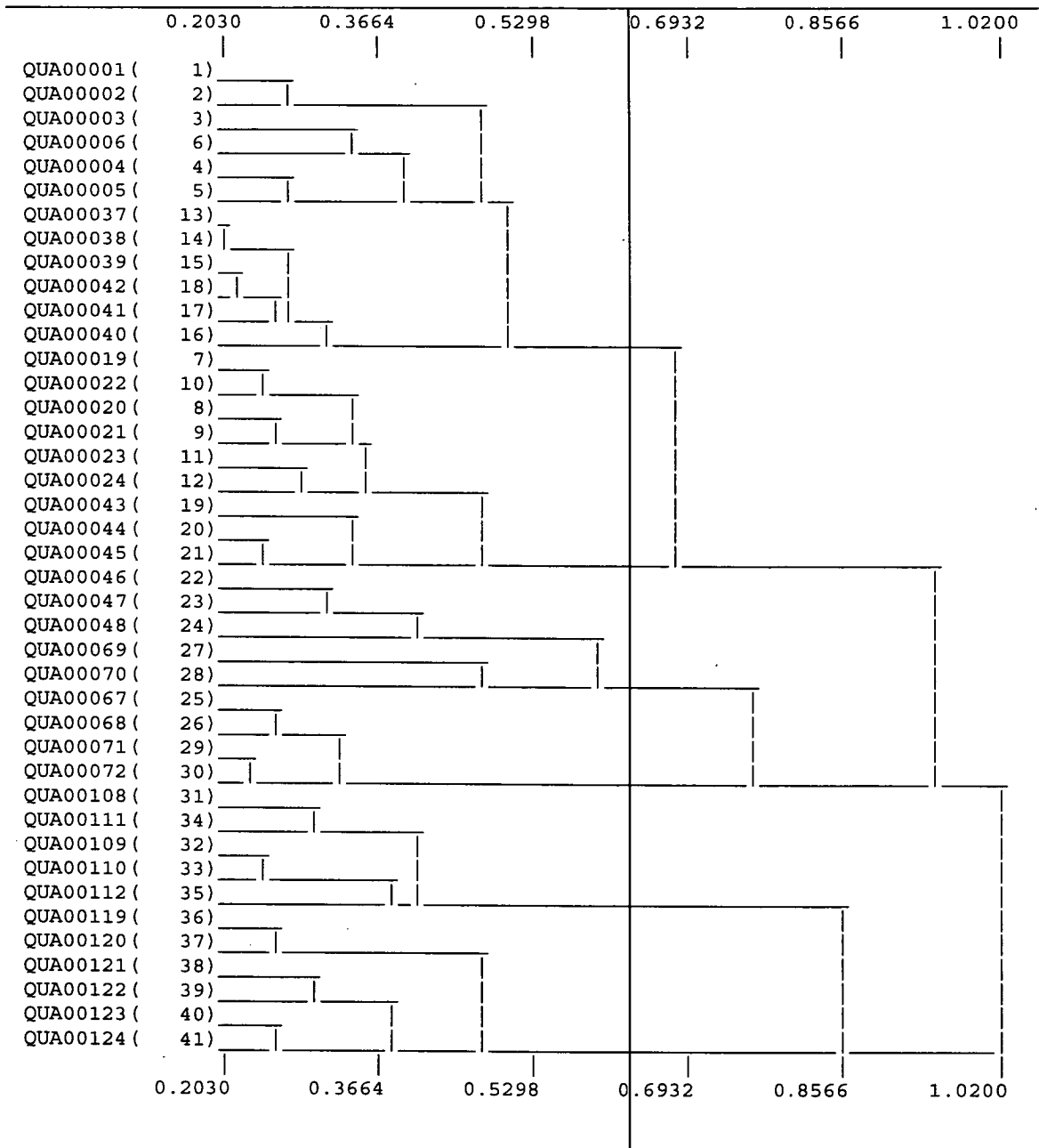


Figure 3.2 Dendrogram of the 41 native forest control quadrat classification showing line that defines the six groups. Group 1, quadrats 1-6 and 37-42 = Table Mountain grassy forest; group 2, quadrats 19-24 and 43-45 = Table Mountain shrubby forest; group 3, quadrats 46-48 = Table Mountain shrubby forest, quadrats 69-70 = Glenmark shrubby forest; group 4, quadrats 67-68, 71-72 = Glenmark shrubby forest; group 5, quadrats 108-112 = Clarence Lagoon shrubby forest; group 6, quadrats 119-124 = Mt Franklin grassy forest.

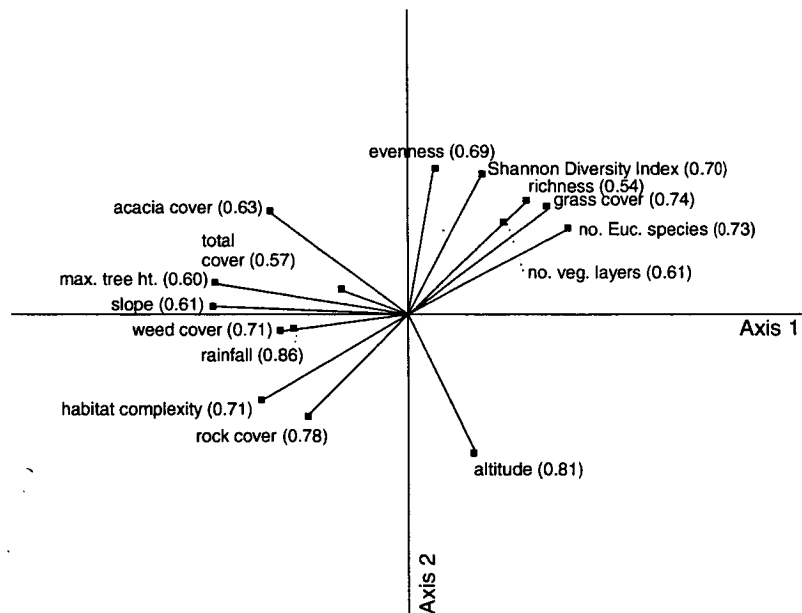
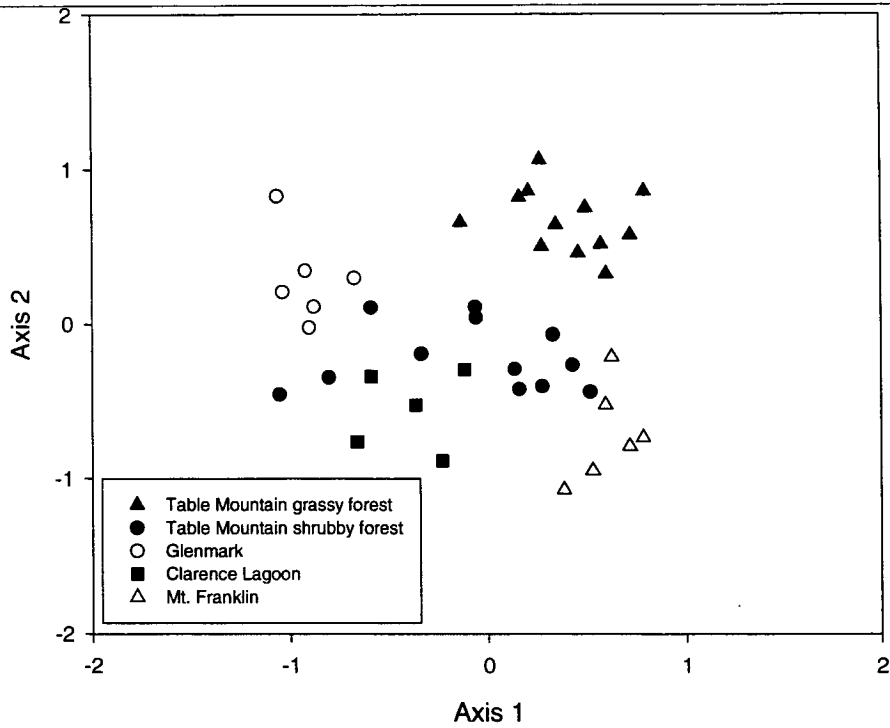


Figure 3.3a SSH ordination in three dimensions (stress = 0.16), showing the five area/forest types and significant ($P < 0.05$) fitted vectors for environmental variables with respect to axis 1 against axis 2. Each fitted vector is displayed with R value

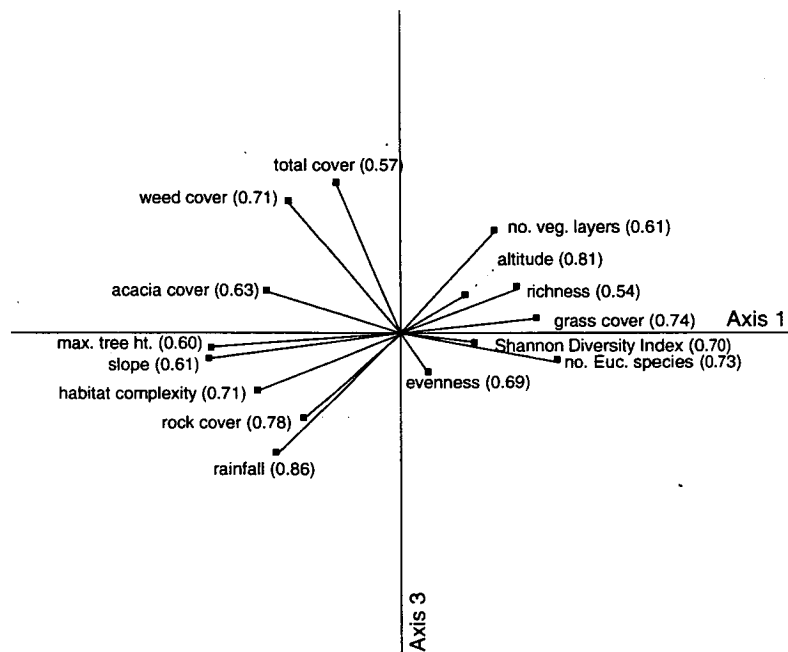
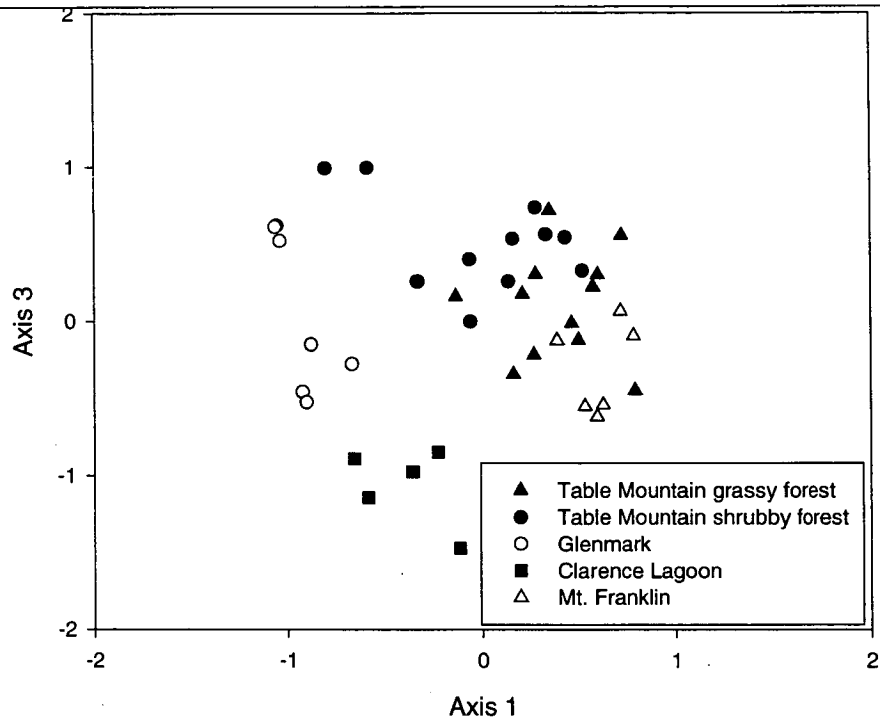


Figure 3.3b SSh ordination in three dimensions (stress = 0.16), showing site/forest types and significant ($P < 0.05$) fitted vectors for environmental variables with respect to axis 1 against axis 3. Each fitted vector is displayed with R value.

3.3.2 Temporal effects

To assess temporal effects of logging, an ordination of the entire data set is presented with group centroids calculated for each unlogged control and each logged coupe, and each coupe is labelled with the date of logging (Fig. 3.4). The group centroids were used because any temporal pattern would be easier to discern without the clutter of 91 quadrats. Examination of the ordination, however, shows no clear temporal pattern, for example, the oldest logged quadrats at Mt Franklin (1977/78) display the same spatial separation from the Mt Franklin controls as more recently logged quadrats do from their site controls (Fig.3.4).

These first analyses show the strong floristic separations between the different areas, with greater similarity between control quadrats and logged quadrats within each area than between logging treatments across areas (also see Appendix 1, species frequency and mean cover data at each site). It was concluded that none of the forest types could be considered as replicates but represent the range of forest communities that collectively come under *E. delegatensis* forest types. It was decided, therefore, to determine common patterns of change post logging between the five area/forest types: Table Mountain grassy *E. delegatensis* and Table Mountain shrubby *E. delegatensis* forests, Glenmark shrubby *E. delegatensis* forest, Clarence Lagoon shrubby *E. delegatensis* forest and Mt. Franklin grassy *E. delegatensis* forest.

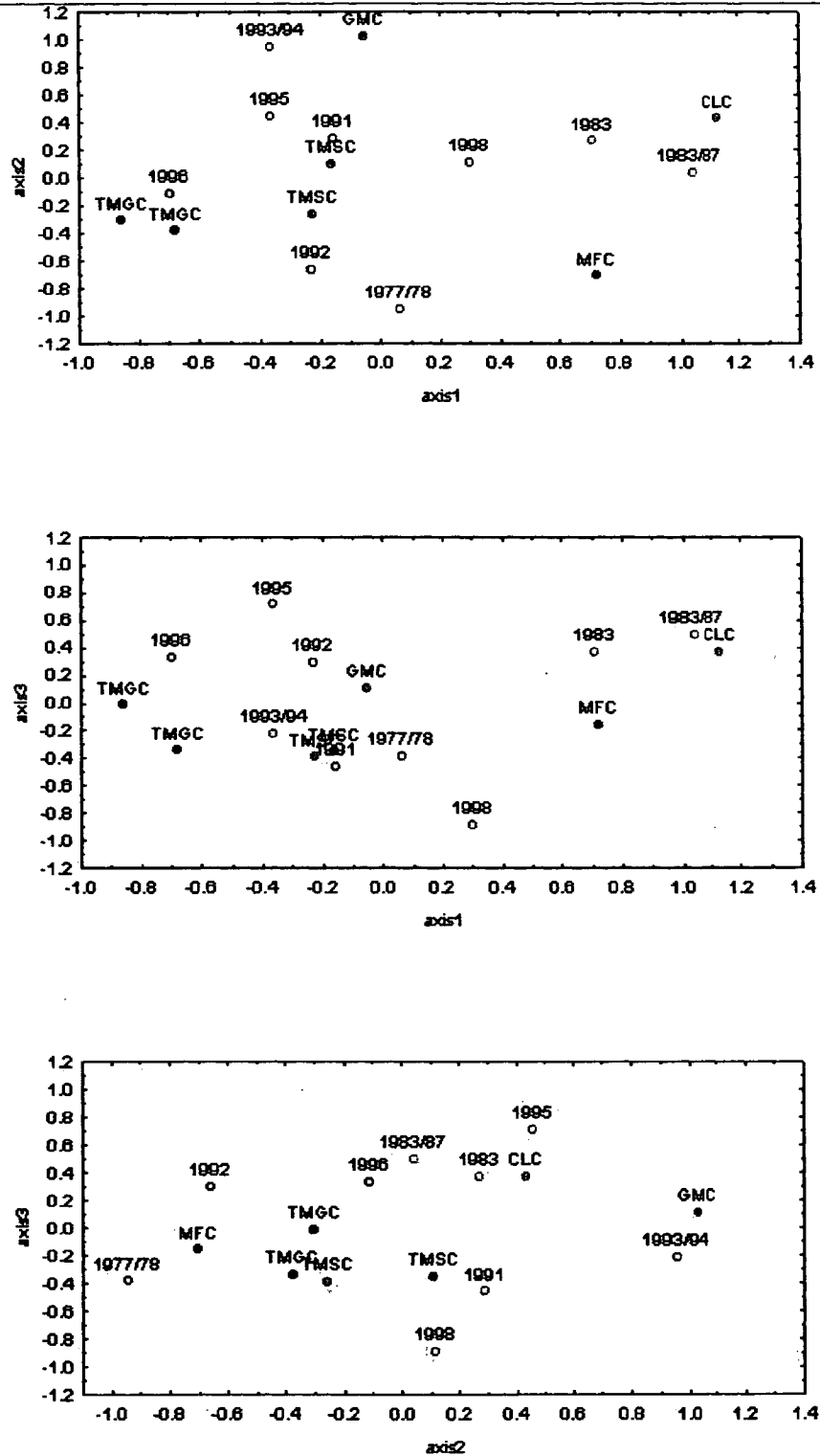


Figure 3.4 SSH ordination in three dimensions (stress = 0.16) of the group centroids of nine logged coupes and seven controls. TMGC = Table Mtn. grassy control, TMSC = Table Mtn. shrubby control, GMC = Glenmark control, CLC = Clarence Lagoon control, MFC = Mt. Franklin control. Logged coupes displayed with date logged.

3.3.3 Effects of logging within similar forest types.

3.3.3.1 Table Mountain grassy *E. delegatensis* forest

The results of the classification and ordination suggest that the management regime of partial logging was the most important factor separating these quadrats in the ordination space (Fig. 3.5a, b). The ANOSIM analysis found the logged quadrats to be significantly floristically different to the control quadrats (Table 3.1).

Two classifications were carried out, a site classification of 24 quadrats (Fig. A.4.1 Appendix 4), and a species classification of 88 species (Fig. A.4.2 Appendix 4) that resulted in the four site groups and six species groups, of Table 3.2. The three dimensional ordination indicated four clusters, the same four groups produced by the classification procedure, clearly separating the logged quadrats from the control quadrats. The vector for *type* (a dummy variable where 1 = controls, 2 = logged quadrats, $r = 0.94$) was associated with logged quadrats and antagonistic to the next strongest variable of increasing *basal area* ($r = 0.91$) associated with controls. The other significant variables can be split into two groups more or less parallel to axis 2. Increased *habitat complexity*, *number of eucalypt classes*, *number of vegetation layers* and *maximum understorey height* were associated with the controls, whereas increased *bare ground*, *weed cover*, *slope*, *altitude* and *aspect* were associated with logged quadrats.

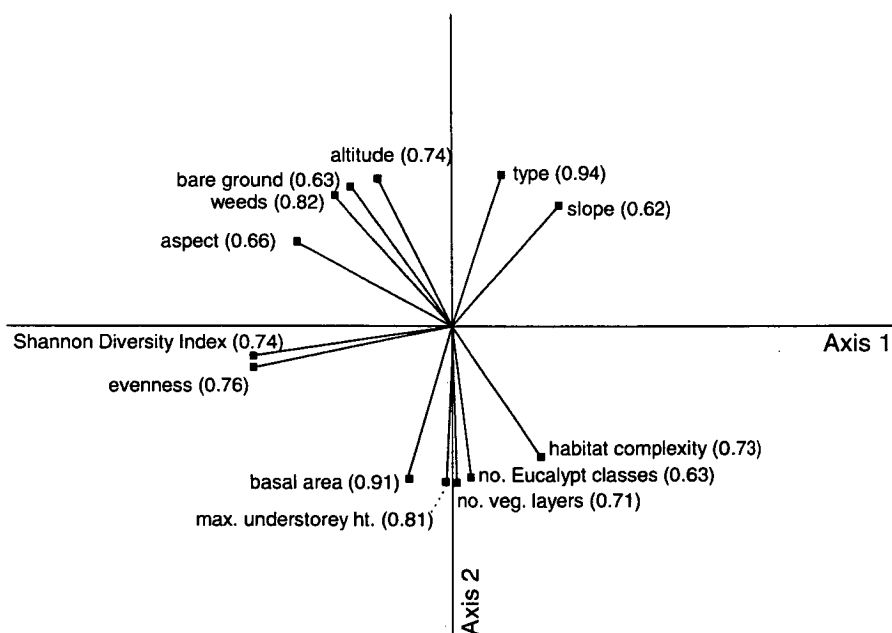
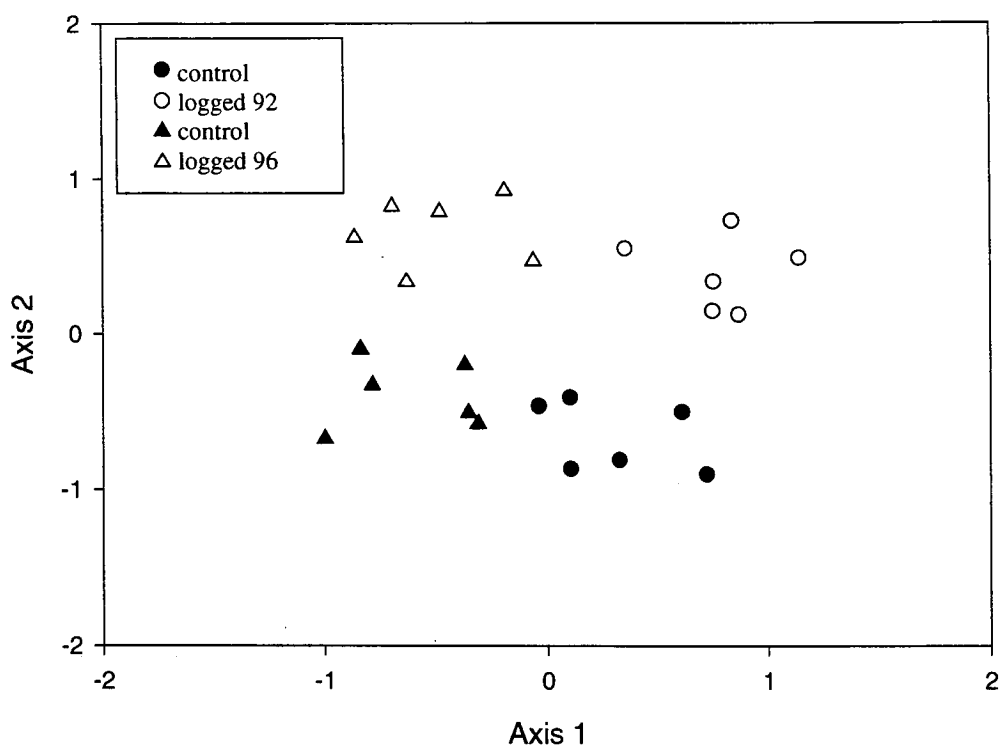


Figure 3.5a SSH ordination in three dimensions (stress = 0.17) of Table Mtn. grassy forest quadrats and significant ($P < 0.05$) fitted vectors for environmental variables with respect to axis 1 against axis 2. Each fitted variable displayed with R value.

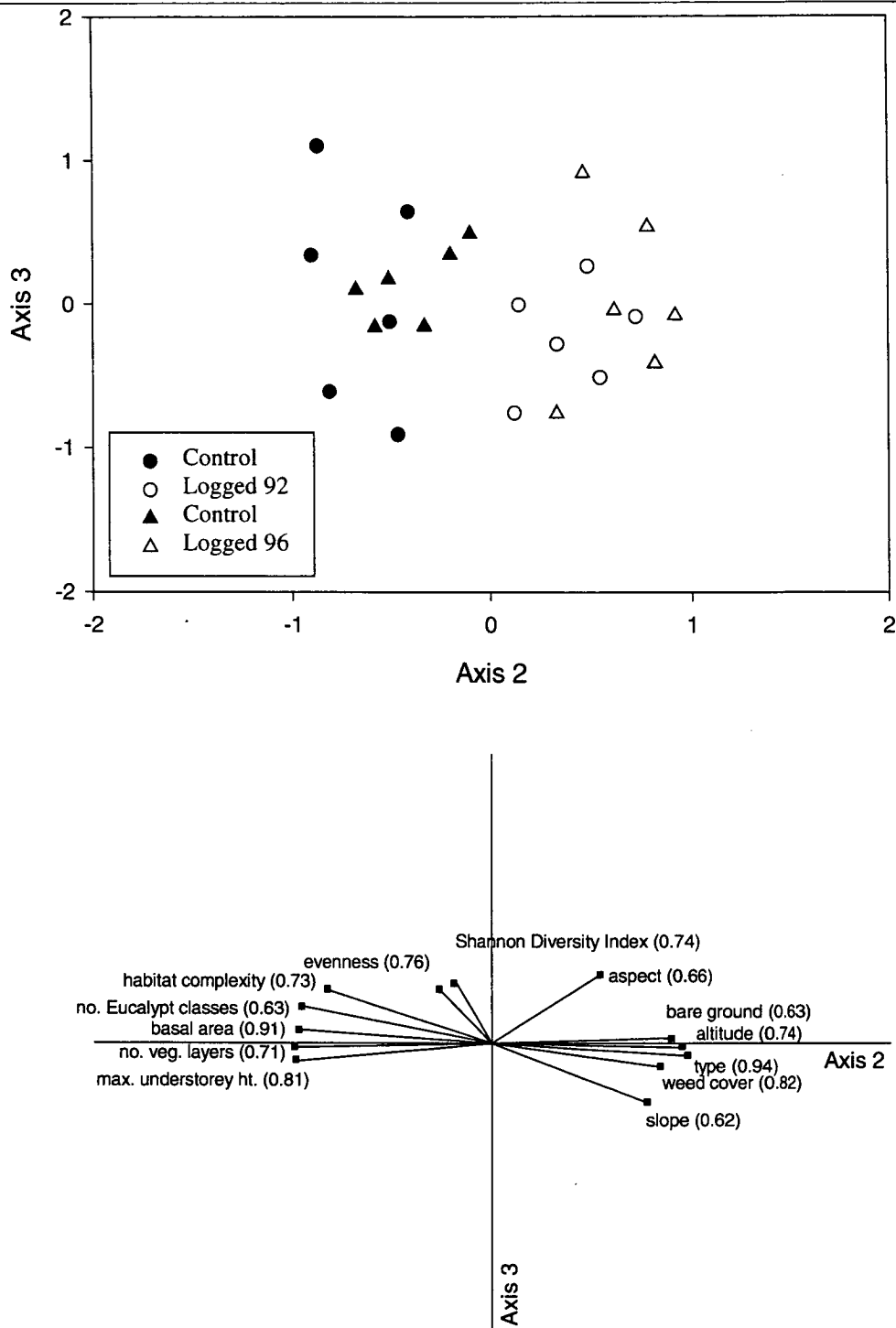


Figure 3.5b SSH ordination in three dimensions (stress = 0.17) of Table Mtn. grassy forest quadrats and significant ($P < 0.05$) fitted vectors for environmental variables with respect to axis 2 against axis 3. Each fitted variable displayed with R value.

| | unlogged | | logged | |
|----------------------------------|----------|---------|---------|--------|
| | | | 1992 | 1996 |
| | 000000 | 122222 | 000111 | 111111 |
| | 123456 | 901234 | 789012 | 345678 |
| <i>Acacia dealbata</i> | 22121 | 121111 | + + + + | r+122+ |
| <i>Pteridium esculentum</i> | 111+11 | 221111 | + +r+1 | ++112r |
| <i>Leucopogon hookeri</i> | 122221 | 221221 | 11+rr+ | + 1rr+ |
| <i>Lomatia tinctoria</i> | 22211+ | 1 1 12 | 111+11 | 11222r |
| <i>Acaena novae-zelandiae</i> | r r | 1+11++ | 111r1r | 1121r+ |
| <i>Hydrocotyle hirta</i> | 11rrrr | 121111 | r rrrr | 112212 |
| <i>Cyathodes parvifolia</i> | + | 11+11+ | r1 r r | +2211+ |
| <i>Lomandra longifolia</i> | 221+12 | 111+ | 222222 | r |
| <i>Poa gunnii</i> | 222222 | 222112 | 111+21 | 222222 |
| <i>Poa rodwayi</i> | 11 | 1+1111 | | ++122r |
| <i>Acacia melanoxylon</i> | 22 | | r | 2 |
| <i>Scleranthus biflorus</i> | r | 11 | | r |
| <i>Acaena echinatus</i> | r r | + + + r | r r r r | r |
| <i>Drymophila cyanocarpa</i> | rr rrr | + +r | r+rr r | rr |
| <i>Veronica calycina</i> | rrrr | +++ +r | r+rr | r r |
| <i>Poranthera microphylla</i> | rr | +++ + | r+rrrr | r rr |
| <i>Wahlenbergia</i> spp | rrrr | ++++ r | r+rrrr | rrrr |
| <i>Geranium sessiliflorum</i> | r rrr | 1++1+r | r+r rr | rrrr1r |
| <i>Lagenophora stipitata</i> | rrrrr | +++++ | r+r rr | +rr1 |
| <i>Hypericum japonicum</i> | rrrrrr | 1++++r | rrr | rrrr r |
| <i>Pratia pedunculata</i> | rrr r | +++++ | r rrrr | rr12r1 |
| <i>Ranunculus scapiger</i> | rrr rr | rr++rr | r+rrr | +rrrrr |
| <i>Gonocarpus serpyllifolius</i> | rrrrrr | 11111+ | r+rrrr | ++11r+ |
| <i>Viola hederacea</i> | 111rrr | 11111r | +r+rr | +r r |
| <i>Euchiton collinum</i> | r | r ++ | r | r r1+ |
| <i>Hypochaeris radicata*</i> | | + r r | rr+r | rr rrr |
| <i>Poaceae</i> | rrrrr | ++ | r+r rr | 1122r+ |
| <i>Pultenaea juniperina</i> | r | + r r | 1 +++ | 111211 |
| <i>Galium australe</i> | rrrr r | ++1++r | r | r r |
| <i>Viola betonicifolia</i> | r r | +++ +r | | rr |
| <i>Pterostylis</i> spp | r rrr | ++ +r | | |
| <i>Veronica gracilis</i> | r r | ++ r | | r r |
| <i>Arthropodium milleflorum</i> | r r | | r+rrrr | r |
| <i>Senecio gunnii</i> | r rr | | r+rrrr | |
| <i>Brachyscome spathulata</i> | r r | | +rr | r |
| <i>Diplarrena moraea</i> | r | | rrr | r |
| <i>Helichrysum scorpioides</i> | rr | rr+r | r+r rr | r |
| <i>Luzula</i> spp | rrr r | r | r+rrrr | rrr |
| <i>Dianella tasmanica</i> | r2 r+ | r | + r | |
| <i>Brachyscome decipiens</i> | rr | r | | r |
| <i>Chiloglottis gunnii</i> | 1r | + | | r |
| <i>Drosera peltata</i> | rr | | | r |
| <i>Caladenia alpina</i> | r rr+ | | | |
| <i>Carex breviculmis</i> | r r | | | |
| <i>Cirsium vulgare*</i> | | | r+rrr | rlrrr |
| <i>Epilobium sarmentaceum</i> | r | | r1 rr | rrr1 r |
| <i>Oxalis perennans</i> | rrr | | r | rrr r |
| <i>Leontodon taraxacoides*</i> | | | r+ | 1 |
| <i>Leptospermum lanigerum</i> | | | | r+ 1 |
| <i>Oreomyrrhis eriopoda</i> | | | | r r r |
| <i>Taraxacum officinale*</i> | | | | rr r |
| <i>Comesperma volubile</i> | | | rr | |
| <i>Hypericum gramineum</i> | | | rr | r |
| <i>Myotis australis</i> | | | | rr |
| <i>Carex raleighii</i> | | ++ | | |
| <i>Dichondra repens</i> | | 111++r | | |
| <i>Vulpia megalura*</i> | | + 1+ | | |
| <i>Juncus gregiflorus</i> | | 1 + | | |
| <i>Microseris scapigerus</i> | | r++ r | | |
| <i>Plantago glabrata</i> | | +++ r | | |
| <i>Acianthus</i> spp | r r | | | |
| <i>Craspedia glauca</i> | r r | | r | |
| <i>Gonocarpus tetragynus</i> | r | | r | |
| <i>Pimelea humilis</i> | r | | | |
| <i>Asplenium flabellifolium</i> | r | | | r |
| <i>Cardamine</i> spp* | r | | | r |

Table 3.2 Two-way table of Table Mountain grassy forest showing the six classification defined species groups and the four site groups. Quadrat groups are controls = 1-6, 19-24, logged 92 coupe = 7-12, logged 96 coupe = 13-18. * denote introduced species. Table values were derived from an arbitrary scale where a blank denotes absence, and +, r, 1, 2 denotes increasing cover/abundance.

Six species groups were defined by the classification procedure and show the highly site-specific nature of species distributions in these forests. Each group of control quadrats and each group of logged quadrats have species present that are absent from the other quadrat groups (Table 3.2). Logging, however, does result in two consistent changes across the two coupes; 1) increased cover of five forbs, some grasses, and the shrub *Pultenaea juniperina*; and 2) decreased cover of two forbs, the orchid *Pterostylis* spp. and the shrub *Leucopogon hookeri* (see Appendix 1).

3.3.3.2 Glenmark shrubby forest

Examination of the ordination suggests that partial logging was causing the separation of the three coupes in the ordination space. The classification procedure produced three site groups corresponding to the two sampled coupes and the controls and these can be clearly seen in the ordination (Fig. 3.6) and five species groups (Table 3.3).

Classification dendrograms of site are displayed in Appendix 4. ANOSIM analysis was carried out on only two groups, both logged coupes were combined and tested against the control group, and were found to be significantly different (Table 3.1)

The logged quadrats were clearly differentiated from the control quadrats and were associated with the vector for increasing type ($r = 0.86$). Other significant vectors can be divided into two groups. The first, associated with the controls, included increasing *acacia cover* ($r = 0.79$), *rock cover* ($r = 0.71$), *basal area* ($r = 0.70$) and *habitat complexity* ($r = 0.76$). The second group, antagonistic to the first, and associated with logged quadrats include increasing *grass cover* ($r = 0.77$), *Shannon Diversity Index* ($r = 0.60$), and *species richness* ($r = 0.68$). The significantly correlated vectors *altitude* ($r =$

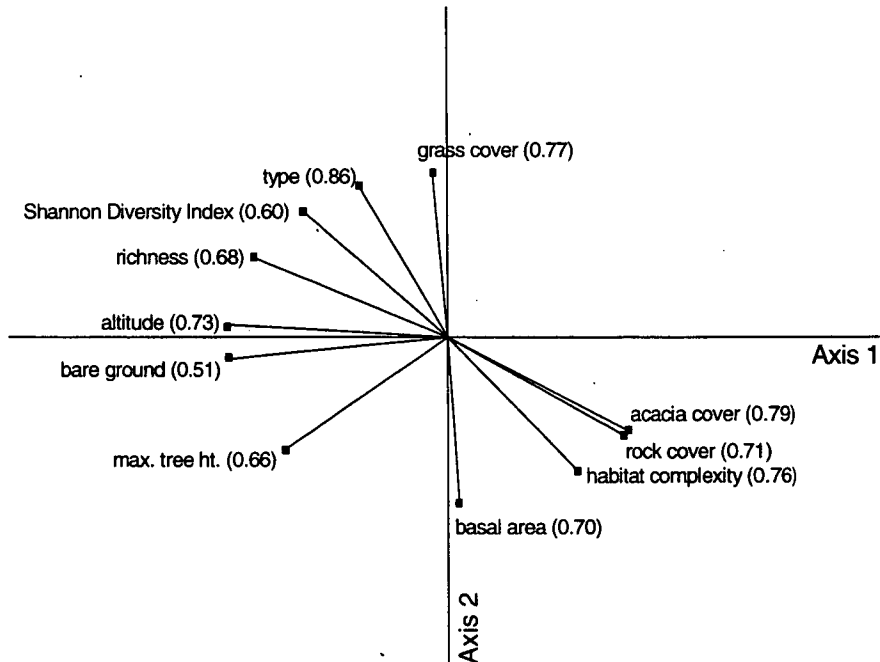
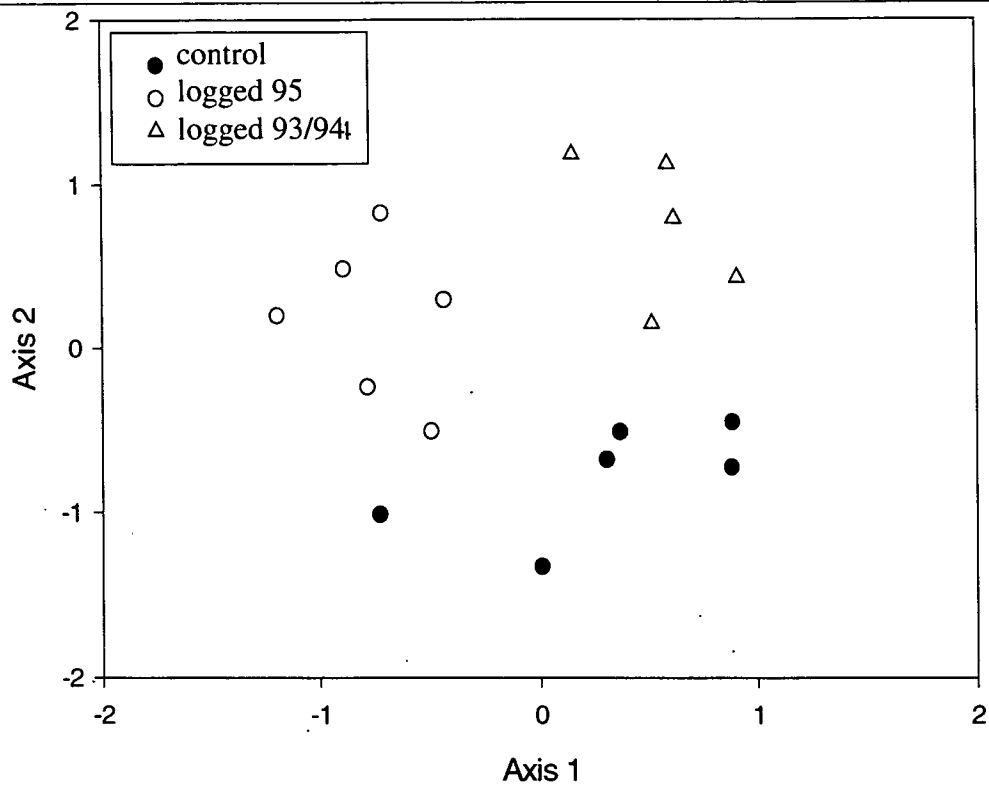


Figure 3.6 SSH ordination in two dimensions (stress = 0.22) of Glenmark shrubby forest quadrats and significant ($P < 0.05$) fitted vectors for environmental variables. Each fitted variable displayed with R value.

0.73) and *bare ground* ($r = 0.51$) reflect the fact that the 1995 coupe was 20-30m higher in altitude, and had higher bare ground cover, than the controls and the 1993/94 logged coupe.

Species increasing in cover in logged coupes included three forbs, one shrub and the grass *Poa gunnii*; species decreasing in cover were three shrubs and the orchid *Pterostylis* spp. (Table 3.3, Appendix 1).

The remaining three area/forest types, Table Mountain shrubby forest, Clarence Lagoon shrubby forest (Table 3.4) and Mt. Franklin grassy forest (Table 3.5) displayed the same general trends with respect to logging, i.e. logged quadrats clearly separated from control quadrats in the ordination space, and associated with increased bare ground, forb and grass cover, and decreased basal area, habitat complexity, shrub and orchid cover as those exhibited above and so will not be presented here.

3.4 Discussion

3.4.1 Floristic change

The floristic analyses across all areas shows that there are floristic differences between areas that override the differences between controls and logged coupes. However, the pattern analysis did reveal significant differences between logged coupes and adjacent controls at all areas. The differences are largely due to the altered cover of species in logged coupes, rather than changes in species presence/absence, although weed species were more common in logged coupes.

| | unlogg ed | logged | |
|----------------------------------|--------------|--------|-------|
| | 000111 | 000000 | 11111 |
| | 789012 | 123456 | 34567 |
| <i>Acacia dealbata</i> | r1 | + 1 + | +r111 |
| <i>Acaena novae-zelandiae</i> | + +r | 1111+1 | 122+1 |
| <i>Poa gunnii</i> | r | 2111 + | 11112 |
| Poaceae | 1 r | +1+ | 21 |
| <i>Hydrocotyle hirta</i> | 1+1+1r | 111111 | r r |
| <i>Polystichum proliferum</i> | +r11 | ++ 111 | + r++ |
| <i>Cyathodes parvifolia</i> | 11r112 | 121211 | 11+11 |
| <i>Pultenaea juniperina</i> | 22 12 | 222 22 | 1++12 |
| <i>Poa tenesis*</i> | 1 r | 21 | 1 + |
| <i>Deyeuxia monticola</i> | +r | +1 | +1r + |
| <i>Lomatia tinctoria</i> | 11 11 | | 12111 |
| <i>Pteridium esculentum</i> | 222 2+ | 2 1 | 21122 |
| <i>Asperula gunnii</i> | | r 1++ | rrr |
| <i>Leucopogon hookeri</i> | | r1+ | r r1 |
| <i>Oxalis perennans</i> | rr | r + | r |
| <i>Poa pratensis*</i> | | 1+ | + |
| <i>Poa rodwayi</i> | | r | +1r |
| <i>Asperula conferta</i> | +r+rr | 1+ | |
| <i>Pterostylis</i> spp. | rr r | r | |
| <i>Ranunculus scapiger</i> | + r | r | r |
| <i>Drymophila cyanocarpa</i> | +r rrr | r++r+ | r r |
| <i>Lagenophora stipitata</i> | +rrrrr | +r++++ | r rr |
| <i>Pimelea drupaceae</i> | +r1+rr | r r+r+ | r |
| <i>Geranium potentilloides</i> | + r | +r+ | rrrrr |
| <i>Helichrysum scorpioides</i> | 1r r | r r+ | r |
| <i>Galium australe</i> | +rrr r | ++1+r+ | r r |
| <i>Viola hederacea</i> | r r | ++1+r+ | r r |
| <i>Geranium sessiliflorum</i> | +r r | 1+1 r+ | |
| <i>Scleranthus biflorus</i> | | r + | rr |
| <i>Acacia verniciflua</i> | 11 22 | | + |
| <i>Notolea ligustrina</i> | 1r +1 | | r |
| <i>Olearia phlogopappa</i> | +r | | |
| <i>Olearia viscosa</i> | 1+12++ | 11 | |
| <i>Epilobium sarmentaceum</i> | | | rr +r |
| <i>Ranunculus lappaceus</i> | | | r r |
| <i>Huperzia australiana</i> | | | rr |
| <i>Australopyrum pectinatum</i> | | rr 1 + | r |
| <i>Gonocarpus serpyllifolius</i> | | rr+1 + | |
| <i>Senecio minimus</i> | | ++ + + | |
| <i>Hypericum japonica</i> | | rr +r+ | r |
| <i>Euchiton collinum</i> | | rr++ | |
| <i>Uncinia elegans</i> | | r++r | |
| <i>Cirsium vulgare*</i> | | + ++ + | |
| <i>Luzula</i> spp | | r + + | |
| <i>Poranthera microphylla</i> | r | + ++ | r |
| <i>Dicksonia antarctica</i> | r | 1+ | |
| <i>Echinopogon ovatus</i> | | r r | |
| <i>Tasmannia lanceolata</i> | | r r | |
| <i>Bedfordia salicina</i> | | + + | |
| <i>Gonocarpus teucრიoides</i> | | + r+ | |
| <i>Veronica notabilis</i> | | r r | r |
| <i>Veronica calycina</i> | + | r | |

Table 3.3 Two-way table of Glenmark shrubby forest showing the five classification defined species groups and the three site groups. Quadrat groups are control = 7-12, logged 93/95 coupe = 13-17, logged 95 coupe = 1-6. * denotes introduced species. Table values were derived from an arbitrary scale where a blank denotes absence of the species, and +, r, 1, 2 denotes increasing cover/abundance.

| | logged | | control | |
|----------------------------------|--------|--------|---------|---|
| | 000000 | 000111 | 11111 | |
| | 123456 | 789012 | 34567 | |
| <i>Acaena novae-zelandiae</i> | lr + | rrr | | |
| <i>Pteridium esculentum</i> | | l++ | | |
| <i>Euchiton collinum</i> | r | rr | | |
| <i>Ranunculus scapiger</i> | | rrr | | |
| <i>Viola hederacea</i> | r | rr | | |
| <i>Asperula gunnii</i> | | r rr | | |
| <i>Hydrocotyle hirta</i> | + | rr rr | + | |
| <i>Lagenophora stipitata</i> | +r | rr rr | | |
| <i>Gonocarpus serpyllifolius</i> | | rr r | r | |
| <i>Leucopogon hookeri</i> | l | r | | |
| <i>Oreomyrrhis eriopoda</i> | r | r | | |
| <i>Aristotelia peduncularis</i> | r+ | r | + | |
| <i>Luzula</i> spp | r | r | + | + |
| <i>Veronica notabilis</i> | + | r | + | |
| <i>Blechnum</i> spp | | r r | | |
| <i>Hypericum japonicum</i> | r | r | | |
| <i>Hypochaeris radicata</i> * | rr | r | | |
| <i>Asplenium flabellifolium</i> | | | r +r+ | |
| <i>Deyeuxia monticola</i> | | | r+ | |
| <i>Billardierei longifolia</i> | r +r | | r + | |
| <i>Coprosma hirtella</i> | rr++ | r | r r+ | |
| <i>Gonocarpus teucroides</i> | | | r r | |
| <i>Coprosma quadrifida</i> | rr | | rr + | |
| <i>Pittosporum bicolor</i> | r | | r | |
| <i>Stylidium graminifolium</i> | r rr | | | |
| <i>Cardamine</i> spp* | | | r r | |
| <i>Bedfordia linearis</i> | 22211+ | 2 r+2r | 21211 | |
| <i>Lomatia tinctoria</i> | 222121 | 211111 | 111+1 | |
| <i>Pultenaea juniperina</i> | 222222 | 222222 | 22222 | |
| <i>Cyathodes parvifolia</i> | 111+1+ | 21+r++ | +1++ | |
| <i>Diplarrena latifolia</i> | 211+11 | r++112 | 1+1++ | |
| <i>Poa gunnii</i> | 212+1+ | 2111+1 | r+1 | |
| <i>Dianella tasmanica</i> | + | 1+r + | + r | |
| <i>Hakea lissosperma</i> | 1 rlr | 2 + | r 1r | |
| <i>Notolea ligustrina</i> | ++r | rr+r | ++1++ | |
| <i>Drymophila cyanocarpa</i> | 1rrrlr | rrr++r | r +r | |
| <i>Senecio linearifolius</i> | 1rr +r | r+++rr | r+ + | |
| <i>Helichrysum scorpioides</i> | r rr+r | rrr++r | r+r+ | |
| <i>Olearia erubescens</i> | rrrr+r | rrrrr | rr+r+ | |
| <i>Tasmania lanceolata</i> | rr r | rrrrrr | ++r+ | |
| <i>Olearia viscosa</i> | r rr | rr++ + | +r+ | |
| <i>Pimelea nivea</i> | rr r+r | r r | r+ + | |
| <i>Geranium sessiliflorum</i> | rr r | rr rr | +r+ | |
| Orchidaceae | r rr+r | rrrr | + +r+ | |
| <i>Poranthera microphylla</i> | r r+r | r rrr | r r+ | |
| <i>Galium australe</i> | r | rrr | rr+ + | |
| <i>Goodenia lanata</i> | r r + | r rrr | + | |
| <i>Olearia phlogopappa</i> | 1 r+r | + r | r | |

Table 3.4 Two-way table of Clarence Lagoon shrubby forest showing the ten classification defined species groups and the three site groups. Quadrat groups are unlogged controls = 13-17, logged 83/87 coupe = 1-6, logged 83 coupe = 7-8. * denotes introduced species. Table values were derived from an arbitrary scale where a blank denotes absence of the species, and +, r, 1, 2 denotes increasing cover/abundance.

The effect of partial logging on understorey is, therefore, likely to be very site specific with respect to species and will be influenced by the initial floristic composition at each

site. There were general trends, however, and partial logging was found to be associated with an increase in, bare ground, weed, and grass cover and a decrease in the structural complexity of the vegetation at all areas.

| | logged 000000 123456 | unlogged 000111 789012 |
|----------------------------------|----------------------------|------------------------------|
| <i>Acaena novae-zelandiae</i> | +r++++ | +++rrr |
| <i>Gonocarpus serpyllifolius</i> | ++rr++ | +++rrr |
| <i>Veronica calycina</i> | ++++r+ | +++ rr |
| <i>Viola hederacea</i> | rrr+ | + + r |
| <i>Leucopogon hookeri</i> | 11111+ | +++rr+ |
| <i>Diplarrena moraea</i> | + rr+ | rrrr |
| <i>Poranthera microphylla</i> | rr+ | + rr |
| Orchidaceae | rrrr + | r +rlr |
| <i>Helichrysum scorpioides</i> | r + | +rrr |
| <i>Coprosma quadrifida</i> | r | +++ r |
| <i>Olearia erubescens</i> | r + | +++rrr |
| <i>Geranium sessiliflorum</i> | | + rr |
| <i>Wahlenbergia</i> spp | r | + rr |
| <i>Craspedia glauca</i> | rr | |
| <i>Drymophila cyanocarpa</i> | r | r |
| <i>Epilobium sarmentaceum</i> | + + | |
| <i>Galium australe</i> | rrrr+ | ++ |
| <i>Hydrocotyle hirta</i> | +++rr+ | ++ r |
| <i>Euchiton collinum</i> | +rrr + | + + |
| <i>Hypericum japonicum</i> | +rrrr+ | + r |
| <i>Senecio gunnii</i> | +rrr + | r |
| <i>Ranunculus scapiger</i> | +r++r+ | r |
| <i>Geranium mollis</i> * | ++rrr+ | |
| <i>Luzula</i> spp | rrrr+ | |
| <i>Hypochaeris radicata</i> * | +r | rr |
| <i>Oreomyrrhis eriopoda</i> | +r | |
| <i>Plantago glabrata</i> | +r r | r |
| <i>Brachyscome spathulata</i> | r | +r |
| <i>Stylidium graminifolium</i> | | +r |
| <i>Microseris scapigerus</i> | | + + |
| <i>Cyathodes parvifolia</i> | 1+1222 | 222222 |
| <i>Poa gunnii</i> | 222222 | 11++21 |
| <i>Deyeuxia monticola</i> | r | +1+ |
| <i>Pultenaea juniperina</i> | | +r11 |
| <i>Hakea lissosperma</i> | | + r2+ |
| <i>Pultenaea gunnii</i> | | +1+121 |
| <i>Lomatia tinctoria</i> | + + | 1+++11 |
| <i>Euphrasia collina</i> | | r + |
| <i>Callistemon viridiflorus</i> | | 1+ |

Table 3.5 Two-way table of Mt Franklin grassy forest showing the six classification defined species groups and the three site groups. Quadrat groups are control = 7-12, logged 77/78 coupe = 1-6. * denotes introduced species. Table values were derived from an arbitrary scale where a blank denotes absence of the species, and +, r, 1, 2 denotes increasing cover/abundance.

The use of unstandardised data in the ordination and classification analysis produced the clearest site groupings even though, in most cases, some form of data standardisation improves the relationship between compositional dissimilarity of quadrats and ecological distance (Faith *et al.* 1987). A site standardisation by sample total has the effect of placing all species within a quadrat on the scale zero to one, giving equal weight to all sites (i.e. species rich plots do not dominate the ordination), a sample (species) standardisation tends to equalise the contribution of all species. Without standardisation, the analysis is biased by those species with high modal abundance. Unequivocal recommendation for standardisation, however, cannot be given as it may cause deterioration in the predictive value of the analysis by increasing the effective weight of sporadic species that never attain high abundances (Kent & Coker 1999, Faith *et al.* 1987). It appears, therefore, that in these high altitude forests logging primarily affects the cover of the dominant species, and that this altered cover may persist for many years.

3.4.2 Implications and pragmatic ecology

The results of this exploratory analysis suggest that partial logging has altered the floristics and structure of the understorey vegetation across a range of understorey/site types and that these changes persist for at least 21 years after logging.

This form of *post-hoc* analysis (also called a retrospective and/or space-for-time analysis) can produce misleading results caused by initial floristic difference between control and logged areas. However, the possibility of this occurring with six randomly distributed plots in each of the five area/forest types is very low. Taking the worst case

scenario, if it is assumed that logging has no impact and that differences are entirely due to vegetation differences between plots, the chance of this giving consistent results, such as increased weed or grass cover, are $(1/2)^5 = 0.03$. In reality, given the spatial distribution of plots, the chances are somewhat closer to $(1/2)^{90}$. In short, it is extremely unlikely that the observed differences between logged and unlogged plots have occurred by chance.

As with any retrospective study, there were problems in adequate representation across sites, specifically with coupe ages not represented across all sites and low sample sizes for some of the older logged sites. While such *post hoc* analysis is inevitably weakened due to these constraints (though the analysis above suggests it is still strong) in order to draw conclusions about long-term trends there is no alternative and many researchers in forest ecology face the same dilemma. Designed field experiments are rare in forest research, so other types of studies must make contributions to informing ecologically sustainable forest management (Lindenmayer 1999).

Descriptive studies, as used here, are a powerful way of studying the joint relationship of species/quadrats and environmental variables, discerning underlying patterns in the data (Kent & Coker 1999). Pragmatic ecological research depends on these descriptive studies, as both a vital first step leading to an experimental approach to the analysis of causes (James & McCulloch 1990), and to form part of the process of development of theories that are generally lacking in plant ecology (Kirkpatrick 1997b).

As the five area/forest types displayed a floristic variation that was continuous, rather than structured into definitive floristic groups, each area was assessed separately in regard to the impact of logging. The use of inferential statistics to assess the significance of each of the individual five area/forest types would have led to a level of replication

for testing a treatment effect (in this case partial logging), that was low (2 replicates each for Table Mtn grassy and shrubby forest), or non-existent (Glenmark, Clarence Lagoon and Mt Franklin), and this would have constituted pseudoreplication (*sensu* Hurlbert 1984). Pseudoreplication is defined as the use of inferential statistics to test for treatment effects with data from treatments that are not replicated, although the samples may be. The rationale for proper replication relates to the known heterogeneity of the environment. It is argued that, in the absence of replication, responses may relate to environmental variation rather than treatment effects (Kirkpatrick 1997a) and weaken any inference drawn from the research (Scheller & Mladenoff 2002). Pseudoreplication, however, is relatively easily avoidable by following current guidelines for experimental design and statistical analysis (see Benedetti-Cecchi 2001, Margules *et al.* 1998, Underwood 1993, Hurlbert 1984).

Because of the above problems a more robust, replicated analysis based on repeated measures analysis of variance (Glasby 1997, Underwood 1993) was carried out in the next chapter (Chapter 4). In addition, it was noted that some of the fitted environmental vectors in the ordinations above, primarily *rock cover* and *aspect*, were associated with the logged quadrats and could be influencing the floristic difference between logged and control quadrats. Thus, the replicated analysis of the next chapter is used to examine: 1) if other environmental variables could be contributing to logged coupe/control differences; 2) whether partial logging has changed understorey floristics and structure; and 3) how floristic composition and vegetation structure alter with time after logging.

4. Understorey dynamics following partial logging of *E. delegatensis* forests of the Central Plateau, Tasmania

4.1 Introduction

This chapter examines both the short- and long-term impacts of partial logging on the structure and understorey composition of highland forests. The long-term impacts detected in Chapter 3 reflect changes in the cover of understorey species and a simplification of the vegetation structure that persisted 21 years after logging. This chapter assesses these results in a more robust, replicated experimental design.

Two studies were undertaken: the first was a long-term study utilising the floristic and environmental data set of partially logged coupes of varying ages (1-21 years old) used in Chapter 3; and the second consisted of a short-term study of two years duration. The long-term study uses a space-for-time technique on replicate environmental variable groups and lifeform groups. The short-term study was a before-after-control-impact (BACI) design (Underwood 1993, 1991).

Specifically, this chapter examines: 1) whether the long-term impacts detected by multivariate analysis in Chapter 3 are detected by a replicated experimental design, i.e. is partial logging changing understorey floristics and structure? 2) do other environmental variables contribute to logged coupe/control differences? and 3) how does understorey floristics and structure alter with time after logging?

4.2 Methods

Site descriptions, and multivariate analysis techniques that were common to chapters 3, 4, 5 and 7 are detailed in chapter 2.

4.2.1 Data collection

The 20 m x 20 m quadrat based floristic and environmental data collected for the pattern analysis in Chapter 3 were used in the space-for-time survey of this chapter.

The floristic and environmental data for the BACI study of this chapter were collected using 2 m x 2 m quadrats in grassy understorey forest at Table Mountain (Fig. 2.1, 4.1). The pre-logging data (prelog) were collected in October 1999. The site was then partially logged (basal area of forest reduced from 28 m²ha⁻¹ to 9 m²ha⁻¹) in November 1999–February 2000 in a 34 ha coupe. Data were collected within the coupe from a 10ha area of relatively flat forest surrounding a 1ha area that was excluded from logging and acted as the control. The first post-logging data (postlog 1) were collected immediately following the harvest operation in March–April 2000 and the second (postlog 2) a year later in April–May 2001. At each sample period, floristic data were collected around a total of 15 randomly situated trees (three in control) of four eucalypt species (*E. delegatensis*, *E. dalrympleana*, *E. amygdalina* and *E. rodwayi*) and 14 randomly situated canopy gaps (two in control) within the study area. A canopy gap was defined as a hole in the overstorey canopy with a clear sky view and the mean size was 125 m². For each tree, eight 2 m x 2 m quadrats were placed in two rings of four, one ring adjacent to the trunk and the other ring under the outer edge of the canopy, for each gap five 2 m x 2 m quadrats were used, four situated on canopy edge and one in the gap centre (Fig.4.2).

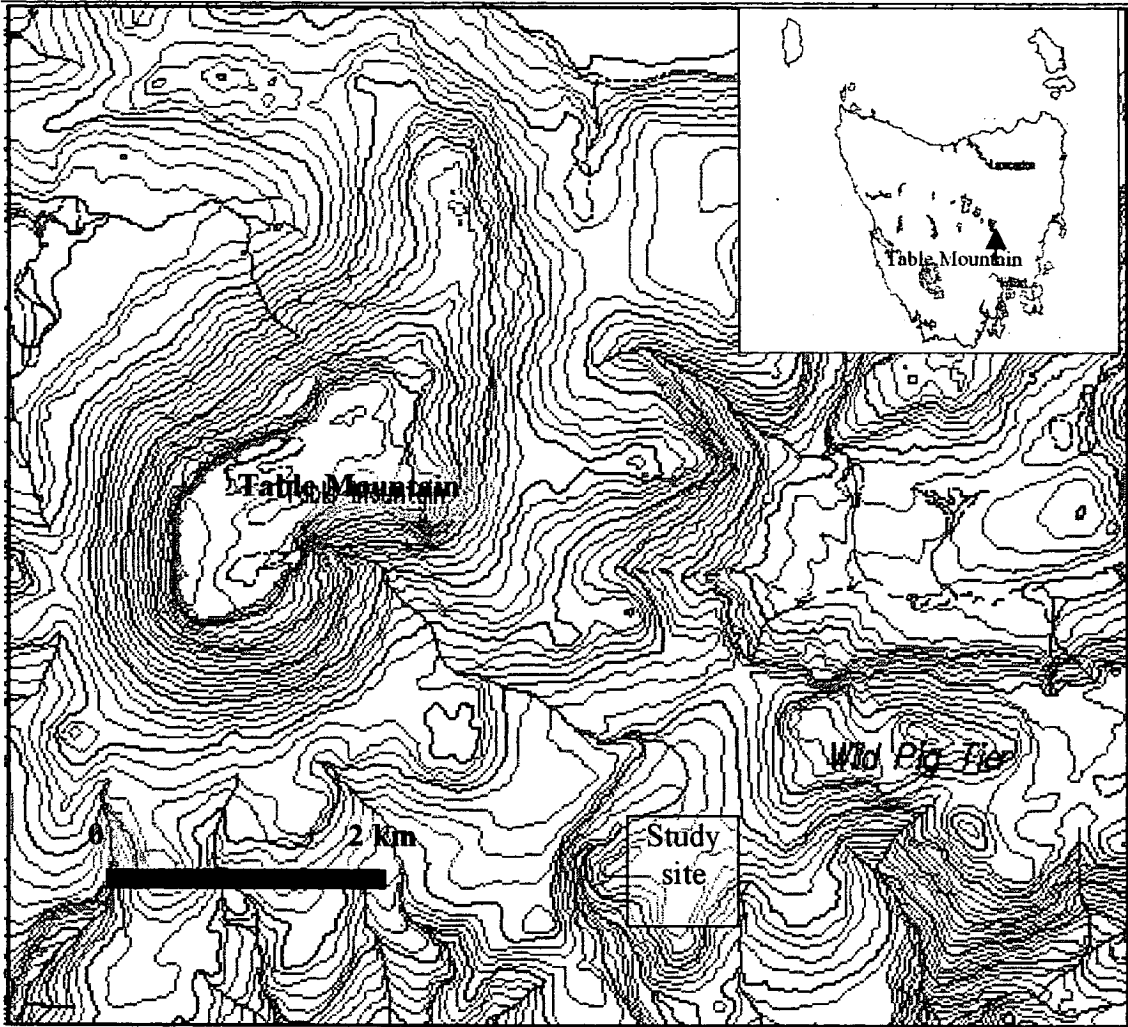


Figure 4.1 Location of BACI and Halo study site near Table Mountain, Tasmania

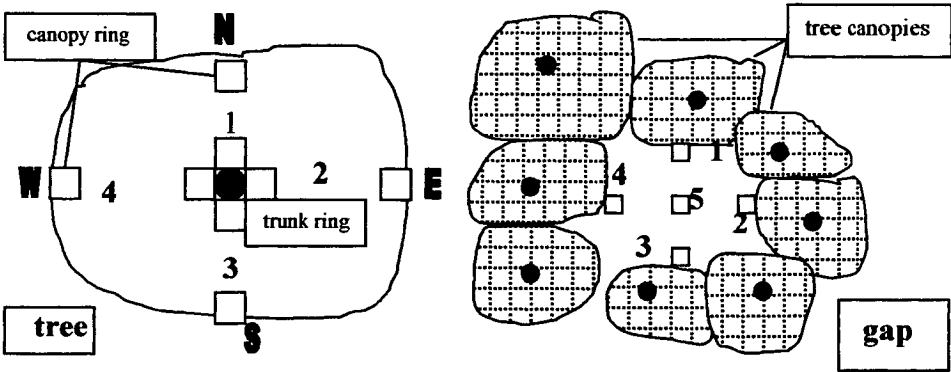


Figure 4.2 Quadrat placement for BACI study showing the eight quadrats under each tree canopy and the five quadrats in each forest gap.

Rainfall data were collated for the BACI study from the closest Bureau of Meteorology station Interlaken Estate (altitude 831m), for the three periods April 98 -March 99, April 99- March 00 and April 00-Mar 01. This data was collected to check for undue fluctuations in annual rainfall over the period of sampling that may be influencing understorey floristics.

4.2.2 Data analysis

4.2.2.1 Understorey lifeform groups and environmental variables

Species were grouped into seven vegetation lifeform groups: shrubs, grasses, non-graminoid monocots (monocots), native forbs (nforbs), introduced forbs (iforbs), ferns, and orchids for the space-for-time and the BACI survey.

Tests for significant difference ($P < 0.05$) in mean lifeform percentage cover between logged coupes and control sites, and for effects and interactions between site, treatment (logged/controls), forest type (grassy/shrubby), and time since logging (1-3 years, 5-8 years, 16-21 years and controls) for the space-for-time study were carried out using a repeated measures ANOVA. Tests for significant difference ($P < 0.05$) in environmental variable means in response to treatment, forest type and time since logging in the space-for-time study were carried out using factorial ANOVA and *post-hoc* Tukey test for all areas (9 replicates; different coupes logged at different times).

The BACI analysis was carried out on the mean cover values of each species around each tree, derived from the eight quadrats under each tree, and the five quadrats in each gap. This gave a total of 24 logged quadrats and 5 control quadrats for each of the three sample times prelog, postlog1 and postlog2. Tests for significant difference ($P < 0.05$) in

mean lifeform group percentage cover, and environmental variable means for the BACI study between the three sampling times, prelog, postlog1 and postlog2, in the logged area, (24 replicates), and the control (5 replicates) were detected using repeated measures ANOVA and *post hoc* Tukey test.

Space-for-time and BACI analyses were carried out in STATISTICA (StatSoft, Inc. 2001), and all data were natural log transformed prior to analysis.

4.2.2.3 Species analysis

Two species analyses were carried out in both the space-for-time and the BACI study. The first using a mean relative importance value calculated as follows:

$$P_i = \% C_i / \sum \% C_q$$

where the relative importance (P_i) of a species (i) is the percent cover of this species ($\% C_i$) divided by the total percent cover of all species for the quadrat (C_q).

The second using the mean percentage cover of a species in a quadrat. Significant differences in P_i and species percentage cover were tested between logged and control quadrats in the space-for-time study, and between the three sample times, prelog, postlog1 and postlog2, for logged and control areas in the BACI study using a Monte Carlo randomisation test (Manly 1991) in the Pop tools (Hood 2002) add-in, in Excel.

4.3 Results

4.3.1 Space-for-time environmental variables

Logged coupes and controls were comparable in terms of the basic environmental attributes, with no significant differences in altitude, rainfall, aspect, slope or rock cover. As a result of logging, however, coupes had a reduced number of vegetation layers, maximum understorey height, and eucalypt classes, and a reduced habitat complexity score (Table 4.1). Six environmental variables (basal area, habitat complexity, grass cover, number of eucalypt species, bare ground cover and evenness) were found to have a significant interaction between forest type and time since logging. Basal area of the overstorey steadily increased with time since logging in both forest types but had not reached control levels 16-21 years later (Fig. 4.3a). Over the same time period, habitat complexity had recovered in grassy forest but not in shrubby forest (Fig. 4.3b). Grass cover and number of eucalypt species was higher in grassy forest but showed inconsistent, site specific, responses with time since logging (Fig. 4.3b). There was a higher proportion of bare ground exposed in grassy forest 1-3 years after logging but this had recovered to levels similar to the controls in both forest types 5-8 years after logging. Vegetation evenness displayed opposite trends in each forest type, decreasing in grassy forest 5-21 years after logging, and tending to increase slightly in shrubby forest over the same time period (Fig. 4.3a).

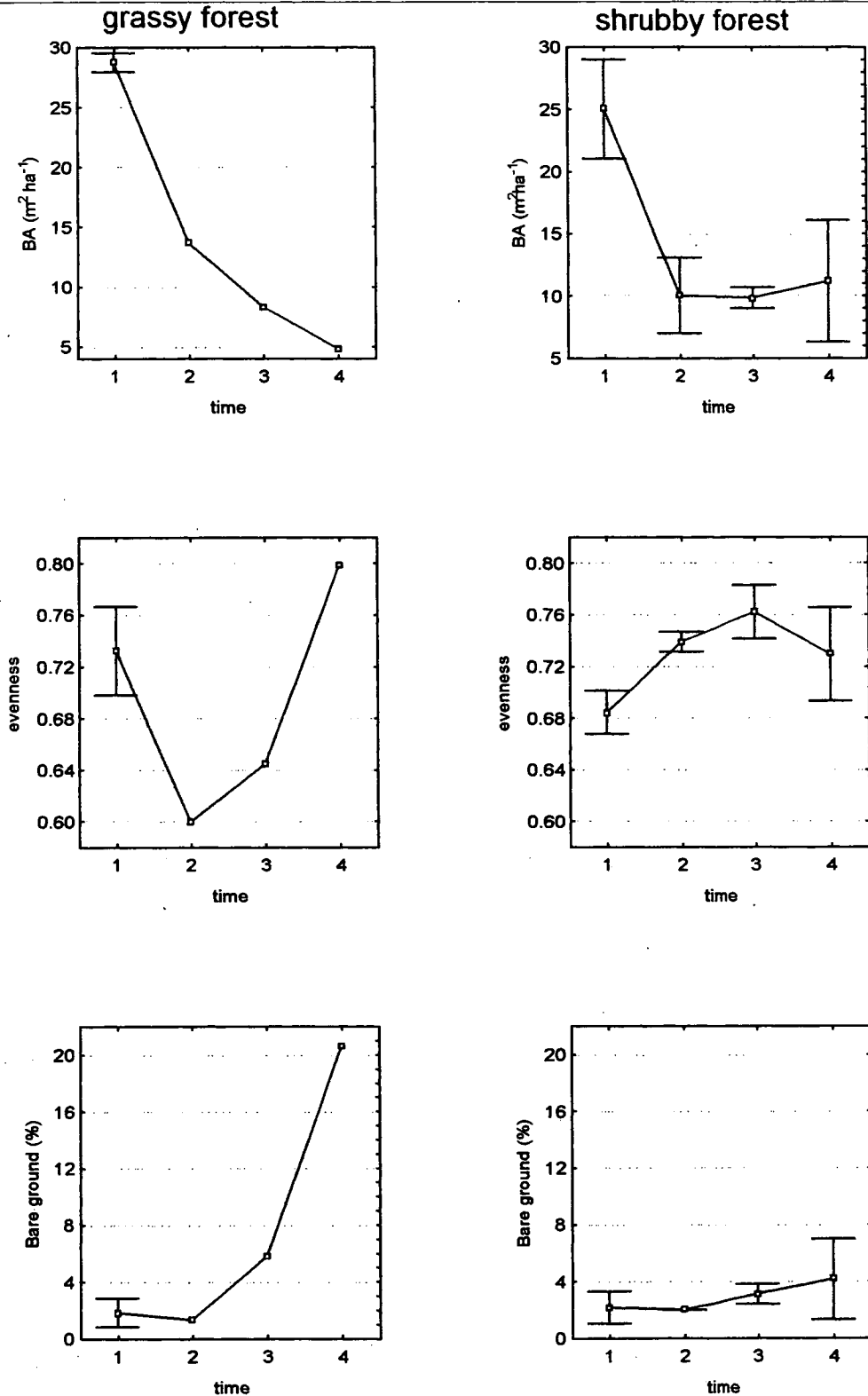


Figure 4.3a Mean \pm sem of the three significant ($P < 0.05$, ANOVA and *post hoc* Tukey test) environmental variables basal area, evenness and bare ground in the space-for-time study with respect to forest type and time since logging. Time categories 1 = controls, 2 = 16-21 years after logging, 3 = 5-8 years, 4 = 1-3 years.

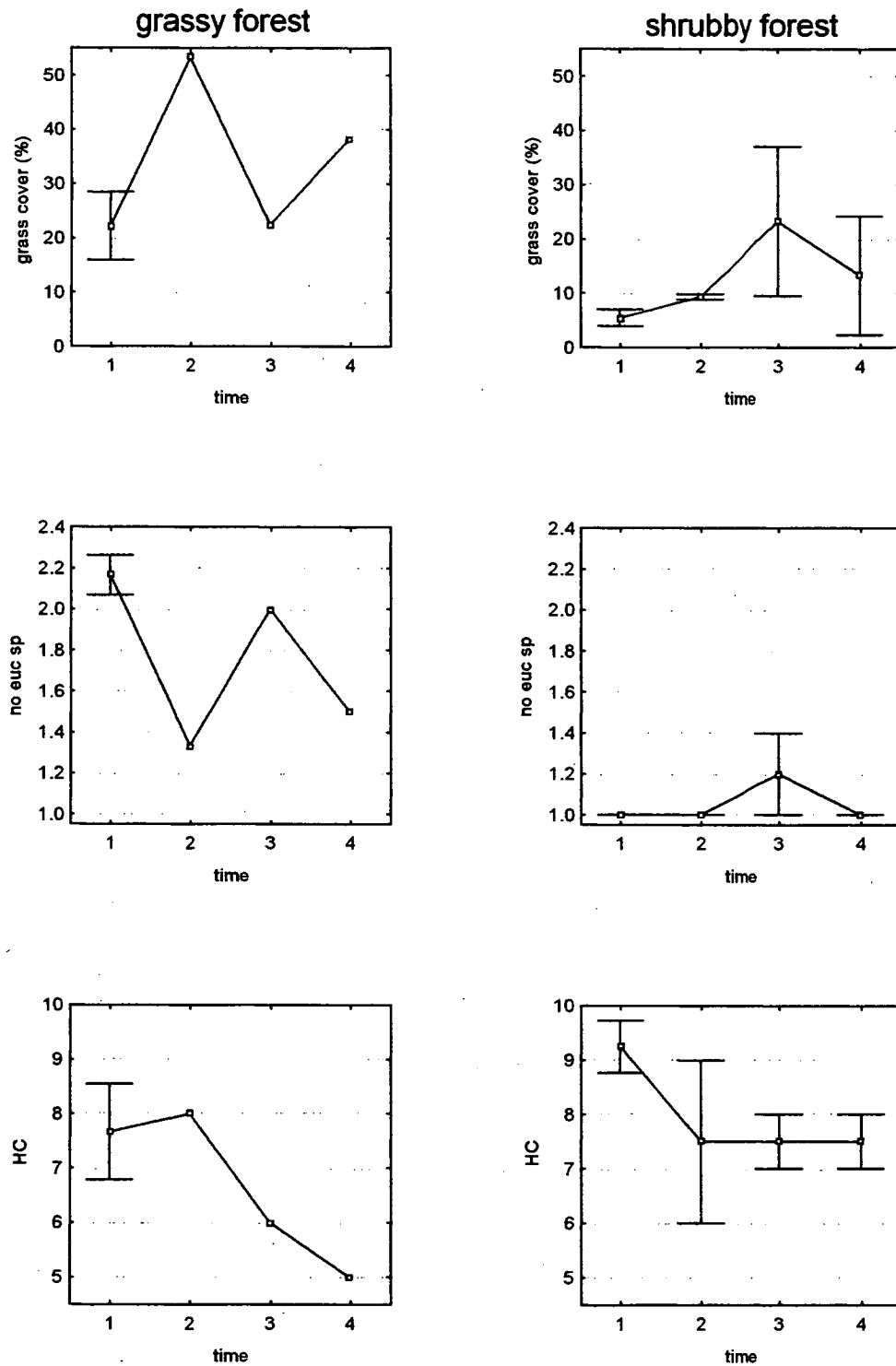


Figure 4.3b Mean \pm sem of the three significant ($P < 0.05$, ANOVA and *post hoc* Tukey test) environmental variables grass cover, number of eucalypt species and habitat complexity in the space-for-time study with respect to forest type and time since logging. Time categories 1 = controls, 2 = 16-21 years after logging, 3 = 5-8 years, 4 = 1-3 years.

Table 4.1 Mean values (\pm SEM) of environmental variables in the space-for-time study. Treatments sharing the same letter for each variable between logged and control quadrats were not significantly different at $P < 0.05$ (ANOVA and *post-hoc* Tukey test).

| Variable | Control ($n = 7$) | Logged ($n = 9$) |
|---|------------------------|-----------------------|
| altitude (m) | 834 \pm 34a | 832 \pm 25a |
| rainfall (mm) | 784 \pm 29a | 807 \pm 28a |
| aspect ($^{\circ}$) | 148 \pm 24a | 159 \pm 20a |
| slope ($^{\circ}$) | 5.6 \pm 1.4a | 6.0 \pm 1.2a |
| no. of veg layers | 4.2 \pm 0.3a | 3.6 \pm 0.1b |
| max tree ht (m) | 31.9 \pm 1.7a | 28.4 \pm 3.1a |
| max understorey ht (m) | 10.8 \pm 1.1a | 6.7 \pm 1.2b |
| euc classes | 3.3 \pm 0.2a | 2.5 \pm 0.1b |
| acacia cover (%) | 11 \pm 4a | 4 \pm 1a |
| grass cover (%) | 13 \pm 4a | 23 \pm 6a |
| no euc sp | 1.5 \pm 0.2a | 1.2 \pm 0.1a |
| basal Area (m^2ha^{-1}) | 27 \pm 2a | 10 \pm 1b |
| richness | 24 \pm 2a | 24 \pm 1a |
| total cover (%) | 143 \pm 10a | 141 \pm 12a |
| J | 0.70 \pm 0.02a | 0.72 \pm 0.02a |
| H' | 2.2 \pm 0.1a | 2.3 \pm 0.1a |
| habitat complexity | 9 \pm 0.5a | 7 \pm 0.4b |
| weed cover (%) | 3 \pm 1a | 8 \pm 3a |
| litter (%) | 38 \pm 3a | 33 \pm 3a |
| rock (%) | 37 \pm 10a | 40 \pm 10a |
| bare ground (%) | 2 \pm 1a | 5 \pm 2a |

4.3.2 Space-for-time lifeform groups and species

Significant difference in the cover of the lifeform groups were observed in response to treatment, forest type ($P < 0.01$), and time since logging ($P < 0.05$) (Table 4.2).

Table 4.2 Statistical significance of effects on log transformed percentage cover of understorey lifeform groups analysed with repeated measures ANOVA in the space-for-time survey. S = site, Tr = treatment, F = forest type, Ti = time. ns = not significant, - term not included in model, $\dagger = P < 0.10$, $* = P < 0.05$, $** = P < 0.01$, $*** = P < 0.001$, $**** = P < 0.0001$.

| S | Tr | F | Ti | S x Tr | S x F | S x Ti | Tr x F | Tr x Ti | F x Ti | S x Tr x F | S x Tr x Ti | S x F x Ti | Tr x F x Ti | S x Tr x F x Ti |
|----|----|----|----|--------|-------|--------|--------|---------|--------|------------|-------------|------------|-------------|-----------------|
| ns | ** | ** | * | - | ns | ns | ns | ns | ns | - | - | ns | ns | ns |

Shrub and orchid cover were decreased in logged coupes, whereas cover of introduced forbs, grass and monocots were increased compared to cover proportions in the controls (Table 4.3). The two forest understorey types differed in cover proportions of two of the lifeform groups with grassy forest displaying decreased shrub and increased grass cover compared to shrubby forest (Table 4.3).

The analysis of time since logging identified two lifeform groups displaying significant differences across the four time periods. Shrub cover was lowest at 5-8 years, and introduced forb cover was highest at 1-3 years after logging (Fig. 4.4, Table 4.4).

Table 4.3 Summary of space-for-time lifeform group means \pm se for the main effects of treatment and forest type using repeated measure ANOVA and post hoc Tukeys test. nforbs = native forbs, iforbs = introduced forbs. † = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, **** = $P < 0.0001$, ns = not significant.

| | treatment | | | | |
|-----------|----------------|---|----------------|---|-------|
| | control | | logged | | sign. |
| lifeforms | mean \pm se | n | mean \pm se | n | |
| shrubs | 82.7 \pm 9.0 | 7 | 60.1 \pm 5.5 | 9 | ** |
| grass | 16.4 \pm 5.0 | 7 | 27.1 \pm 6.5 | 9 | † |
| monocots | 6.0 \pm 2.5 | 7 | 11.5 \pm 6.6 | 9 | † |
| nforbs | 21.3 \pm 5.3 | 7 | 27.4 \pm 5.7 | 9 | ns |
| iforbs | 0.9 \pm 0.3 | 7 | 2.3 \pm 0.7 | 9 | ** |
| ferns | 13.9 \pm 5.0 | 7 | 11.6 \pm 4.8 | 9 | ns |
| orchids | 1.2 \pm 0.4 | 7 | 0.4 \pm 0.2 | 9 | ** |

| | forest type | | | | |
|-----------|----------------|---|----------------|----|-------|
| | grassy forest | | shrubby forest | | sign. |
| lifeforms | mean \pm se | n | mean \pm se | n | |
| shrubs | 52.4 \pm 6.7 | 6 | 80.5 \pm 6.0 | 10 | * |
| grass | 33.8 \pm 6.2 | 6 | 15.6 \pm 4.9 | 10 | * |
| monocots | 15.6 \pm 9.7 | 6 | 5.2 \pm 1.8 | 10 | ns |
| nforbs | 27.9 \pm 6.6 | 6 | 22.9 \pm 5.1 | 10 | ns |
| iforbs | 2.4 \pm 1.0 | 6 | 1.3 \pm 0.3 | 10 | ns |
| ferns | 5.9 \pm 2.8 | 6 | 16.6 \pm 4.8 | 10 | ns |
| orchids | 1.0 \pm 0.4 | 6 | 0.7 \pm 0.2 | 10 | ns |

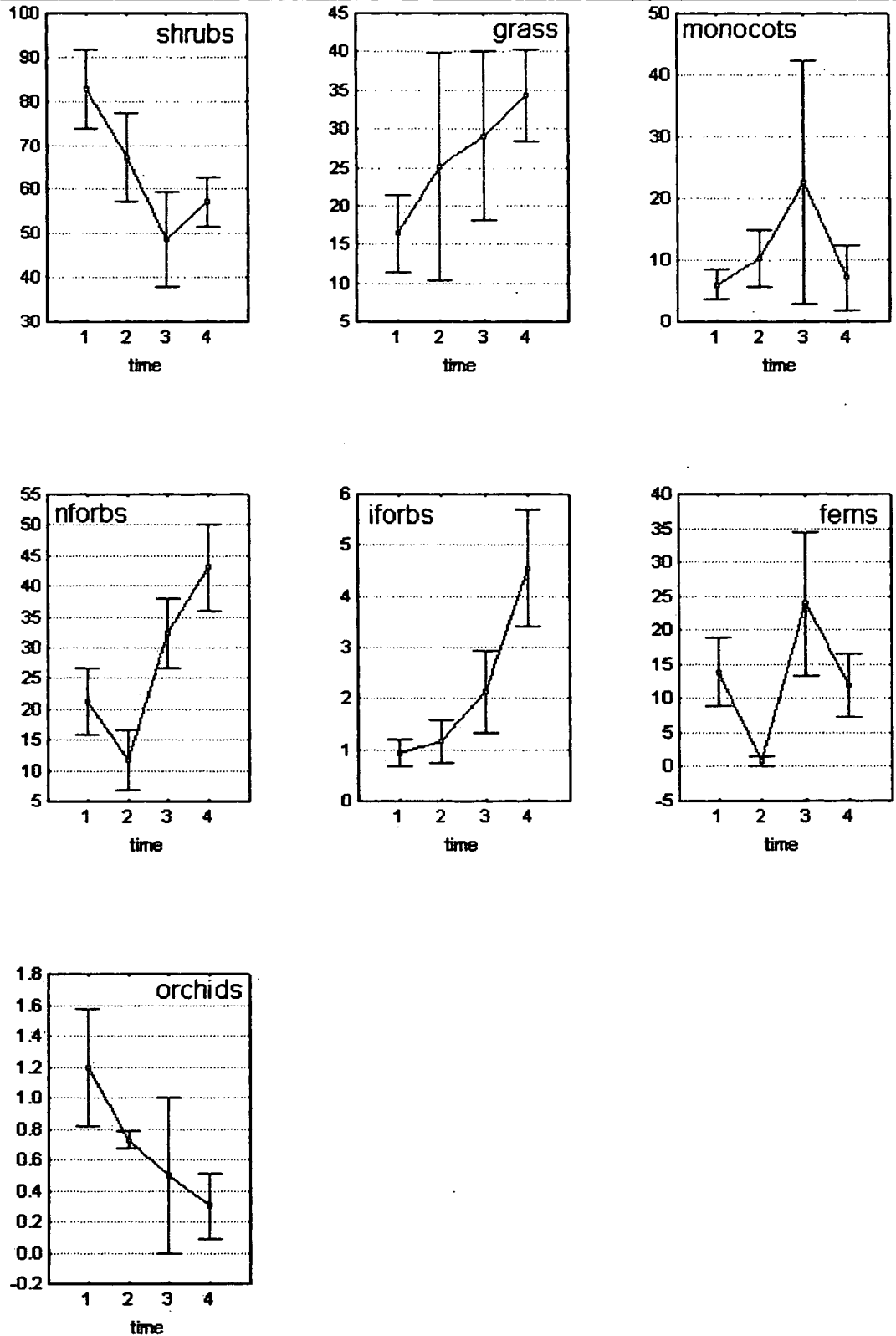


Figure 4.4 Change in mean \pm sem percentage cover of understorey guilds over time in the space-for-time survey. Time scale 1 = controls, 2 = logged 16-21 years ago, 3 = 5-8 years ago, 4 = 1-3 years ago. Nforbs = native forbs, iforbs = introduced forbs. Note different percentage cover scale for each graph.

Table 4.4 Summary of lifeform group means \pm se for time since logging. Nforbs = native forbs, iforbs = introduced forbs. Different letters show significant difference between quadrats logged at different times using post hoc Tukeys test. N = 7 in controls, 3 in 16-21 years, 5-8 years and 1-3 years time categories.

| lifeforms | control | 16-21 years | 5-8 years | 1-3 years |
|-----------|-----------------|------------------|------------------|-----------------|
| shrubs | 82.7 \pm 9.0a | 67.4 \pm 10.0a | 48.7 \pm 10.6b | 57.2 \pm 5.5a |
| grass | 16.4 \pm 5.0a | 25.1 \pm 14.7a | 29.1 \pm 11.0a | 34.3 \pm 6.0a |
| monocots | 6.0 \pm 2.5a | 10.4 \pm 4.6a | 22.6 \pm 19.8a | 7.1 \pm 5.2a |
| nforbs | 21.3 \pm 5.3a | 11.7 \pm 4.9a | 32.3 \pm 5.6a | 43.1 \pm 7.1a |
| iforbs | 0.9 \pm 0.3a | 1.2 \pm 0.4a | 2.1 \pm 0.8a | 4.6 \pm 1.1b |
| ferns | 13.9 \pm 5.0a | 0.8 \pm 0.7a | 24.0 \pm 10.6a | 11.9 \pm 4.6a |
| orchids | 1.2 \pm 0.4a | 0.7 \pm 0.1a | 0.5 \pm 0.5a | 0.3 \pm 0.2a |

Four understorey groups are proposed based on their response to logging over time, 1) immediate decreaseers-orchids and shrubs displayed a reduction in cover 1- 3 years after logging, 2) delayed decreaseers-shrubs cover continued to decline reaching a minimum 5-8 years after, 3) immediate increaseers - grass, nforbs and iforbs, with forbs displaying greatest cover 1-3 years after logging, 4) delayed increaseers - monocot and fern cover were not initially affected by logging, but then increased reaching greatest cover 5-8 years after logging (Table 4.4, Fig 4.4). The cover of all lifeform groups approached the levels in controls 16-21 years after logging.

Significantly greater species importance values and species percentage cover were found in logged coupes compared to controls, however, no significant reductions (Table 4.5). Five forbs, the monocot *Luzula* spp., and the grass *Poa gunnii* had greater P_1 and percent cover (Table 4.5, Appendix 1)).

Table 4.5 Species with significant ($P < 0.05$) mean relative importance value (P_I) and percentage cover in space-for-time logged quadrats. Greater P_I and percentage cover equals greater importance or cover in logged quadrats, no species displayed significantly lower P_I or cover, * denotes introduced species. Vegetation guilds defined as (S) = shrubs, (F) = forbs, (G) = grass, (M) = other monocots, (Fe) = ferns and (O) = orchids.

| species with greater P_I | species with greater percentage cover |
|-----------------------------------|---------------------------------------|
| <i>Acaena novae-zelandiae</i> (F) | <i>Acaena novae-zelandiae</i> (F) |
| <i>Epilobium sarmentaceum</i> (F) | <i>Epilobium sarmentaceum</i> (F) |
| <i>Euchiton collinum</i> (F) | <i>Luzula</i> spp (M) |
| <i>Hypochaeris radicata</i> * (F) | <i>Ranunculus scapiger</i> (F) |
| <i>Luzula</i> spp (M) | |
| <i>Poa gunnii</i> (G) | |

4.3.3 BACI ordination

Floristic composition changes are clearly shown in the ordination of logged and control quadrats over the three sample periods (Fig 4.5). While control quadrats stay clustered around the prelog quadrats, the postlog 1 and 2 quadrats are widely spread out along axis 4, showing an increased variability of community pattern. The plotted vectors of *soil disturbance* and *bare ground* cover are positively correlated with these changes in ordination scores and associated with the logged quadrats. Antagonistic to these variables and associated with prelog and control quadrats are the vectors for increased vegetation layers, cover, species richness, grass cover, understorey height and basal area.

4.3.4 BACI environmental variables

Annual rainfall for the three periods April 98 -March 99, April 99- March 00 and April 00-Mar 01 were 743, 474 and 663mm respectively. The long-term mean annual rainfall for the area is 743 mm.

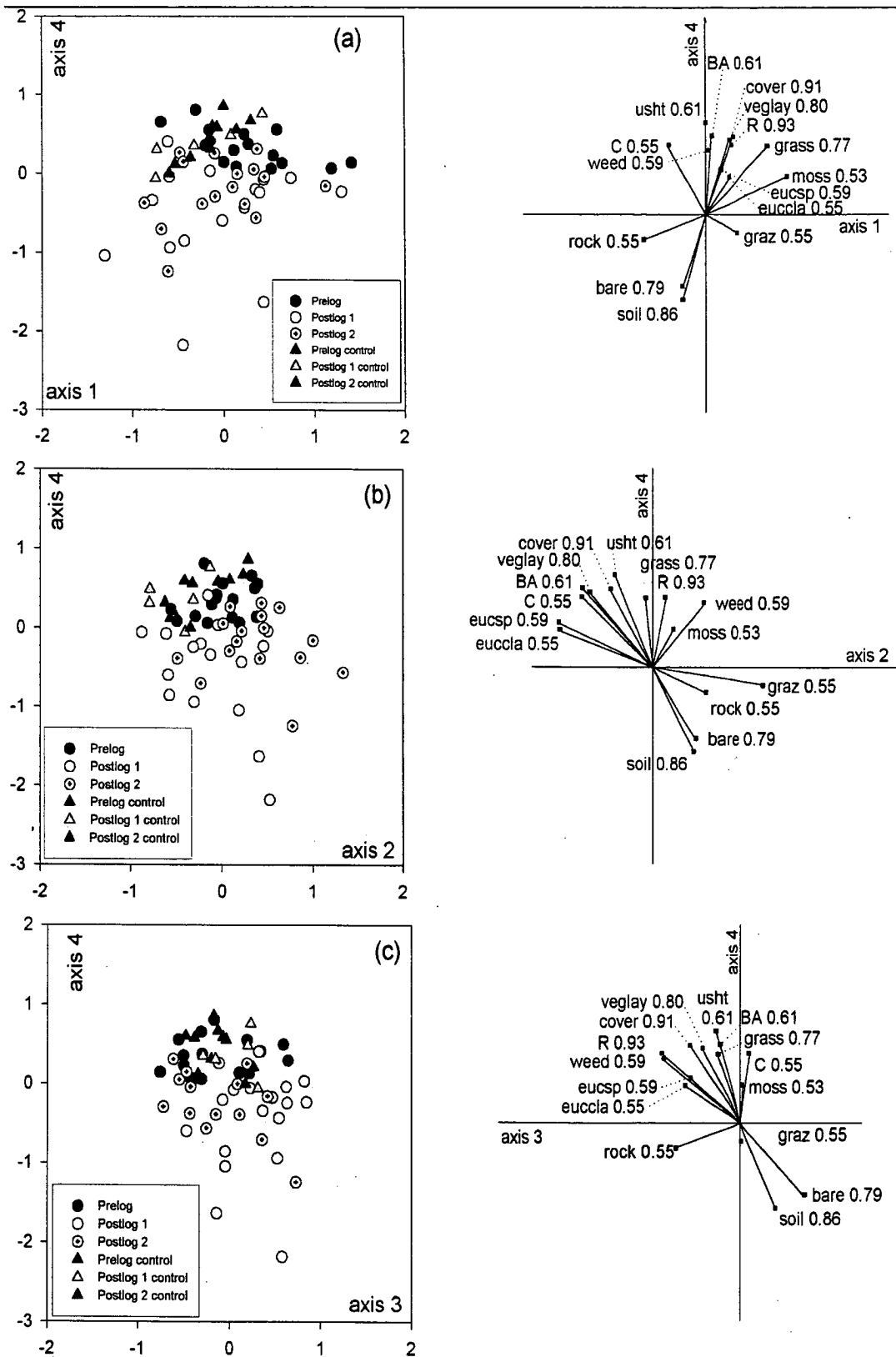


Figure 4.5 SSH ordination and significant fitted vectors of BACI site using cover-abundance of all species in quadrats at Table Mountain in four dimensions (stress = 0.16), for axes a) 1 & 4, b) axes 2 & 4, c) axes 3 & 4 of control, prelog, postlog 1 and postlog 2 quadrats, vectors displayed with correlation of each attribute in the ordination space.

Logging was associated with a reduction in the number of vegetation layers, understorey height, eucalypt classes, eucalypt species, eucalypt understorey height, species richness, grass, weed, moss, lichen and total cover, and an increase in bare ground cover and soil disturbance. Decreased weed cover was the only significant environmental variable occurring simultaneously within the control area (Table 4.6).

Table 4.6 Means \pm sem for environmental variables at three different sample times (prelog, postlog 1 and postlog 2) in logged and control quadrats of BACI study. Treatments sharing the same letter for each variable between the three sample times were not significantly different at $P < 0.05$ (ANOVA and *post-hoc* Tukey test).

| | logged | | | control | | |
|---------------------------------------|--------------------|-----------------------|-----------------------|-------------------|----------------------|----------------------|
| | prelog (n = 24) | postlog 1 (n = 24) | postlog 2 (n = 24) | prelog (n = 5) | postlog 1 (n = 5) | postlog 2 (n = 5) |
| no. veg layers | 2.7 \pm 0.1a | 1.7 \pm 0.1b | 1.8 \pm 0.1b | 2.6 \pm 0.7a | 2.7 \pm 0.1a | 2.6 \pm 0.1a |
| max understorey ht (m) | 1.5 \pm 0.2a | 0.6 \pm 0.1b | 0.6 \pm 0.1b | 1.3 \pm 0.1a | 1.2 \pm 0.1a | 1.3 \pm 0.2a |
| euc classes | 1.2 \pm 0.1a | 0.5 \pm 0.1b | 0.5 \pm 0.1b | 1.1 \pm 0.3a | 1.0 \pm 0.2a | 1.2 \pm 0.2a |
| euc species | 1.1 \pm 0.1a | 0.5 \pm 0.1b | 0.6 \pm 0.1b | 0.8 \pm 0.1a | 0.9 \pm 0.1a | 1.0 \pm 0.1a |
| euc u/s ht | 1.9 \pm 0.5a | 0.7 \pm 0.2b | 0.5 \pm 0.1b | 0.9 \pm 0.4a | 0.5 \pm 0.2a | 1.0 \pm 0.2a |
| grass cover (%) | 34 \pm 2.9a | 21 \pm 3.0b | 20 \pm 2.5b | 42 \pm 7.0a | 38 \pm 8.7a | 25 \pm 5.0a |
| BA (m ² ha ⁻¹) | 28 \pm 1.3a | 9 \pm 1.0b | 9 \pm 1.0b | 34 \pm 3.2a | 30 \pm 4.4a | 30 \pm 4.4a |
| soil disturbance | 1.0 \pm 0a | 1.9 \pm 0.1b | 1.6 \pm 0.1b | 1.1 \pm 0.1a | 1.1 \pm 0.1a | 1.0 \pm 0a |
| grazing | 1.2 \pm 0a | 1.1 \pm 0a | 1.4 \pm 0.1b | 1.0 \pm 0a | 1.0 \pm 0a | 1.0 \pm 0a |
| total cover (%) | 115 \pm 5.9a | 64 \pm 6.8b | 68 \pm 6.2b | 139 \pm 9.5a | 128 \pm 13.1a | 109 \pm 12.0a |
| species richness | 16.3 \pm 0.7a | 10.4 \pm 0.8b | 13.8 \pm 0.9c | 17.5 \pm 1.6a | 13.9 \pm 1.6a | 16.9 \pm 2.0a |
| weed cover (%) | 2.3 \pm 0.2a | 0.4 \pm 0.1b | 1.1 \pm 0.2c | 2.1 \pm 0.4a | 0.8 \pm 0.3b | 0.8 \pm 0.1b |
| Litter (%) | 45 \pm 3.7a | 44 \pm 3.0a | 47 \pm 3.0a | 51 \pm 8.0a | 42 \pm 5.0a | 46 \pm 7.8a |
| Moss (%) | 18 \pm 3.5a | 6 \pm 1.5b | 6 \pm 1.7b | 8 \pm 3.4a | 7 \pm 4.3a | 8 \pm 5.2a |
| Rock (%) | 10 \pm 1.8a | 10 \pm 2.0a | 6 \pm 1.7a | 1 \pm 0.7a | 2 \pm 0.7a | 1 \pm 0.6a |
| Bare ground (%) | 1 \pm 0.3a | 20 \pm 2.9b | 10 \pm 2.0c | 2 \pm 1.1a | 1 \pm 0.9a | 1 \pm 0.4a |
| Lichen (%) | 8 \pm 1.7a | 5 \pm 0.6b | 2 \pm 0.4b | 6 \pm 2.3a | 6 \pm 1.8a | 2 \pm 0.4a |

4.3.5 BACI lifeform groups

In logged areas, five of the seven lifeform groups (shrubs, grass, native forbs, introduced forbs and orchids) displayed reduced cover between prelog and postlog 1, and this reduced cover was still evident at postlog 2, although both native and introduced forbs had started to recover (Figure 4.6). The ferns also showed a recovery by postlog 2 due to

a rapid increase in the cover of *Pteridium esculentum*. In the control area, shrubs, grass, monocots, native forbs and ferns displayed no significant cover changes over the three sample times but introduced forbs and orchids were reduced in cover. In contrast to the logged area, the ferns had reduced in cover by postlog 2 (Fig.4.6).

4.3.6 BACI species

The analysis of species importance values and percentage cover predominantly reflect the lifeform changes mentioned above (see also raw data in Appendix 2). In the logged area, four species showed an increase in contribution including two forbs, Poaceae spp., and the monocot *Luzula* spp. Species decreasing in importance included two shrubs, the monocots *Arthropodium milleflorum* and *Drymophila cyanocarpa*, six forbs, the orchids and the grass *Poa gunnii* (Table 4.7, 4.8, Appendix 2). In control areas (Table 4.8, 4.9, Appendix 2) there was a decrease in contribution of one forb, the grass *Poa rodwayi* and the fern *Pteridium esculentum*.

4.4 Discussion

4.4.1 Floristic changes

This study has shown that partial logging in *E. delegatensis* forests causes significant changes in floristics, at the lifeform and species level, and in vegetation structure, in both the short and longer term. The BACI data presented here show that while control sites displayed limited temporal floristic shifts, the magnitude of change was small compared to the logged sites.

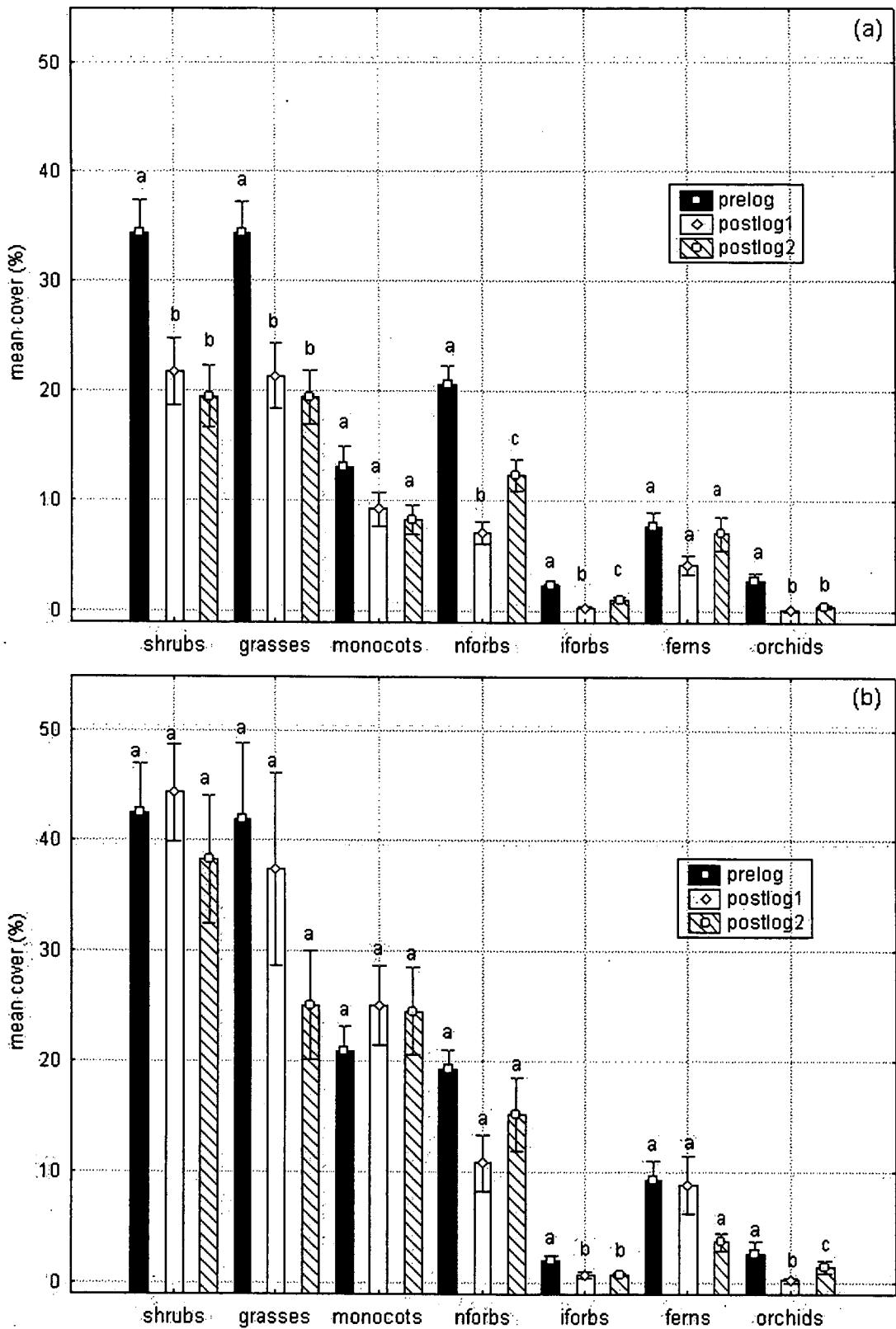


Figure 4.6 Mean percentage cover of seven understorey lifeform groups in (a) logged quadrats and (b) control quadrats at the BACI site over the three sample times, prelog, postlog1 and postlog2. Different letters indicate a significant difference (ANOVA, Tukeys test, $P < 0.05$).

Table 4.7 Species with significant ($P < 0.05$) change in mean percentage cover in logged quadrats between each of the three sampling times prelog, postlog 1 and postlog 2. Vegetation guilds defined as (S) = shrubs, (F) = forbs, (G) = grass, (M) = other monocots, (Fe) = ferns and (O) = orchids. * denotes introduced species.

| Species with increasing percentage cover | | |
|--|-------------------------------------|-----------------------------------|
| Prelog/Postlog 1 | Prelog/Postlog 2 | Postlog 1/Postlog 2 |
| <i>Cirsium vulgare</i> * (F) | <i>Cirsium vulgare</i> * (F) | <i>Brachyscome decipiens</i> (F) |
| | | <i>Cirsium vulgare</i> * (F) |
| | | <i>Euchiton collinum</i> (F) |
| | | <i>Geranium sessiliflorum</i> (F) |
| | | <i>Luzula</i> spp (M) |
| | | Orchidaceae (O) |
| | | Poaceae spp. (G) |
| | | <i>Poranthera microphylla</i> (F) |
| | | <i>Ranunculus scapiger</i> (F) |
| | | <i>Wahlenbergia</i> spp. (F) |
| Species with decreasing percentage cover | | |
| Prelog/Postlog 1 | Prelog/Postlog 2 | Postlog 1/Postlog 2 |
| All Poaceae (G) | <i>Arthropodium milleflorum</i> (M) | <i>Drymophila cyanocarpa</i> (M) |
| <i>Arthropodium milleflorum</i> (M) | <i>Galium australe</i> (F) | |
| <i>Brachyscome decipiens</i> (F) | <i>Leucopogon hookeri</i> (S) | |
| <i>Diplarrena moraea</i> (M) | <i>Lomatia tinctoria</i> (S) | |
| <i>Drymophila cyanocarpa</i> (M) | Orchidaceae (O) | |
| <i>Euchiton collinum</i> (F) | <i>Poa gunnii</i> (G) | |
| <i>Galium australe</i> (F) | <i>Pratia pedunculata</i> (F) | |
| <i>Geranium sessiliflorum</i> (F) | <i>Veronica calycina</i> (F) | |
| <i>Lomatia tinctoria</i> (S) | <i>Veronica gracilis</i> (F) | |
| <i>Luzula</i> spp. (M) | <i>Wahlenbergia</i> spp. (F) | |
| Orchidaceae (O) | | |
| <i>Poa rodwayi</i> (G) | | |
| Poaceae spp. (G) | | |
| <i>Poranthera microphylla</i> (F) | | |
| <i>Pratia pedunculata</i> (F) | | |
| <i>Pteridium esculentum</i> (F) | | |
| <i>Senecio gunnii</i> (F) | | |
| <i>Veronica calycina</i> (F) | | |
| <i>Veronica gracilis</i> (F) | | |
| <i>Viola hederacea</i> (F) | | |
| <i>Wahlenbergia</i> spp. (F) | | |

Table 4.8 Species with significant ($P < 0.05$) change in mean species importance value (P_1) in logged and control quadrats between each of the three sampling times prelog, postlog 1 and postlog 2. Vegetation guilds defined as (S) = shrubs, (F) = forbs, (G) = grass, (M) = other monocots, (Fe) = ferns and (O) = orchids. * denotes introduced species.

| Logged | | |
|--|--|---|
| Species with greater P_1 | | |
| Prelog/Postlog 1 | Prelog/Postlog 2 | Postlog 1/Postlog 2 |
| <i>Cirsium vulgare</i> * (F) | <i>Cirsium vulgare</i> * (F) <i>Euchiton collinum</i> (F) <i>Luzula</i> spp. (M) Poaceae (G) | <i>Brachyscome decipiens</i> (F) <i>Cirsium vulgare</i> * (F) <i>Geranium sessiliflorum</i> (F) <i>Euchiton collinum</i> (F) <i>Hypericum japonicum</i> (F) <i>Luzula</i> spp. (M) Poaceae (G) <i>Poranthera microphylla</i> (F) <i>Viola hederacea</i> (F) <i>Wahlenbergia</i> spp. (F) |
| Species with less P_1 | | |
| Prelog/Postlog 1 | Prelog/Postlog 2 | Postlog 1/Postlog 2 |
| <i>Arthropodium milleflorum</i> (M) <i>Brachyscome decipiens</i> (F) <i>Dryophila cyanocarpa</i> (M) <i>Hypericum japonicum</i> (F) <i>Lagenophora stipitata</i> (F) <i>Luzula</i> spp. (M) Orchidaceae (O) <i>Pratia pedunculata</i> (F) <i>Veronica gracilis</i> (F) <i>Viola hederacea</i> (F) <i>Wahlenbergia</i> spp. (F) | <i>Dryophila cyanocarpa</i> (M) <i>Lagenophora stipitata</i> (F) Orchidaceae (O) <i>Veronica gracilis</i> (F) | <i>Dryophila cyanocarpa</i> (M) <i>Pratia pedunculata</i> (F) |
| Control | | |
| Species with greater P_1 | | |
| Prelog/Postlog 1 | Prelog/Postlog 2 | Postlog 1/Postlog 2 |
| <i>Poa gunnii</i> (G) | | Poaceae (G) <i>Viola hederacea</i> (F) <i>Wahlenbergia</i> spp. (F) |
| Species with less P_1 | | |
| Prelog/Postlog 1 | Prelog/Postlog 2 | Postlog 1/Postlog 2 |
| <i>Luzula</i> spp. (M) Orchidaceae (O) <i>Poa rodwayi</i> (G) Poaceae (G) | <i>Lagenophora stipitata</i> (F) <i>Poa rodwayi</i> (G) | |

Table 4.9 Species with significant (< 0.05) change in mean percentage cover in control quadrats between each of the three sampling times prelog, postlog 1 and postlog 2. Vegetation guilds defined as (T) = trees, (S) = shrubs, (F) = forbs, (G) = grass, (M) = other monocots, (Fe) = ferns and (O) = orchids. * denotes introduced species.

| Species with increasing percentage cover | | |
|--|----------------------------------|----------------------|
| Prelog /Postlog 1 | Prelog /Postlog 2 | Postlog 1 /Postlog 2 |
| | | Poaceae spp. (G) |
| Species with decreasing percentage cover | | |
| Prelog /Postlog 1 | Prelog /Postlog 2 | Postlog 1 /Postlog 2 |
| <i>Luzula</i> spp. (M) | <i>Pteridium esculentum</i> (Fe) | |
| Orchidaceae (O) | | |
| <i>Poa rodwayi</i> (G) | | |
| Poaceae spp. (G) | | |
| <i>Viola hederacea</i> (F) | | |

Short-term changes are expected given the ground-based nature of forest operations, however, some of these changes persist. The variability of community pattern increased as a result of logging and was evident as: 1) the error bars of the space-for-time lifeform analysis i.e. greater variance of lifeform percentage cover, particularly grass, monocots, iforbs, ferns and orchids in logged quadrats (Fig. 4.4); and 2) the increased spread of the postlog quadrats in the BACI ordination (Fig. 4.5). This increased variability of community pattern following the logging has been reported as both a consequence of disturbance (Underwood 1991) and an indicator of disturbance impact (Clarke 1993), and can preclude the detection of all but a very large impact (Hewitt *et al.* 2001, Glasby 1997, Underwood 1993), [see Chapter 8 for further discussion].

This study revealed a short-term increase in soil disturbance and bare ground cover, and a decrease in species richness, shrub, forb, grass, orchid, moss and lichen cover. Several of the short-term trends, principally reduced forb and orchid cover, were occurring simultaneously in the control area (Table 4.8, 4.9 and Fig. 4.6) suggesting that

logging was not directly responsible for these changes. This decrease in forb and orchid cover was likely to be a result of natural environmental fluctuations, in this case probably moisture availability, given the low rainfall in the year prior to prelog 1 sampling.

The reductions in both grasses and forbs in logged areas are short lived, however, and 2-3 years after logging both will increase in cover and importance in the more open environment of the logged coupes. The rapid response of bracken to the disturbance contrasted markedly with its decline in the control area over the same time frame.

The occurrence of orchids is highly variable year to year and it is possible that seasonal crypsis could confound abundance measurements despite precautions taken during data collection. Given the rapid response of orchids to rainfall fluctuations at the BACI site, orchid abundance is probably correlated with fluctuations in available soil and/or air moisture. However, a longer-term reduction of shrubs and orchids was observed in logged areas (Fig. 4.4). Abundance of ground orchids has been seen to increase in elevated (deeper?) soils at the base of tree trunks (Lunt 1990), and decrease in association with grazing in Australia (McIntyre *et al.* 1995, Leigh and Holgate 1979), and with logging, in montane old-growth forests of coastal British Columbia (Beese and Bryant 1999). It is suggested that a reduction in available soil moisture is an indirect effect of logging in these forests. This reduction in soil moisture is probably the result of increased evapotranspiration rates mediated by increases in the intensity of solar radiation, the wind speed, and the temperature range, of the forest floor. Orchids clearly respond rapidly to short-term fluctuations in available soil moisture, however, it appears that a logging induced reduction in available moisture is imposed on top of the climatic fluctuations and has long-term effects on orchid abundance.

A suite of forbs (*Acaena novae-zelandiae*, *Cirsium vulgare**, *Epilobium sarmentaceum*, *Geranium sessiliflorum*, *Hypochaeris radicata** and *Ranunculus scapiger*) had greater cover at all of the longer-term logged sites, as did the native grass *Poa gunnii*. These species were able to rapidly colonise bare ground following logging as a function of their life history attributes (McIntyre *et al.* 1995). Species that are able to disperse effectively and exploit resources rapidly, i.e. annuals, wind/animal dispersed taxa and flat rosettes, are associated with soil disturbance.

Previous research has shown that logging of eucalypt forests in Tasmania has led to the following changes: increased solar radiation reaching the ground (Bowman & Kirkpatrick 1986a, Keenan 1986, Nunez & Sander 1982); expanded diurnal temperature range (Keenan 1986, Nunez & Bowman 1986); increased soil disturbance (Peacock 1994, Dickinson & Kirkpatrick 1987); introduction of weeds; and increased volume of slash on the ground (Peacock 1994). The extent and interaction of these factors at each site may be different, but they appear to result in some general trends in both the short and long terms.

The understorey response to the disturbance caused by partial logging in these forests is similar to the effects of grazing on grassland and grassy *E. gunnii* forest on the Central Plateau of Tasmania (Gibson and Kirkpatrick 1989), and on forests of the Southern Tablelands of N.S.W (Leigh and Holgate 1979). Each study found that increased grazing increased bare ground and rosette herb cover, and led to an increase in species richness, but a decrease in shrub cover and structural complexity, although increased grazing also led to decreased grass cover. McIntyre *et al.* (1995) showed that increased grazing was associated with higher proportions of annuals, flat rosettes and species with adhesive seeds (mainly grasses). Undisturbed sites in their study had more shrubs, vegetatively

reproducing species and geophytes (a life form with persistent buds buried to a depth of 2-3 cm e.g. Orchidaceae).

It is clear that understorey composition after partial logging in these forests will be determined by the species present on the site before logging and this has been reported by other authors. Initial floristic composition after disturbance were found to largely determine species composition in wet *Eucalyptus regnans* forest in Victoria (Ough 2001) and dry mixed eucalypt forests in Tasmania (Dickinson & Kirkpatrick 1987). As no two areas of forest will be identical, it is probable that small initial differences in floristics will be exaggerated following disturbance and have led to the very site-specific responses noted here. For example some species displayed contrasting response at different sites; *Leucopogon hookeri* and *Hypericum japonicum* showed decreased cover after logging at Table Mountain and Mt Franklin, but increased in cover at Glenmark and Clarence Lagoon. Similarly, *Lomatia tinctoria* showed decreased cover after logging at Table Mountain, Glenmark and Mt. Franklin, but increased in cover at Clarence Lagoon, whereas *Pultenaea juniperina* decreased in cover at Mt Franklin, but increased in cover at Table Mountain. Such variable responses to disturbance have been reported by other authors (Bauhus *et al.* 2001, Beese and Bryant 1999, Gibson and Kirkpatrick 1989, Alaback and Herman 1988) and clearly reinforce the concept that impact of logging will have a strong site-specific component.

4.4.2 Forest type and time

The response to logging differs between the two forest understorey types. In the grassy forest understorey, lifeform cover, bare ground and habitat complexity recovered to control levels 21 years after logging, whereas, in the shrubby forests the shrub

lifeform group and habitat complexity were still very different 16 years after logging.

This may just reflect the difference in recovery time between the two forest types. The two forest understorey types also showed contrasting responses in the vegetation evenness or equitability measure (J). Grassy forest had a very even spread of species in both, controls and in coupes, immediately after logging. Five to 21 years after logging, however, J had dropped, reflecting the increased dominance of a single grass species, *Poa gunnii*. Conversely, in shrubby forest J increased over the same time period due to the partial removal of the dominant shrub species, usually *Cyathodes parvifolia* or *Olearia viscosa*, allowing the expansion of other species.

A similar delayed response is apparent in other environmental variables and also in four of the lifeform groups, grass, shrubs, monocots and ferns, suggesting that these understorey species may take years readjusting to the altered microclimate of the forest floor following logging. Cover of all lifeform groups, however, was approaching that of the controls 16 years after logging in grassy forest, and 21 years after logging in shrubby forest.

4.4.3 Vegetation structure and habitat complexity

Partial logging of native forest has a pronounced and persistent impact on the vegetation structure due to the inevitable damage to the understorey tree and shrub layer. This reduction of the middle stratum of the forest was obvious in recently logged coupes in both forest types, and in shrubby forest, had not recovered 16 years after logging. It has been suggested that a single event thinning of *Eucalyptus sieberi* L. Johnson

regrowth forest reduces structurally complexity in the understorey in the long term (Kutt *et al.* unpublished).

Reduced habitat complexity can directly influence the distribution and abundance of small ground-living fauna (Catling & Burt 1995) and arboreal fauna (Lindenmeyer & Cunningham 1997, Lindenmayer *et al.* 1994, Lindenmayer *et al.* 1991a, b, Braithwaite *et al.* 1984) in south-eastern Australia. The abundance of small species, such as *Antechinus stuartii* and *A. swainsonii* were positively correlated with habitat complexity, while large grazing species such as *Vombatus ursinus* and *Macropus giganteus* were negatively correlated with habitat complexity (Catling & Burt 1995). The direction of relationships with habitat complexity is considered to reflect the requirements of faunal species of different sizes for cover or herbaceous food (Cork & Catling 1996) and it is likely that a threshold exists with regard to understorey complexity, below which forests are unsuitable for small ground dwelling fauna (Catling & Burt 1995).

In the longer term, the complexity of grassy forest logged coupes studied here recovered to the control levels despite the reduced ground cover of logs, branches and litter on the coupe floor. This was due to the recovery of the shrub, monocot and forb lifeform groups. Of more concern, however, is the reduction of the middle layer connecting understorey stratum in shrubby forest. Along with the increased spacing of overstorey trees in the post-logging environment of the coupe, this could significantly affect the abundance of arboreal marsupials and some birds.

4.4.4 Experimental design

In order to understand longer term responses it was necessary to use a retrospective (space-for-time) study and, as with any retrospective study, there were problems with

adequate representation across sites, specifically with coupe ages not represented across all sites, and low sample sizes for the older logged sites. This space-for-time study, however, was not undertaken in isolation but rather within the broader context of the space-for-time study, the BACI study and the multivariate analysis from Chapter 3. The same general long-term trends that were found by the multivariate analysis (increased bare ground, weed and grass cover, decreased habitat complexity) were also found with the use of inferential statistics in the replicated analysis of this chapter. This suggests that the conclusions reached here are robust.

There were three other factors, however, that influenced the analysis of the logging impact. 1) There was a dichotomy in the estimation of the duration of logging impacts on understorey floristics. For example, the lifeform analysis of this chapter suggests that all lifeform groups were approaching control levels of cover 16-21 years after logging, whereas the multivariate analysis suggests that in logged areas the cover of the understorey species were still different 16-21 years after logging. 2) A number of the quadrats in logged coupes were in areas undisturbed by machinery etc while still being within the coupe. These quadrats were included as post logged data since the intention was to assess impact on a coupe scale of, not only the actual logging operation, but also any post logging environmental changes. This contributes to the next factor. 3) There was increased variability in species covers following logging, and, some species responded differently in different areas (Kirkpatrick *et al.* 2002). These three factors will be discussed in detail in Chapter 8. What these factors suggest, however, is that the impact of logging is likely to be greater than is reported here.

4.4.5 Long-term ecological trends and conclusions

The short term impacts of partial logging are a reduction in the cover of shrubs, grasses, forbs and orchids, greater bare ground cover and soil disturbance, and a consequent reduction in habitat complexity. In the longer term, lifeform group cover and measured environmental variables recovered to control levels with the exception of the basal area of the overstorey eucalypts in both forest types, and the habitat complexity score in shrubby forest. The multivariate analysis in Chapter 3, however, revealed consistent floristic differences between 16 and 21 years old coupes and their adjacent controls. These differences were primarily the result of altered cover values for some of the dominant shrubs and forbs, increases for dominant grasses and reductions for moisture sensitive species. This suggests that some of the trends noted in this chapter may persist for more than 20 years (Fig. 4.6). Three hypotheses acting either independently or in concert are consistent with the observed longer-term reduction of shrub cover and habitat complexity in logged areas of these high altitude forests: (1) long term successional change, (2) cold induced photoinhibition, (3) increased dryness.

(1) Long term successional change

Successional change in floristics and structure following disturbance will be very slow in these cool and dry, high altitude forests. Slow but significant changes in vegetation structure and composition occurred over several decades after grazing had stopped in alpine Tasmania (Gibson & Kirkpatrick 1989), and 20-40 years were required for elimination of bare ground upon cessation of grazing in subalpine environments of mainland Australia (Leigh *et al.* 1987). The basal area, and number of classes, of the

eucalypt overstorey at the two oldest logged sites were still significantly reduced. If the overstorey canopy has not reached pre-log density in 15-20 years, it is unlikely that an understorey adapted to lower light, sheltered environments can achieve pre-harvest floristics.

(2) *Cold induced photoinhibition*

The increase in radiation reaching the ground, the greater diurnal temperature range and increased incidence in frost (Nunez & Sander 1982) in partially logged areas could be enough to affect susceptible species, adapted to the lower light and higher minimum temperature environment under the forest canopy. The data presented here showed that the shrub cover continued to drop for 5-8 years after logging. There was a rapid vegetative growth response of the shrubs, *Leucopogon hookeri* and *Lomatia tinctoria*, immediately after logging in autumn, however, the majority of these shoots died back as winter progressed. Although these shrubs can rapidly recover by vegetative means after disturbance, the removal of much of the canopy with the concomitant increased irradiance and water stress, and decreased minimum temperatures, predisposes them to photoinhibition. This differs from natural regeneration following wildfire where the eucalypt overstorey canopy recovers quickly due to epicormic bud development along the branches and trunk of the trees.

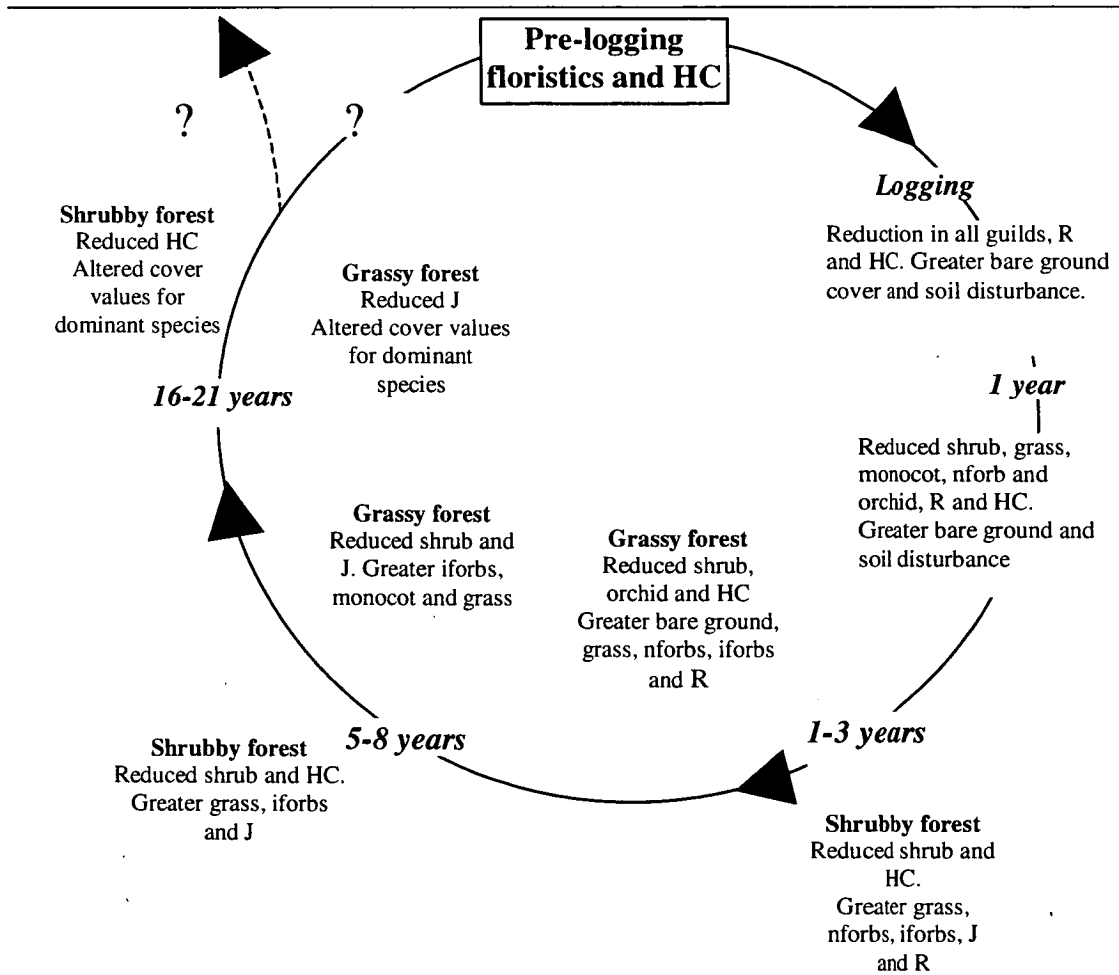


Figure 4.6 Hypothesised understorey dynamics following partial logging in grassy and shrubby *E. delegatensis* forests. The dotted line arrow shows that the floristic and structural endpoint of this succession may differ substantially from the original due to 1) the influence of stochastic events imposed on top of the logging induced disturbance, eg. fire, or 2) the influence of logging induced effects such as increased grazing/browsing, altered microclimate and soil depletion. The seven lifeform groups are shrubs, grass, monocots, nforbs (native forbs), iforbs (introduced forbs or weeds), ferns and orchids. HC = habitat complexity, J = evenness, R = species richness.

(3) *Decreased moisture availability due to surface soil drying.*

It is also likely that, in both the short (< 2 years) and long term (16-21 years) the forest floor will experience drier conditions due to increased radiation/wind speed. On the wetter sites of Clarence Lagoon and Glenmark, the logged coupes showed a floristic

transition to species more characteristic of the drier, high light environment at Table Mountain (such as *Cirsium vulgare*, *Euchiton collinum*, *Hypochaeris radicata*, *Epilobium sarmentaceum*, *Hypericum japonicum*, *Scleranthus biflorus*, *Poa gunnii*, *Gonocarpus serpyllifolius*, *Leucopogon hookeri*, *Luzula* spp, and *Poa rodwayi*).

A combination of all three factors is probably occurring in the more open environment of the forest post-logging and suggests that understorey recovery will differ from regeneration following wildfire where the eucalypt overstorey canopy recovers in 1-2 years. Although the majority of the environmental variables and the cover of all lifeform groups measured here had returned to control levels 16-21 years after logging the return to original floristics and structure was slow as indicated by the increased variance of lifeform cover and environmental variable measures, the behaviour of species evenness and habitat complexity, the absence of any recovery in the overstorey, and the site specific differences in species cover/abundance in logged vs. control quadrats. These changes in the vegetation can act in a positive feedback process with site factors and may maintain understorey differences for a long time in these forests. (see Keenan 1986, Keenan & Candy 1983, Webb *et al.* 1983, Forestry Commission of NSW 1983, Nunez & Sander 1982).

5. Individual tree influence, or the ‘halo effect’, on patterns of understorey distribution in *E. delegatensis* forests of Tasmania

5.1 Introduction

Canopy species can profoundly affect the distribution of the understorey vegetation in a wide variety of woodland communities (Vetaas 1992, Belsky *et al.* 1989, Maranon 1986, Parker and Muller 1982), including a range of Australian forests (Gibbs *et al.* 1999, Kirkpatrick 1997b, Scanlan and Burrows 1990, Lamont 1985, Lange and Reynolds 1981, Specht and Morgan 1981, del Moral *et al.* 1978). This effect is often characterised as a zone of influence on the understorey biomass, cover or diversity and can take the form of suppression (Scanlan and Burrows 1990, Walker *et al.* 1986, Lamont 1985, Parker and Muller 1982, Lange and Reynolds 1981, del Moral *et al.* 1978) or facilitation (Vetaas 1992, Belsky *et al.* 1989,). The predominant effect under a eucalypt canopy in the Australian flora is one of suppression, which, in its most extreme form, produces a sparser, lower, less diverse but more xerophytic understorey vegetation (Lamont 1985, Lange and Reynolds 1981, del Moral *et al.* 1978). These circular zones of altered growth around trees, or ‘halos’ (*sensu* Lange and Reynolds 1981) are often conspicuous on aerial photographs and to the ground observer. These effects, however, are often not as simple as a general suppression or enhancement of plant growth around particular trees (Lange and Reynolds 1981). Halos may be subtler shifts in floristic

composition of the area surrounding trees compared to adjacent forest gaps. Gaps may have increased total understorey cover (McGuire *et al.* 2001, Walker *et al.* 1986, Specht and Morgan 1981), herb cover (Moore and Vankat 1986) and, possibly, increased species richness (Collins and Pickett 1987).

Various biophysical factors have been implicated in these tree-understorey patterns, including alteration in light (Gibbs *et al.* 1999, Belsky *et al.* 1989), temperature (Nunez and Bowman 1986), moisture (Belsky *et al.* 1989, Lamont 1985), soil nutrient levels (Gibbs *et al.* 1999, Belsky *et al.* 1989), litter (Wilson and Zammit 1992, Sydes and Grime 1981), allelopathy (del Moral *et al.* 1978), sub-canopy fauna (Vetaas 1992, Belsky *et al.* 1989) and, possibly, mycorrhizal associations (Ellis & Pennington 1992).

The influence of canopy species ameliorating the combined effect of low temperature and high light intensity on cold-induced photoinhibition of understorey species has received little attention in Australian eucalypt forests. It has been demonstrated that the distributions of the seedlings (where the majority are under the southern sector of a mature tree canopy) of two overstorey species, *Eucalyptus pauciflora* (Ball *et al.* 1991) and *Nothofagus solandri* (Ball 1994) are consistent with reduced exposure to extreme low temperatures and prolonged high irradiance during winter. In a similar way cold-induced photoinhibition may lead to predictable distributions of some understorey species, particularly in higher altitude forests (Kirkpatrick 1997b).

This study was carried out in the grassy *E. delegatensis* forest site at Table Mountain, where the BACI data of Chapter 4 were collected. At this site the greatest changes in understorey lifeform cover occurred 5-8 years after partial logging of the eucalypt overstorey (basal area reduced from 33 to 10 m² ha⁻¹). If these changes were the result of

the more open overstorey, then the overstorey trees might be expected to cause patterns or “halos” in the distribution of the understorey species beneath them.

This study investigates the nature of the understorey vegetation patterns in an *E. delegatensis* forest. Specifically, are there discernable shifts in understorey species cover beneath individual overstorey eucalypts, producing a halo effect in understorey species composition and distribution? Does the halo effect, if any, differ in magnitude under two different areas of the overstorey eucalypt canopy i.e. directly adjacent to the trunk compared to under the canopy edge? How does the tree halo effect, if any, compare with the understorey patterns in adjacent forest gaps? Does aspect influence species cover under trees and in canopy gaps? Which biophysical factors associated with individual trees are causing the observed understorey patterns and could cold-induced photoinhibition be contributing to understorey patterns in these forests?

5.2 Methods

Site descriptions, and multivariate data analysis techniques were common to chapters 3, 4, 5 and 7, and are detailed in chapter 2.

5.2.1 Survey design and data collection

The floristic, structural and environmental data were collected around 15 trees of four eucalypt species (*E. delegatensis*, *E. dalrympleana*, *E. amygdalina* and *E. rodwayi*) and 14 randomly situated canopy gaps within the study area. A canopy gap was defined as a hole in the overstorey canopy with a clear sky view and mean size was 125 m². This was

the prelog data of the chapter 4 BACI study and general comments on data collection can be seen there. The details of quadrat placement are as follows. Eight 2 m x 2 m quadrats were sampled beneath each tree, arranged in two rings of four: one ring directly adjacent to the base of the trunk (trunk ring), and the other ring directly underneath the edge of the tree canopy (canopy ring). Within each ring a quadrat was positioned at each of the four cardinal points north (N), east (E), south (S) and west (W) (Fig 5.1). Five 2 m x 2 m quadrats were situated within each canopy gap, one at the N, E, S and W position at the gap edge and one in the centre (C) (Fig. 5.1).

5.2.2 Chlorophyll fluorescence

Photoinhibition is defined as the light dependent loss in photosynthetic functioning of photosystem II (PSII) and is manifested in whole leaves as a decline in the quantum efficiency of photosynthesis (i.e. mol CO₂ fixed of mol O₂ evolved per mol photons absorbed under limiting light intensities) (Osmond 1994). This reduction can be measured using the technique of chlorophyll fluorescence (see Schreiber & Bilger 1993 for review) through the ratio of variable to maximal fluorescence (F_v/F_m) that has been shown to be 0.78-0.86 at maximal PSII efficiency (Adams *et al.* 1994, Bjorkman & Demmig 1987). In the context of this experiment chlorophyll fluorescence measurements could directly measure if a plant was suffering stress in a position of increased radiation i.e. in a partially logged forest compared to unlogged forest.

Chlorophyll fluorescence measurements were carried out on three plant species, the sedge *Lomandra longifolia*, the shrub *Lomatia tinctoria* and the grass *Poa gunnii* at the site using a PAM-2000 fluorometer and 2030-B leaf-clip holder (Heinz Walz GmbH,

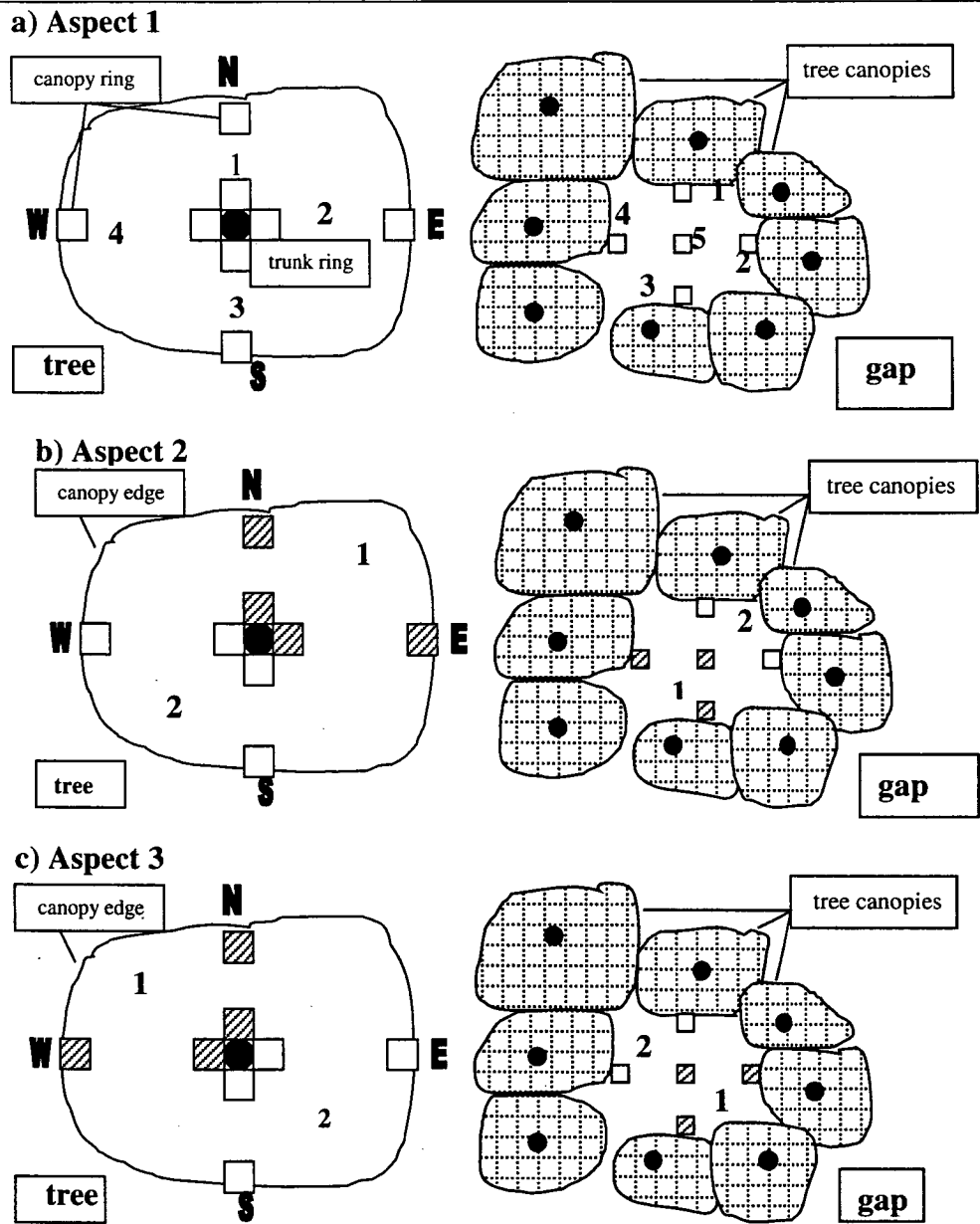


Figure 5.1. Quadrat groupings for the three aspect variables analysis, under individual trees (left column), and in forest gaps (right column). a) aspect 1 or individual quadrat effect, b) aspect 2 and c) aspect 3. Aspect 2 and aspect 3 quadrats in two groups 1) open boxes, 2) shaded boxes.

Effeltrich, Germany). The three species each represent a different lifeform group, and were dominants in the understorey of the grassy forest at the Table Mountain site.

Photochemical efficiency, F_v/F_m , was assessed on 3rd and 9th August 2000 on three dark-

adapted individuals in two treatments, partially logged (basal area $9.2 \text{ m}^2 \text{ ha}^{-1}$) and unlogged forest (basal area $27.9 \text{ m}^2 \text{ ha}^{-1}$), of each of the three species. Single measurements were made on each leaf of the most recently expanded pair and on a single older leaf for *L. longifolia* and *L. tinctoria*. For *P. gunnii*, due to the narrow diameter of leaves, measurements were made on several of the green leaves laid in an unbroken row in the leaf-clip holder.

Fluorescence data were analysed with a t-test to determine if the three species differed significantly in stress levels between the partially logged coupe and the unlogged control.

5.2.3 Temperature

Hourly temperature data were collected around three trees and three gaps for a 24-day period in autumn, 23rd March -15th April 2001 using “Tiny talk data loggers” (Hastings Data Loggers). Four temperature loggers were placed around each of the three trees in a north trunk, north canopy, south trunk and south canopy position and one logger placed in the centre of each of the three gaps.

Maximum and minimum temperatures for the north trunk, north canopy, south trunk and south canopy positions of trees and centres of gaps were calculated from the temperature data and displayed graphically. Differences between positions were assessed with analysis of variance and *post-hoc* Tukeys test.

5.2.4 Halo and aspect analysis

The effects of overstorey canopy cover and aspect were tested on the 37 species with greatest abundance (those occurring in > 20 quadrats). The cover scores for these species were converted to mid-point percentage values and then tested for significant differences in cover for two halo effects, three aspect effects and their interactions using a split-plot design in ANOVA in the statistical package SPLUS 2000. The two halo analyses carried out were 1) tree or gap i.e. did a significant difference in individual species cover exist from being under a tree compared to being in a forest gap, and 2) trunk ring or canopy ring i.e. did a significant difference in individual species cover exist between the trunk ring compared to the canopy ring. The three aspect analyses carried out were:

1. Aspect 1 - individual quadrat effect with quadrats labelled as 1 = N, 2 = E, 3 = S, 4 = W and 5 = C (Fig. 5.1a). This analysis was used to determine any significant differences in cover occurring in quadrats of a particular compass direction (either N, E, S, W or C).
2. Aspect 2 - cold photoinhibition effect where quadrats were split into two sectors. The N and E quadrats under trees and the S, W and C quadrats in gaps as sector 1, and S and W quadrats under trees and N and E quadrats in gaps as sector 2 (Fig 5.1b). The N and E quadrats under trees and S, W and C quadrats in gaps are the ones most exposed to morning sun while tree S and W, and gap N and E quadrats are shaded from morning sun, particularly in winter.
3. Aspect 3 - dryness effect where quadrats were split into two sectors. The N and W quadrats under trees and S, E and C quadrats in gaps as sector 1 and S and E quadrats under trees and N and W quadrats in gaps as sector 2 (Fig.5.1c). Tree N and

W and gap S, E and C quadrats are more exposed to hot afternoon sun than tree S and E, and gap N and W quadrats.

For aspect analyses 2 and 3 above, the centre gap quadrat was always grouped with the S gap quadrat, as a separate analysis (not shown) showed their species cover to be more similar to the south gap quadrats than the north gap quadrats.

5.3 Results

5.3.1 Ordination, classification and general halo effects

The classification procedure (not shown) defined three floristic groups displayed in the first ordination (Fig. 5.2). Group 1 (129 quadrats), called “ubiquitous” for the remainder of this chapter, represents the dominant vegetation type at the site, occupying the centre of the ordination space, occurring in canopy and trunk rings under *E. delegatensis*, *E. dalrympleana*, and *E. amygdalina* (mean basal area of 31 m²/ha), and in forest gaps. It was species rich (mean richness for a 4 m² quadrat = 17.6) and had a relatively low litter cover of 46% (see Table 5.1 and 5.2). Group 2 (23 quadrats), called “gap/open forest”, partially overlaps the “ubiquitous” group in the ordination. It was also species rich (mean richness = 17.7) but with a lower understorey height and was associated with gaps and a more open (basal area 23 m²/ha) forest under *E. dalrympleana*. Group 3, called “trunk/canopy”, is comprised of species poor (mean richness = 10.6) quadrats with very high litter cover (mean = 73%), little grass, low total cover (Table 5.1) and is essentially associated with the trunk and canopy rings of very large *E. delegatensis*.

Table 5.1 Means and standard deviations for significant numerical environmental variables of floristic groups 1, 2 and 3. Different letters denote significant differences at $P < 0.05$ determined by ANOVA and post hoc Tukey test.

| environmental variables | ubiquitous | | gap/open forest | | trunk/canopy | |
|---------------------------------|------------|-----|-----------------|-----|--------------|-----|
| | mean | sd | mean | sd | mean | sd |
| slope (°) | 2.4a | 2.9 | 1.9a | 1.5 | 5.8b | 6.3 |
| vegetation layers | 2.8a | 0.7 | 2.3b | 0.7 | 2.5c | 0.7 |
| understorey height (m) | 1.7a | 1.9 | 0.7b | 0.4 | 1.4c | 1.2 |
| grass cover (%) | 39a | 19 | 40a | 22 | 14b | 10 |
| basal area (m ² /ha) | 31a | 6 | 23b | 4 | 27c | 8 |
| total cover (%) | 128a | 33 | 114b | 28 | 71c | 28 |
| species richness | 17.6a | 3.5 | 17.7a | 4.2 | 10.6b | 5.0 |
| weed cover (%) | 2.7a | 1.9 | 1.7b | 1.9 | 1.0c | 1.6 |
| litter (%) | 46a | 21 | 34b | 20 | 73c | 20 |
| rock (%) | 7a | 8 | 13b | 13 | 12b | 13 |
| canopy size (m ²) | 171a | 106 | 63b | 0 | 263c | 131 |
| gap size (m ²) | 108a | 61 | 192b | 19 | 64c | 0 |
| tree height (m) | 30.4a | 5.5 | 23.5b | 0.0 | 34.0c | 3.3 |

An examination of the significant fitted vectors in Figure 5.2 shows two clusters of environmental variables that are antagonistic to each other. The first cluster comprises the vectors for increasing *grass cover*, *gap size*, *species richness* and *halo* (*halo* is whether a quadrat was in a trunk ring, a canopy ring or a gap, so an increasing *halo* vector indicates a trend from the tree trunk → canopy edge → gap) associated with both the ubiquitous and gap/open forest groups. The second cluster of vectors includes increasing *litter cover*, *tree height* and *canopy size* and is associated with the trunk/canopy group.

Individual ordinations for each of these three floristic groups are shown in Figure 5.3 (only one diagram displayed for each group with the two axes best showing the trends in the data). Each of these ordinations displayed a halo trend (trunk quadrats → canopy quadrats → gap quadrats) along one of the axes and this trend is reflected in the fitted vector diagrams where the vector for *halo* is associated with increasing *species richness* and *total cover* in the ubiquitous group (Fig. 5.3a), increasing *weed cover* in the

gap/open forest group (Fig. 5.3b) and increasing *species richness*, *total cover* and *grass cover* in the trunk/canopy group (Fig. 5.3c). The halo vector is also antagonistic to the vectors for increased *canopy size* and *litter cover* in each ordination.

Table 5.2 Representative species with the highest cover for each of the three floristic groups at the Table Mountain study site.

| Group 1 Ubiquitous | |
|----------------------------------|-----------------------------|
| <i>Acacia dealbata</i> | <i>Lomatia tinctoria</i> |
| <i>Arthropodium milleflorum</i> | <i>Luzula</i> spp |
| <i>Brachyscome decipiens</i> | Poaceae spp |
| <i>Galium australe</i> | <i>Poa gunnii</i> |
| <i>Geranium sessiliflorum</i> | <i>Poa rodwayi</i> |
| <i>Gonocarpus serpyllifolius</i> | <i>Pratia pedunculata</i> |
| <i>Hydrocotyle hirta</i> | <i>Pteridium esculentum</i> |
| <i>Hypericum japonicum</i> | <i>Pterostylis</i> spp |
| <i>Lagenophora stipitata</i> | <i>Veronica calycina</i> |
| <i>Leucopogon hookeri</i> | <i>Viola hederacea</i> |
| <i>Lomandra longifolia</i> | <i>Wahlenbergia</i> spp |
| Group 2 Gap/open forest | |
| <i>Ajuga australis</i> | <i>Lomatia tinctoria</i> |
| <i>Geranium sessiliflorum</i> | <i>Plantago glabrata</i> |
| <i>Euchiton collinum</i> | Poaceae spp |
| <i>Gonocarpus serpyllifolius</i> | <i>Poa gunnii</i> |
| <i>Hypericum gramineum</i> | <i>Pratia pedunculata</i> |
| <i>Hypericum japonicum</i> | <i>Ranunculus scapiger</i> |
| <i>Hydrocotyle hirta</i> | <i>Solenogyne gunnii</i> |
| <i>Lagenophora stipitata</i> | <i>Taraxacum officinale</i> |
| <i>Leucopogon hookeri</i> | <i>Veronica calycina</i> |
| <i>Leucopogon stuartii</i> | <i>Viola betonicifolia</i> |
| | <i>Wahlenbergia</i> spp |
| Group 3 Trunk/canopy | |
| <i>Lomatia tinctoria</i> | <i>Poa rodwayi</i> |
| <i>Lomandra longifolia</i> | <i>Pteridium esculentum</i> |
| <i>Poa gunnii</i> | <i>Senecio gunnii</i> |
| | <i>Wahlenbergia</i> spp |

Both ordinations and vector fitting confirm that a halo effect is present and that there are both tree/gap and trunk/canopy floristic differences. The general trends are for increasing species richness, grass cover, total cover, and decreasing litter cover and canopy size, moving from trunk → canopy → gap, and tree → gap, particularly under

the biggest, oldest trees. None of the three aspect vectors (Table 2.2, chapter 2) were found to be significant in the vector fitting analysis.

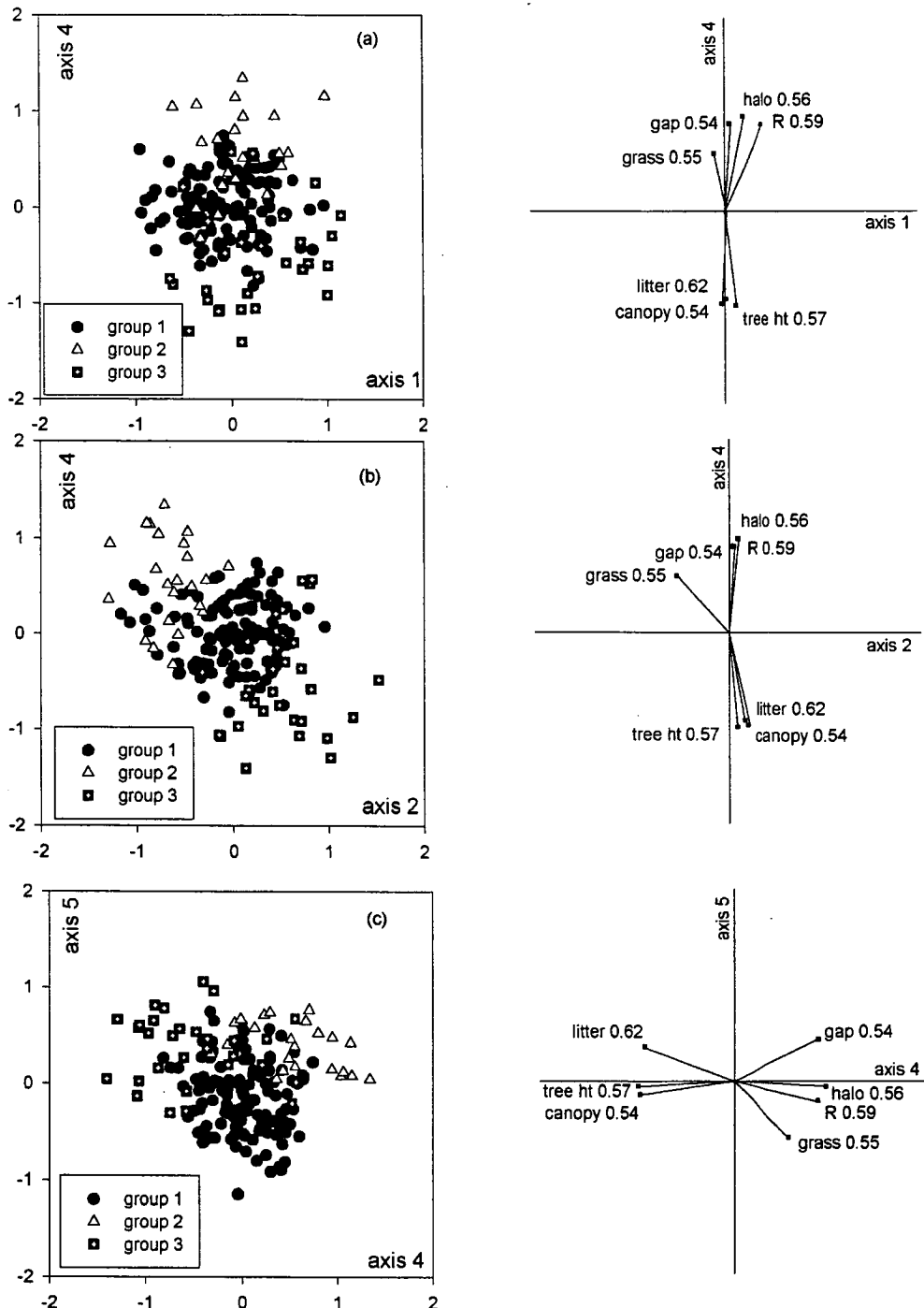


Figure 5.2. Ordination of 182 quadrats in five dimensions (stress = 0.16) from Table Mountain showing the three floristic groups defined by UPGMA classification and associated significant vectors in a) axis 1 against axis 4, b) axis 2 against axis 4, c) axis 4 against axis 5. Group 1 = ubiquitous, group 2 = gap/open forest, group 3 = trunk/canopy.

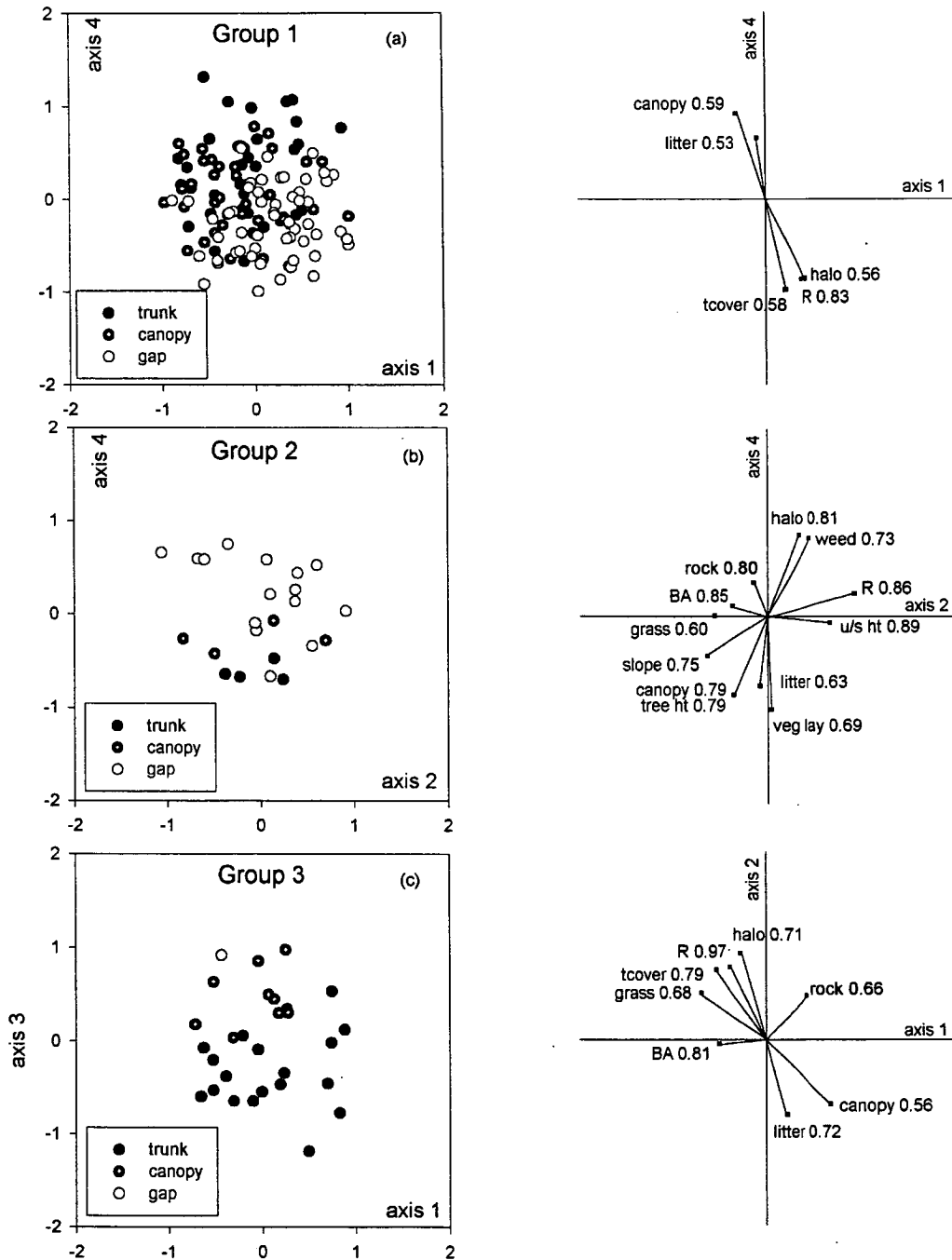


Figure 5.3. Ordinations of each of the three floristic groups showing trunk, canopy and gap quadrats and associated vectors. a) floristic group 1 (ubiquitous) (stress = 0.15 in five dimensions), b) floristic group 2 (gap/open forest) (stress = 0.12 in four dimensions) and c) floristic group 3 (trunk/canopy) (stress = 0.14 in four dimensions).

5.3.2 Specific halo effects

Specific tree/gap effects and their interactions are displayed in Table 5.3 for the 37 most abundant species. Seven species (*Acaena novae-zelandiae*, *Geranium sessiliflorum*, *Hypochaeris radicata*, *Luzula* spp., *Ranunculus scapiger*, *Viola hederacea* and *Wahlenbergia* spp.) had greater cover in gaps than under trees. Two species, (*Ajuga australis* and *Lomandra longifolia*) showed significant *aspect 1* effects, with greater cover in north quadrats, both under trees and in gaps. Two species showed an interaction between tree or gap and *aspect 1*, with *Brachyscome spathulata* found predominantly in north gap quadrats and *Pterostylis* spp. in east gap quadrats.

The second aspect factor (*aspect 2*) was associated with four significant species cover differences: *Ajuga australis*, *G. sessiliflorum* and *Plantago glabrata* displayed highest cover in sector 1 (trees N and E, gap S, W and C), whereas *Galium australe* displayed highest cover in sector 2 (tree S and W, gap N and E). Interactions between *aspect 2* and tree or gap revealed only one significant effect, that of *Leucopogon hookeri* with highest covers in N and E gaps.

The third aspect factor (*aspect 3*) was associated with two significant species cover differences: *Gonocarpus serpyllifolius* and *L. hookeri* were both found in sector 2 (tree S and E, gap N and W); and three interactions, with *Acacia dealbata* and *Cyathodes parvifolia* having highest cover in N and W gaps, and *H. radicata* having highest cover in S and E gaps.

Significant cover differences existed between trunk and canopy rings under trees and there were interactions with two of the three aspect variables (Table 5.4). Eleven species (*Acacia dealbata*, *Brachyscome spathulata*, *G. serpyllifolius*, *Helichrysum scorpioides*, *Hypericum japonicum*, *Lagenophora stipitata*, *Leucopogon. hookeri*, *Luzula* spp., *Poa*

gunnii, *Senecio gunnii*, and *Viola hederacea*) exhibited greater cover in canopy rings than in the ring adjacent to the trunk. Trunk or canopy x *aspect 1* interactions showed only one significant effect, that *B. spathulata* had greater cover in W canopy quadrats. Interaction with *aspect 2* showed that *A. dealbata*, *G. serpyllifolius* and *L. hookeri* exhibited greater cover in N and E canopy quadrats and interaction with *aspect 3* showed no significance.

Table 5.3 Species displaying significant difference in percentage cover between trees and gaps, and the three aspect variables, for the 37 species occurring in at least 20 quadrats in a split-plot ANOVA. $P < 0.05$ in bold, $P < 0.1$ in italics, ns = not significant.

| tree or gap | between plot | within plot | | | | | |
|----------------------------------|------------------|--------------|------------------------|--------------|------------------------|--------------|------------------------|
| | tree or gap | aspect 1 | tree or gap x aspect 1 | aspect 2 | tree or gap x aspect 2 | aspect 3 | tree or gap x aspect 3 |
| <i>Acacia dealbata</i> | ns | ns | ns | ns | ns | ns | 0.045 |
| <i>Acaena novae-zelandiae</i> | 0.017 | ns | ns | ns | <i>0.052</i> | ns | ns |
| <i>Ajuga australis</i> | ns | 0.020 | ns | 0.033 | ns | ns | ns |
| <i>Arthropodium milleflorum</i> | <i>0.074</i> | ns | ns | ns | ns | ns | ns |
| <i>Brachyscome decipiens</i> | ns | ns | ns | ns | ns | <i>0.080</i> | ns |
| <i>Brachyscome spathulata</i> | ns | <i>0.055</i> | 0.004 | ns | <i>0.088</i> | ns | ns |
| <i>Cyathodes parvifolia</i> | <i>0.060</i> | ns | ns | ns | ns | <i>0.056</i> | <0.001 |
| <i>Galium australe</i> | ns | ns | ns | 0.037 | ns | ns | ns |
| <i>Geranium sessiliflorum</i> | <0.001 | ns | ns | 0.007 | ns | ns | ns |
| <i>Gonocarpus serpyllifolius</i> | <i>0.062</i> | ns | ns | ns | ns | 0.040 | ns |
| <i>Helichrysum scorpioides</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Hydrocotyle hirta</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Hypericum gramineum</i> | <i>0.070</i> | ns | ns | ns | ns | ns | ns |
| <i>Hypericum japonicum</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Hypochaeris radicata</i> | <0.001 | ns | ns | ns | ns | ns | 0.038 |
| <i>Lagenophora stipitata</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Leucopogon hookeri</i> | ns | ns | ns | ns | 0.008 | 0.040 | ns |
| <i>Leucopogon stuartii</i> | <i>0.091</i> | ns | ns | ns | ns | ns | ns |
| <i>Lomandra longifolia</i> | ns | 0.021 | ns | <i>0.053</i> | ns | ns | ns |
| <i>Lomatia tinctoria</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Luzula</i> spp | 0.048 | ns | ns | ns | ns | ns | ns |
| <i>Plantago glabrata</i> | ns | <i>0.063</i> | ns | 0.036 | ns | ns | ns |
| Poaceae spp | <i>0.061</i> | ns | ns | ns | ns | ns | ns |
| <i>Poa gunnii</i> | ns | ns | <i>0.064</i> | ns | ns | ns | ns |
| <i>Poa rodwayi</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Poranthera microphylla</i> | ns | <i>0.074</i> | ns | ns | ns | ns | ns |
| <i>Pratia pedunculata</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Pteridium esculentum</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Pterostylis</i> spp | ns | ns | 0.043 | ns | ns | ns | <i>0.073</i> |
| <i>Ranunculus scapiger</i> | 0.020 | ns | ns | ns | ns | ns | ns |
| <i>Senecio gunnii</i> | ns | ns | ns | ns | <i>0.089</i> | <i>0.073</i> | ns |
| <i>Veronica calycina</i> | ns | ns | <i>0.061</i> | ns | ns | ns | ns |
| <i>Viola betonicifolia</i> | ns | ns | ns | ns | <i>0.088</i> | ns | ns |
| <i>Viola hederacea</i> | 0.014 | ns | ns | ns | ns | ns | ns |
| <i>Wahlenbergia</i> spp | 0.001 | ns | <i>0.093</i> | ns | ns | ns | ns |

Table 5.4 Species displaying significant differences in percentage cover between trunk and canopy, and the three aspect variables, for the 37 species occurring at least 20 quadrats in a split-plot ANOVA. $P < 0.05$ in bold, $P < 0.1$ in italics, ns = not significant.

| trunk or canopy | between plot | within plot | | | | | |
|----------------------------------|------------------|--------------|---------------------------------|--------------|-------------------------------|--------------|-------------------------------|
| | trunk or canopy | aspect 1 | trunk or canopy y x aspect 1 | aspect 2 | trunk or canopy x aspect 2 | aspect 3 | trunk or canopy x aspect 3 |
| <i>Acacia dealbata</i> | <0.001 | ns | ns | ns | 0.040 | ns | 0.057 |
| <i>Acaena novae-zelandiae</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Ajuga australis</i> | ns | 0.020 | ns | 0.035 | ns | ns | ns |
| <i>Arthropodium milleflorum</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Brachyscome decipiens</i> | ns | ns | ns | ns | ns | 0.080 | ns |
| <i>Brachyscome spathulata</i> | 0.041 | 0.055 | 0.013 | ns | ns | ns | ns |
| <i>Cyathodes parvifolia</i> | ns | ns | ns | ns | ns | 0.059 | ns |
| <i>Galium australe</i> | 0.057 | ns | ns | 0.034 | ns | ns | ns |
| <i>Geranium sessiliflorum</i> | ns | ns | ns | 0.008 | ns | ns | ns |
| <i>Gonocarpus serpyllifolius</i> | 0.037 | ns | ns | ns | 0.046 | 0.036 | ns |
| <i>Helichrysum scorpioides</i> | 0.010 | ns | ns | ns | ns | ns | ns |
| <i>Hydrocotyle hirta</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Hypericum gramineum</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Hypericum japonicum</i> | <0.001 | ns | ns | ns | 0.088 | ns | ns |
| <i>Hypochaeris radicata</i> | ns | ns | ns | ns | ns | ns | 0.096 |
| <i>Lagenophora stipitata</i> | 0.012 | ns | ns | ns | ns | ns | ns |
| <i>Leucopogon hookeri</i> | 0.002 | ns | ns | ns | 0.003 | 0.032 | ns |
| <i>Leucopogon stuartii</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Lomandra longifolia</i> | ns | 0.023 | ns | 0.058 | ns | ns | ns |
| <i>Lomatia tinctoria</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Luzula</i> spp | 0.044 | ns | ns | ns | ns | ns | ns |
| <i>Plantago glabrata</i> | ns | 0.065 | ns | 0.037 | ns | ns | ns |
| Poaceae spp | ns | ns | ns | ns | ns | ns | ns |
| <i>Poa gunnii</i> | <0.001 | ns | 0.084 | ns | ns | ns | ns |
| <i>Poa rodwayi</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Poranthera microphylla</i> | ns | 0.074 | ns | ns | ns | ns | ns |
| <i>Pratia pedunculata</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Pteridium esculentum</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Pterostylis</i> spp | 0.064 | ns | ns | ns | ns | ns | ns |
| <i>Ranunculus scapiger</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Senecio gunnii</i> | 0.006 | ns | ns | ns | 0.054 | 0.053 | ns |
| <i>Veronica calycina</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Viola betonicifolia</i> | ns | ns | ns | ns | ns | ns | ns |
| <i>Viola hederacea</i> | 0.003 | ns | ns | ns | ns | ns | ns |
| <i>Wahlenbergia</i> spp | ns | ns | ns | ns | ns | ns | ns |

5.3.3 Chlorophyll fluorescence and temperature

While both *L. longifolia* and *L. tinctoria* experienced photoinhibition in the partially logged coupe and control area (Fig. 5.4), F_v/F_m values were significantly ($P < 0.001$) lower in the partially-logged coupe (*L. longifolia*, F_v/F_m partially-logged/unlogged = 0.53/0.56, *L. tinctoria*, F_v/F_m partially-logged/unlogged = 0.44/0.60). The grass *P. gunnii* experienced no photoinhibition ($P > 0.05$), F_v/F_m partially-logged/unlogged = 0.77/0.79.

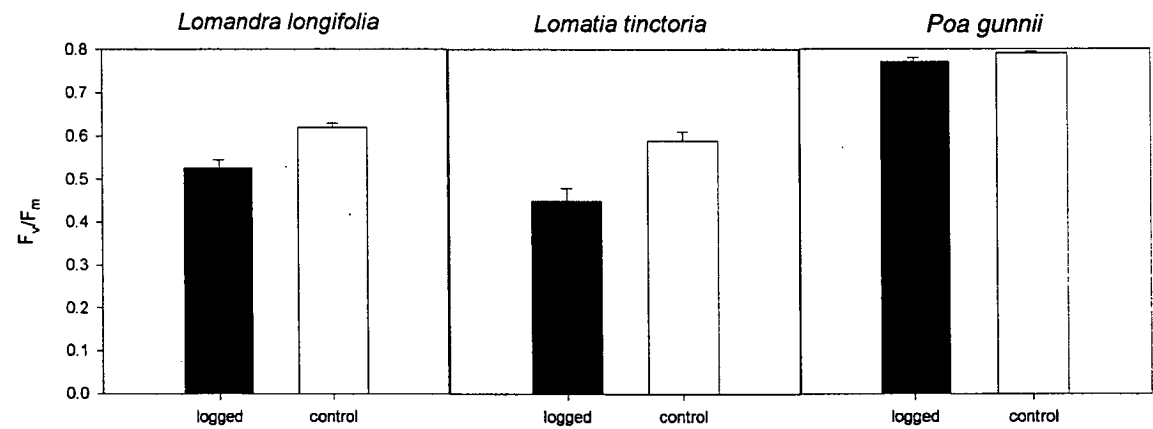


Figure 5.4 Mean chlorophyll fluorescence measurements on three species *Lomandra longifolia*, *Lomatia tinctoria* and *Poa gunnii*, in partially-logged coupes and unlogged controls. Error bars are standard deviation

The only significant difference for temperature was the south trunk position that had a lower maximum temperature (Figure 5.5) than forest gaps (south trunk mean = 16.1°C, gap mean = 21.7°C, $P < 0.001$). The absolute temperature range, however, was greater in forest gaps (-2.2 – 29.9°C) than under tree canopies (-1.8 – 28.0°C).

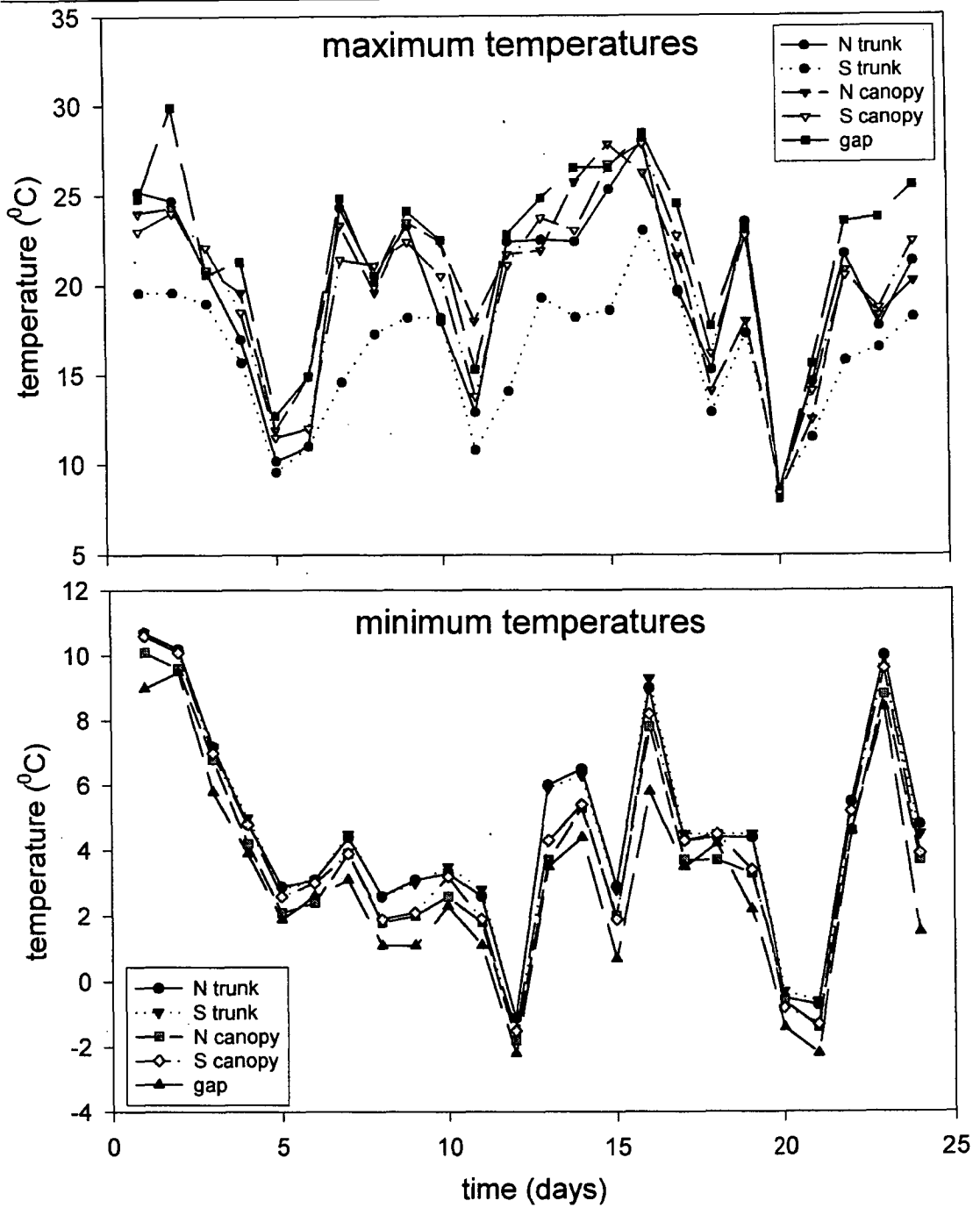


Figure 5.5. Mean maximum and minimum daily temperatures of the four positions under three tree canopies, and one gap position, for grassy forest at Table Mountain over a 23 day period in autumn (March/April 2001).

5.4 Discussion

5.4.1 Halo effects

A definite halo effect exists in these highland forests with the presence of overstorey eucalypts suppressing both the cover and diversity of the understorey (Figure 5.2 & 5.3). There was increased cover of seven species in gaps compared to under trees (Table 5.3), and increased cover of eleven species under the canopy edge compared to being adjacent to the trunk (Table 5.4). This understorey cover difference between trees and gaps is similar to the negative relationship established between understorey yield and tree basal area (Kirkpatrick 1997b, Scanlan and Burrows 1990), and between understorey cover and overstorey cover (Specht and Morgan 1981) in other Australian eucalypt forests. Various biophysical factors have been suggested to account for the way individual eucalypts affect the understorey below them, including: light; temperature; moisture; pH; nutrients; allelopathy; and litter accumulation (Kirkpatrick 1997b). The results from this study suggest that litter accumulation, light and temperature are the most likely factors affecting the distribution of understorey species in this highland forest.

5.4.2 Litter

In this study litter cover was associated with a decrease in species richness and understorey vegetation cover. Similar findings suggest that litter can physically inhibit the establishment of many understorey species (Nash Suding and Goldberg 1999, Kirkpatrick 1997b, Wilson and Zammit 1992, Sydes and Grime 1981). Increasing litter cover was negatively related to the cover of ten of the eleven species around trunks (Table 5.4) (*A. dealbata*, *B. spathulata*, *G. serpyllifolius*, *H. scorpioides*, *H. japonicum*,

L. stipitata, *Luzula* spp., *P. gunnii*, *S. gunnii* and *V. hederacea*). These species reproduce predominantly by seed or are of low stature, with small shoots and straggling growth form, traits associated with greatly reduced cover in areas of high litter (Sydes and Grime 1981). In contrast, the three dominant species in the trunk/canopy group (*L. tinctoria*, *L. longifolia* and *P. esculentum*) all have robust rhizomes and vegetative shoots well adapted to penetration and establishment in deep litter. The distribution of tree litter and the differential ability of ground flora species to emerge through layers of persistent litter are key factors associated with plant distributions on the forest floor (Sydes and Grime 1981). In the highland forest studied here, the suppressive effect of litter is particularly prevalent below very large, old eucalypts where the accumulation of litter results in a floristic shift away from a predominantly grassy, species rich understorey to one dominated by *L. tinctoria*, *L. longifolia* and *P. esculentum*.

5.4.3 Radiation

The generous degree of light penetration through eucalypt canopies does not require understorey plants to be shade-adapted and so the majority of understorey species in eucalypt forests respond positively to increased light levels (Kirkpatrick 1997b). In this study species responding to increased light on northerly aspects under tree canopies and in gaps include seven forbs (*A. novae-zelandiae*, *G. sessiliflorum*, *Hypericum gramineum*, *H. radicata*, *R. scapiger*, *V. hederacea* and *Wahlenbergia* spp.), two monocots (*Arthropodium milleflorum* and *Luzula* spp.), three shrubs (*Cyathodes parvifolia*, *L. hookeri* and *Leucopogon stuartii*), the small tree *A. dealbata* and seven forbs associated with the gap/open forest group (Table 5.3) (*Veronica calycina*, *H. gramineum*, *Viola betonicifolia*, *Ajuga australis*, *Solenogyne gunnii*, *Euchiton collinum*

and *Plantago glabrata*). The grasses also responded to increased light levels in the same fashion. Both forb and grass guilds have been shown to increase in cover following partial logging in this same forest type (Chapter 4), probably because of the increase in radiation reaching the forest floor.

The results presented here are similar to those found in large gaps (1000 to 16000 m²) created in an open canopy, longleaf pine forest in south-western Georgia (McGuire *et al.* 2001). In those forests the growth of understorey vegetation was positively correlated with increased light in gaps; that understorey light increased as a function of distance from gap edges; and there was less light in the southern aspect of gap openings. The Southern Hemisphere study here has less light in the northern aspect of gap openings and thus maximum species cover should develop in the southern aspect of the gaps. This was not the case, however, and it was within the northern aspect of gaps that a large number of species reached their maximum cover values. Thus, another factor was operating here to control the understorey distribution.

5.4.4 Photoinhibition

Despite the positive response to increased radiation mentioned above, light alone does not explain all the understorey patterns displayed here. If increased light were the primary factor, the majority of species would show maximum cover values in the southerly aspect of gaps, but this was only true for four forbs (*H. radicata*, *A. australis*, *G. sessiliflorum*, *P. glabrata*) and the grasses *P. gunnii* and Poaceae spp. Other species all exhibited highest cover in N and/or E gap quadrats. This suggests that for optimum growth these species require some protection from maximum radiation, especially in the morning.

Forest gaps displayed an increase in diurnal temperature range and even a diffuse eucalypt canopy will have a marked effect on the temperature regime, reducing maximum temperatures, increasing minimum temperatures, and reducing radiation frosts, compared to adjacent treeless areas (Bowman & Nunez 1986, Nunez & Sander 1982). Tree canopies are, therefore, affecting both the light and temperature regime beneath their canopy when compared to adjacent cleared areas or large gaps.

Lowered F_v/F_m values, as displayed by *L. longifolia* and *L. tinctoria* in this study, show that these species are exhibiting varying degrees of photoinhibition, and that its severity is increased in areas of higher radiation/lower night temperatures. It has been established that for stress-induced photoinhibition, the cost is decreased efficiency of conversion of intercepted light into dry matter (Long *et al.* 1994) and this should be reflected as less cover on the ground for affected species. Thus it is suggested that cold-induced photoinhibition is one of the factors creating some of the distribution patterns noted above. In *Eucalyptus pauciflora* and *Nothofagus solandri* woodlands, 65% of regenerating seedlings were distributed under the adult canopy in the sector from 165°S to 285°W, where exposure to direct sunlight was minimised throughout the day in winter and during the morning in summer (Ball *et al.* 1994, Ball 1994, Ball *et al.* 1991). This distribution is consistent with minimising exposure during winter to both extreme low temperatures and prolonged high irradiance. However, in the current study the highest cover for many species was in N and E quadrats in gaps. This suggests that once light levels become high enough for optimum growth, it is avoidance of morning sun that then seems to control the distribution of some of the non-shade adapted understorey species.

Three of the dominant species in this forest, *Lomandra longifolia*, *Lomatia tinctoria* and *Leucopogon hookeri* responded with vigorous vegetative growth after destruction of

the above-ground part of the plant during logging operations but after the initial flush of growth, both *L. tinctoria* and *L. hookeri* appeared to suffer frost damage and subsequent reduction in cover. A gap creation experiment in a closed canopy northern hardwood forest on the Allegheny Plateau, North America showed that small forest gaps ($< 150\text{m}^2$) may be below a threshold for pronounced environmental change, apart from increased light on clear summer middays (Collins and Pickett 1987). Thus, the small gap size in our study (125m^2) might not be big enough to elicit the very low night temperatures due to radiation frost experienced in adjacent open areas. The open canopy that results after higher intensity logging (reduction of eucalypt basal area of at least 50%), however, subjects the understorey to lower air and ground temperatures (Nunez and Bowman 1986) and increased sunlight, exposing understorey to photoinhibition. Once leaves become photodamaged, prolonged exposure to high light intensities could result in death of cells and whole leaves (Oquist 1987). Thus, exposed leaves might suffer more damage than shaded leaves, even if there were no difference in night temperatures (Ball 1994).

In the *E. delegatensis* forests of the Central Plateau two patterns of natural regeneration after wildfire are probably occurring. For predominantly sexually reproducing species, seedlings would presumably become established around the mature plant (allowing for species dependent seed dispersal distance) and then be subsequently culled from exposed locations by adverse combinations of high light and low temperature (Ball 1994). Mature plants would tend to be in more favourable locations anyway. Similarly, for species reproducing vegetatively, most new shoots would come from plants with the highest cover that are presumably already in favourable locations and more resistant to litter suppression close to surviving trees. Shoots in areas of high

radiation would also be culled, tending to produce some the spatial patterns observed here. Thus cold-induced photoinhibition will be a major determinant of spatial patterns of regeneration in relation to microclimate in subalpine habitats (Ball *et al.* 1991).

Further research using chlorophyll fluorescence techniques and more precise cover measurements (as opposed to the generalised mid-point percentage cover values used here), and targeting species like the dominant shrubs: *L. tinctoria*, to see if this photoinhibition prone species does actually display distinct patterns on the forest floor; and *L. hookeri* to see if a species that displays distinct cover patterns on the ground is actually photoinhibited, is warranted.

6. Effects of shading and disturbance on three understorey species found in grassy *E. delegatensis* forest of the Central Plateau, Tasmania.

6.1 Introduction

The previous chapters describe understorey patterns that exist in unlogged forest and how these patterns change after partial logging in high altitude *E. delegatensis* forests of the Central Plateau, Tasmania. The understorey patterns in unlogged forests are primarily determined by litter and light levels produced by the overstorey eucalypts. The understorey patterns after partial logging appear to be related to increased light and temperature range, and the disturbance associated with the harvesting operation. Although these processes are associated with the large-scale patterns observed, there is little direct evidence of the effects of light, temperature and disturbance on individuals of understorey species occurring in these forests (although see chlorophyll fluorescence measurements in Chapter 5). This evidence requires experiments with controlled levels of stress and disturbance.

Predictions of plant responses to any change in environment depend on a better understanding of species realised responses to environmental gradients (Austin & Gaywood 1994, Austin 1992). The resulting responses can be drawn as curves relating to a physiological response, (the graph of species performance in relation to variation in some environmental factor), or an ecological response, (the species response in competition with other species) (Austin & Austin 1980). Experimental evidence shows

that species response curves along various environmental gradients in multispecies mixtures differ from those in monoculture (Campbell & Grime 1992, Austin 1982, Austin & Austin 1980).

Experiments of this type are usually carried out as randomised pot designs where each level of the gradient is assigned to a separate small container (Austin *et al.* 1985, Austin & Austin 1980, Austin 1982). This approach has several drawbacks, the major one being the need to guard against edge effects. An effective and simple way to deal with these difficulties is to synthesise artificial communities and construct continuous gradients in single containers (after Campbell & Grime 1992).

In this chapter, the effects of environmental gradients and multispecies competition on vegetation structure are examined using three common understorey species from these forests. Artificial communities, either single-species stands or additive mixed-species stands were established under two continuous gradients: one of shading intensity; one of disturbance intensity.

Three main questions are asked 1) do the three species differ in their response to shading and disturbance? 2) does competition affect the responses of these species to shading and disturbance? and 3) does the shape of the physiological responses curves differ from the ecological response curves for the three species examined?

6.2 Methods

6.2.1 Experimental design

Three plant species were chosen for the experiment: the sedge, *Lomandra longifolia*; the shrub, *Lomatia tinctoria*; and the grass, *Poa labillardierei*. The first two species are

important components of the understorey in grassy *E. delegatensis* forest found near Table Mountain, where the field measurements for the experiment were carried out. The grass species, *Poa gunnii* and *P. rodwayi* are also important components of the understorey but, because of the difficulty in obtaining sufficient number of these two species, the more readily available *P. labillardierei* was used in the experiment even though it does not occur at the site.

The experimental design follows that of Campbell and Grime (1992) in their test of plant strategy theory. The experiment was set up in galvanised steel trays 1200 x 1200 x 200 mm (length x breadth x depth) with holes punched in the bottom to allow drainage. The bottom 50mm of each tray was covered with fine gravel and the remainder filled with a native potting mix. This mix comprised 6 parts pinebark, 4 parts sand and 1 part peatmoss with the addition of dolomite lime (2.7kg/m³), 3-4 month osmocote 19:2.6:10 (1kg/ m³), 8-9 month osmocote 17:1.6:8.7 (2kg/m³), micromax (0.5kg/ m³) and iron sulphate (0.5kg/ m³). Each tray was watered twice daily for a period of 30 minutes in the morning and afternoon to minimise water or nutrient stress for the duration of the experiment, and grazing was excluded.

6.2.2 Shading intensity gradient

A shading intensity gradient was established across each tray with a frame suspended 900 mm above the soil surface supporting three grades of shade cloth with one edge of the tray uncovered. This resulted in four shading intensities running in 250 mm wide strips north-south across each tray corresponding to 0, 50, 75 and 100% shading of full

sunlight. Each tray was surrounded by a 10mm wide buffer area consisting of a strip receiving the same light intensity as the adjacent section of the central area.

6.2.3 Disturbance intensity gradient

A disturbance intensity gradient was created by applying an increasing number of defoliation points in contiguous 330mm wide strips across the soil surface at right angles (east-west) to the shading intensity gradient. Three different intensities of disturbance were applied by removing 0, 50 and 100% of above ground parts of the plants. A 100mm wide buffer area that received the same disturbance intensity as the adjacent section of the central area surrounded the central 1m² area of the tray.

Disturbance was imposed by clipping off all the above ground part of the plant level with the soil surface and removing the clippings. This mimics the damage to understorey plants that occurred in partially logged forests when the passage of machinery scraps above ground parts. Every plant and every second plant were clipped in the 100% and the 50% disturbance intensity strip respectively.

6.2.4 Experimental procedure

Trays were set out in three replicates of four trays each on a flat area at the University of Tasmania farm, Cambridge, Tasmania. Seedlings of each species were planted out on 22-24 February 2000 with each of the three species as a pure stand and one tray planted as a mixed stand based on a Latin Square design (Figure 6.1). This resulted in a plant matrix of $9 \times 8 = 72$ individual plants in each tray. The three replicates of four trays were

orientated north south with the order of the pure and mixed trays arranged randomly within each replicate.

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| P | M | T | M | T | P | T | P | M |
| M | T | P | P | M | T | M | T | P |
| T | P | M | T | P | M | P | M | T |
| M | T | P | M | T | P | T | P | M |
| P | M | T | P | M | T | M | T | P |
| T | M | P | T | P | M | P | T | M |
| M | P | T | P | M | T | T | M | P |
| P | T | M | M | T | P | M | P | T |

Figure 6.1 Mixed species tray design set out in Latin Squares. P = *P. labillardierei*, M = *L. longifolia*, T = *L. tinctoria*.

The shading gradient was established on the 15th March 2000, three weeks after planting and was left intact until completion of the experiment.

The disturbance gradient was imposed at right angles to the shading gradient on 15th May 2000, 11 weeks after planting giving the plants a chance to become properly established and, in the case of *L. tinctoria*, develop small lignotubers just below the soil surface. Only the one disturbance event was imposed thus mimicking a one-off logging event, and the time of disturbance was correlated with what happens in the field, as most logging in highland forests takes place in late summer/autumn.

Weed seedlings were continually removed by hand for the duration of the experiment. Liverwort mats were particularly prevalent in some trays and these were broken up and removed.

6.2.5 Measurements

Measurements were confined to the central 1-m² area of each tray. The imposed gradients resulted in a matrix of 12 330 x 250 mm rectangular areas of differing degrees of shading/disturbance. From 5-7 February 2001 shoot material was removed from contiguous 330 x 250 mm areas of the tray surface at soil level, placed in paper bags, dried at 80 °C and weighed.

Light measurements were taken on 30th January 2001 between 10-11am under clear skies. The quantum flux density was measured with a Li-cor quantum sensor held 40cm above the soil surface under each of the four shading intensities (n = 12 for each intensity).

Chlorophyll fluorescence measurements were carried out on the three species, *L. longifolia*, *L. tinctoria* and *P. labillardierei* at the experimental site in Cambridge using a PAM-2000 fluorometer and 2030-B leaf-clip holder (Heinz Walz GmbH, Effeltrich, Germany). Photochemical efficiency, F_v/F_m , was assessed on 27th July 2000 on three dark-adapted individuals in two treatments, sun (0% shading) and shade (50% shade), of each of the three species. Single measurements were made on each leaf of the most recently expanded pair and on a single older leaf for *L. longifolia* and *L. tinctoria*. Due to the narrow diameter of the leaves of *P. labillardierei*, measurements were made on several of the green leaves laid in an unbroken row in the leaf-clip holder.

6.2.6 Data analysis

Biomass data were analysed as a factorial experiment of a blocked split-plot design. Treatment effects on biomass were analysed by analysis of variance on natural logarithm

transformed data. Trays were treated as main blocks and block, species, competition and species/competition interaction effects were tested against the main block error term. The 12 shade-disturbance matrix levels were treated as sub-blocks and shading, disturbance, species and competition and interaction effects were tested against the residual error.

Competition effects were further examined in two ways, first by calculating the absolute difference between pure-stand and mixed stand biomass (pure – mixed (g/m^2)) and the difference standardised for changes in biomass and productivity across the matrix ((pure – mixed) \times 100/(pure) (%)) (Campbell and Grime 1992). The standardised competition percentages were then tested as above by analysis of variance for interaction effects between species, shading and disturbance. Second, by comparing the relative physiological performance curve and the ecological performance curve for each of the three species in response to both shading and disturbance (Austin 1982, Austin and Austin 1980,). Two types of curve are examined, first the curves of absolute biomass yield, and second, curves standardised to the total yield of the mixture at a particular gradient position. The standardised curves are based on two values i) a relative (or physiological) performance value defined as

$$R_{ij} = Y_{ij}/Y_{mj}$$

where Y_{ij} is the above ground dry weight yield, per unit area, of species i at factor level J and Y_{mj} is the yield for a pure stand of the most productive species, m , at that factor level, and ii) a normalised ecological performance value defined as

$$E_{ij} = Y'_{ij}/Y'_{mj}$$

where Y'_{ij} is the above ground dry weight of species i in mixed stand at factor level J and Y'_{mj} is the yield of the most productive species in the mixed stand at that factor level

(Austin 1982). The reasoning behind this measure is that the biomass of the most productive species provides an estimate of the potential productivity for the factor level. This estimate, however, will be dependent on the particular range of species tested. Both measures are normalised (scaled so that both maxima equal 1.0) and this allows the performance to be corrected for the carrying capacity of a particular environment and is essential if useful comparisons are to be made (Austin 1982)

Fluorescence data were analysed with a t-test to determine differences between shaded and full sun plots at the Cambridge site.

6.3 Results

6.3.1 General observations

All three species grew rapidly after planting out in trays with no mortality in the initial stage of the experiment. Following the disturbance application, however, several individuals of *L. tinctoria* and *P. labillardierei* did not recover. The grass *P. labillardierei* was of much greater stature and vigour compared with the other two species and dominated the mixed trays.

6.3.2 Light

The shading matrix that was the result of the four strips of shade cloth (0, 50, 75, 100% shade) running across each tray actually corresponded to a quantum flux density

of 1446, 624, 265, and 30 $\mu\text{mol}/\text{m}^2/\text{sec}$ respectively. Therefore the actual light intensity of each strip corresponded to 100, 43, 18, and 2 % of full sunlight respectively.

Table 6.1 Statistical significance of effects on log transformed aboveground biomass in Fig. 2. B = block, Sp = species, C = competition, Sh = shading, D = disturbance. Ns = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

| Between effects | | | | | |
|-----------------|-----|-----|--------|--|--|
| B | Sp | C | Sp x C | | |
| ns | *** | *** | *** | | |

| Within effects | | | | | | | | | | | |
|----------------|-----|---------|--------|--------|-------|--------|-------------|------------|-------------|------------|-----------------|
| Sh | D | Sp x Sh | C x Sh | Sp x D | C x D | Sh x D | Sp x C x Sh | Sp x C x D | Sp x Sh x D | C x Sh x D | Sp x C x Sh x D |
| *** | *** | *** | * | ** | * | ns | ns | ns | ns | ns | ns |

6.3.3 Aboveground biomass

After one-year growth, marked differences in biomass distribution had developed in the trays (Fig. 6.2) In the pure stands, *Lomatia tinctoria* and *P. labillardierei* achieved maximum biomass in the lowest shade-lowest disturbance corner of the matrix while *Lomandra longifolia* achieved maximum biomass in the 50% shade-lowest disturbance sector of the matrix. Increased intensities of shade and disturbance both reduced vigour of all three species so that biomass was least with combined high shade and disturbance, although species were affected to different extents by shade and disturbance (Table 6.1). For example, severe shade reduced biomass by 39, 61 and 100% in *L. longifolia*, *L. tinctoria* and *P. labillardierei*, respectively, while severe disturbance reduced biomass by 43, 97 and 66%. Species were ranked for maximum biomass in order *P. labillardierei* > *L. longifolia* > *L. tinctoria* with *P. labillardierei* exhibiting 41% and 76% greater biomass than *L. longifolia* and *L. tinctoria* respectively. When biomass is graphed in relation to total tray productivity all three species display increased biomass with

increasing productivity, however, the rise is of greater magnitude for *P. labillardierei* than for *L. longifolia* and *L. tinctoria* (Fig. 6.3a).

Where the species were combined in the mixed stand, competition altered the biomass distribution patterns (Fig. 6.2 & 6.4, Table 6.2). The competition effect was different for each species and was influenced by shading but not by disturbance (Table 6.2). The fast growing, robust *P. labillardierei* was little affected by the presence of other species, in fact it increased in biomass in the mixed trays continuing to achieve maximum biomass in the sector combining the lowest intensity of both shade and disturbance. The remaining two species were sharply restricted in both biomass and distribution by the presence of other species, principally *P. labillardierei*. Maximum biomass of the shrub *L. tinctoria* was displaced out of the low shade-low disturbance intensity corner towards the mid to high shade-low disturbance sector of the matrix. Maximum biomass of the sedge *L. longifolia* in the mixed stand coincided with the low to mid shade-mid disturbance sector of the matrix (Fig 6.4). An important feature of Figure 6.4 is that there were marked differences in the susceptibility of the three species to competition in the mixed stand. *P. labillardierei* was least affected by competition across the entire matrix and *L. tinctoria* and *L. longifolia* were most affected. When biomass is graphed in relation to total tray productivity in mixed stands *P. labillardierei* follows the same shaped curve as in the pure stands but with greater biomass whereas both *L. longifolia* and *L. tinctoria* show no increase in biomass with an increase in productivity (Fig.6.3b).

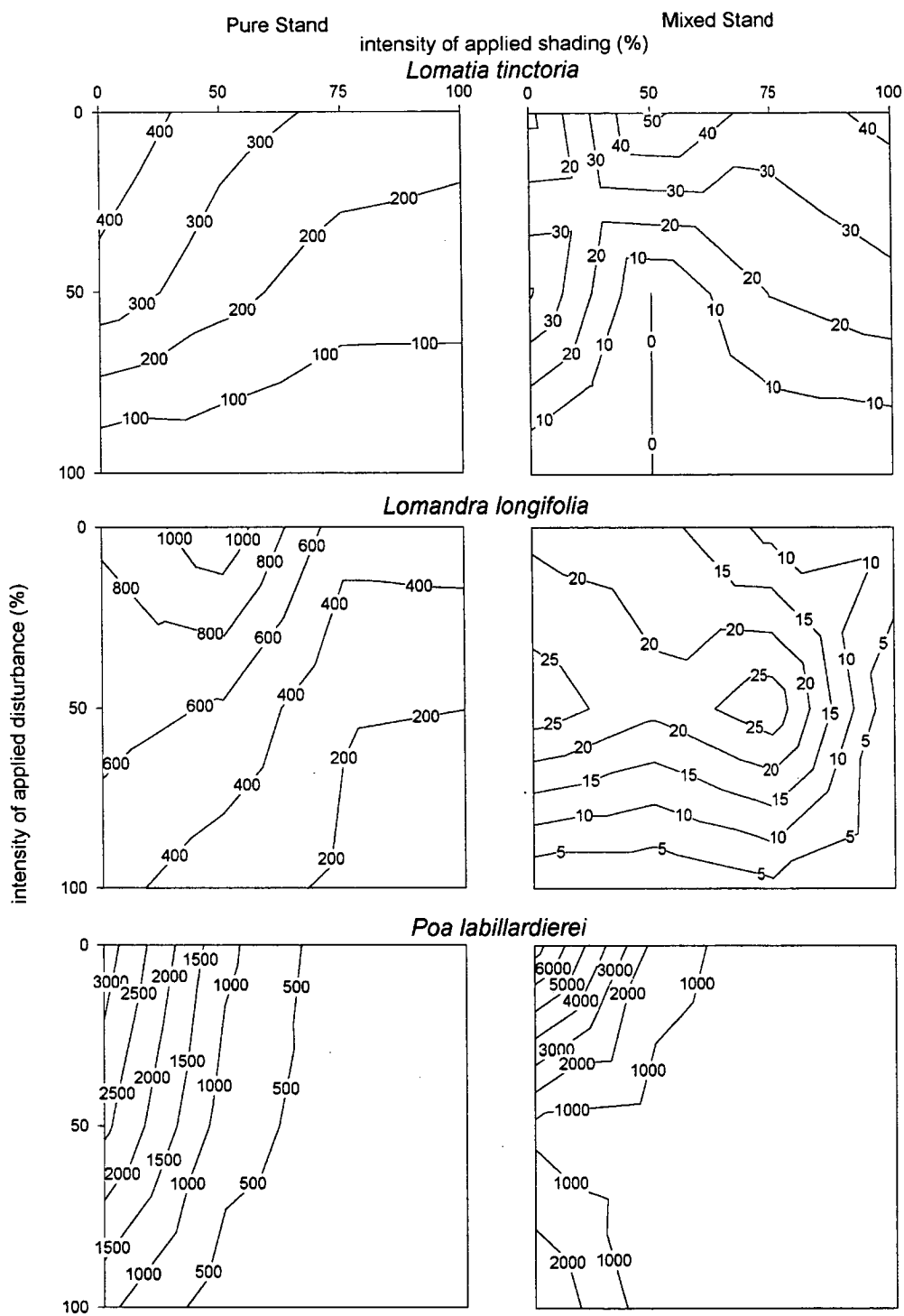


Figure 6.2 Above ground biomass (g/m^2) of the three species grown in pure and mixed stands on an experimental shading-disturbance matrix

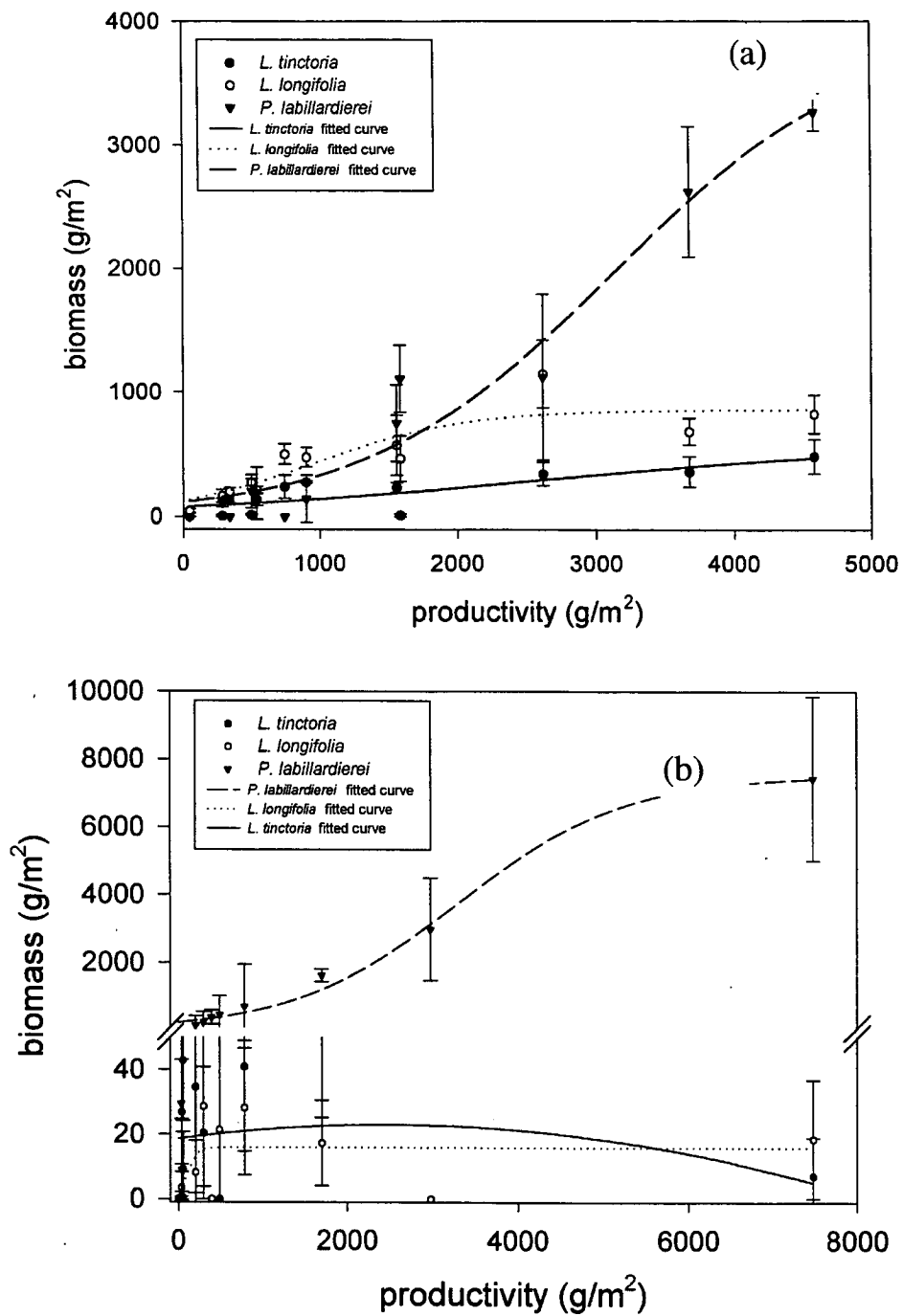


Figure 6.3 Fitted curves of above ground biomass related to total tray productivity for the three species grown on an experimental shading-disturbance matrix in (a) pure stand and (b) mixed stand (note scale change for biomass axis. Error bars = sem).

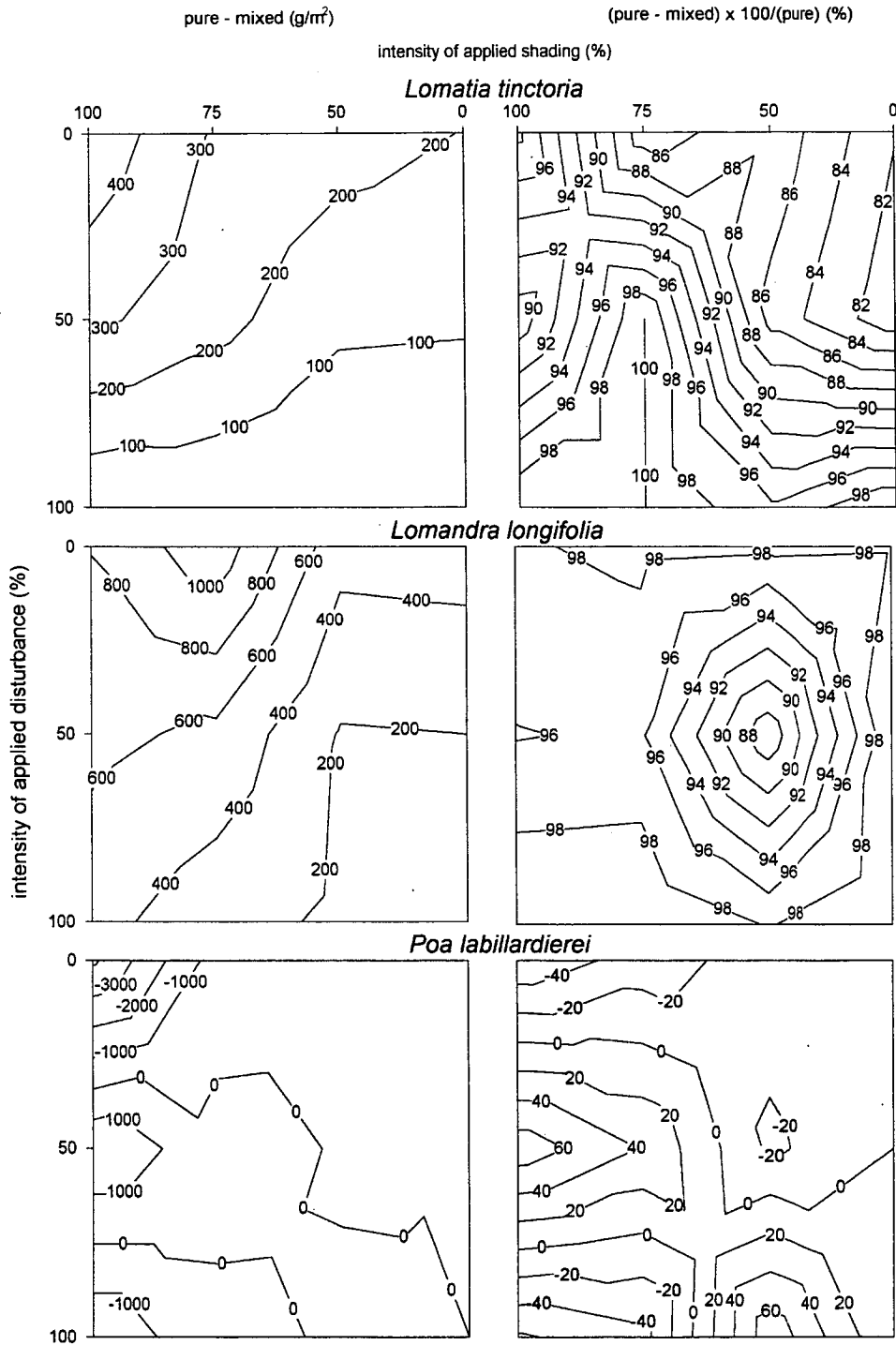


Figure 6.4 Calculated differences between pure and mixed stand above ground biomass for three species grown on an experimental shading-disturbance matrix. Minus values for *P. labillardierei* indicate greater biomass in mixed stands than in pure stands.

Table 6.2 Statistical significance of effects on standardised competition percentages calculated from aboveground biomass in Fig. 6.4. B = block, Sp = species, Sh = shading, D = disturbance. Ns = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

| Between effects | | | | | |
|-----------------|----|---------|--------|--------|-------------|
| B | | | Sp | | |
| ns | | | *** | | |
| Within effects | | | | | |
| Sh | D | Sp x Sh | Sp x D | Sh x D | Sp x Sh x D |
| ** | ns | ** | ns | ns | ns |

6.3.4 Relative physiological and ecological performance curves

Another way of showing the above biomass results is with the physiological and ecological response curves based on absolute yield (Fig. 6.5). Results for the standardised response curves differ substantially, however, with two of the three species (*L. longifolia* and *P. labillardierei*) grown in pure stands having a relative performance value of 1.0 at one or more of the shading intensities. *L. longifolia* and *L. tinctoria* can perform well relative to other species only at higher shading intensities while *P. labillardierei* shows the opposite trend, performing best in full sun. Only *L. tinctoria* was significantly affected by disturbance showing reduced performance at high disturbance intensity. Disturbance had minimal effect on *L. longifolia* and *P. labillardierei* (Fig.6.6).

In mixed trays (ecological performance curves), *P. labillardierei* dominated the trays at lower shading intensities performing better than in the pure stands. At the highest shading intensity *L. tinctoria* outperformed both *L. longifolia* and *P. labillardierei*. The three species show two distinct physiological maxima with respect to the shading and disturbance gradients and these generally occur at the same intensities as the maxima in the relative ecological performance curves (Fig. 6.6).

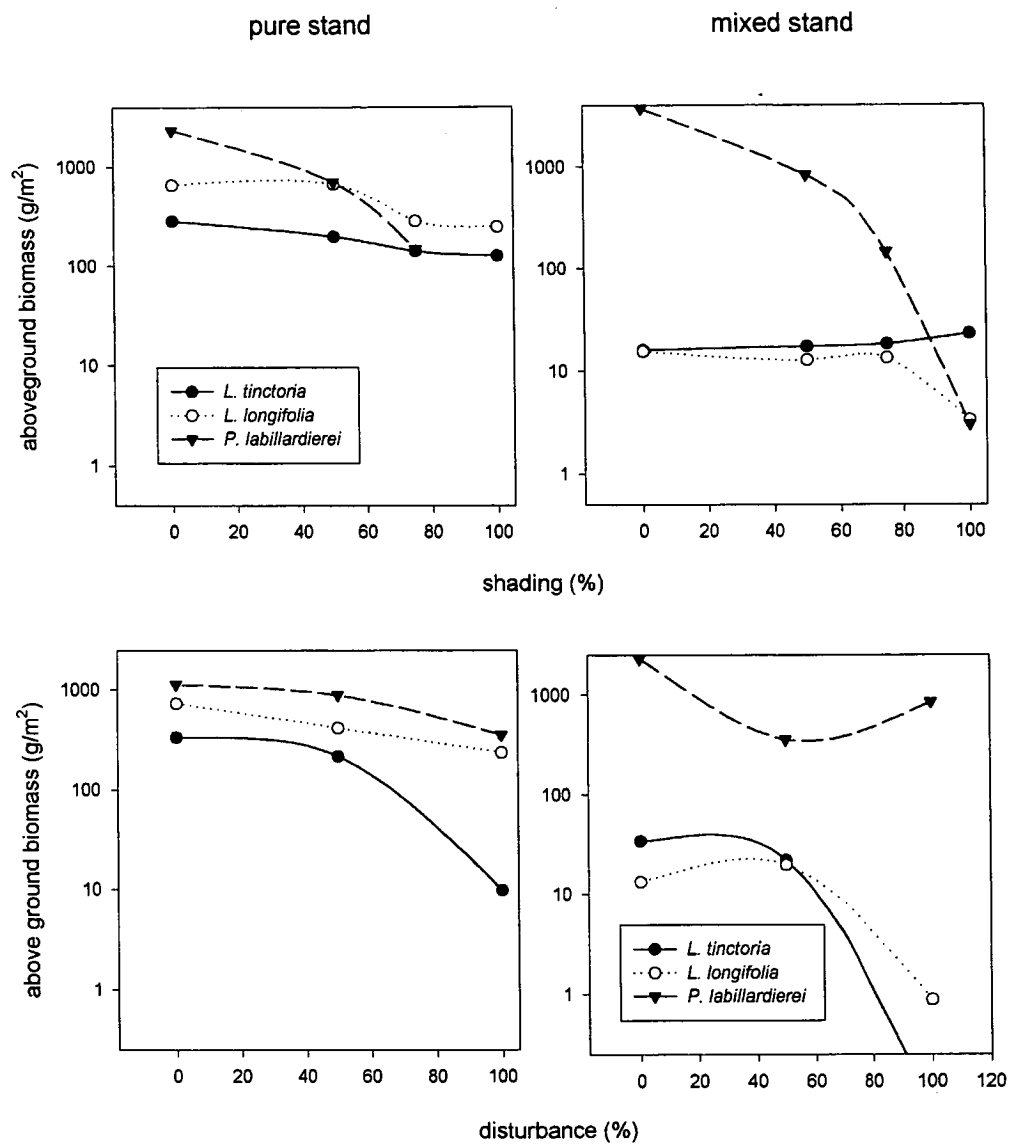


Figure 6.5 Above ground biomass response curves to shading and disturbance for the three species in pure and mixed stands. Note logarithmic scale.

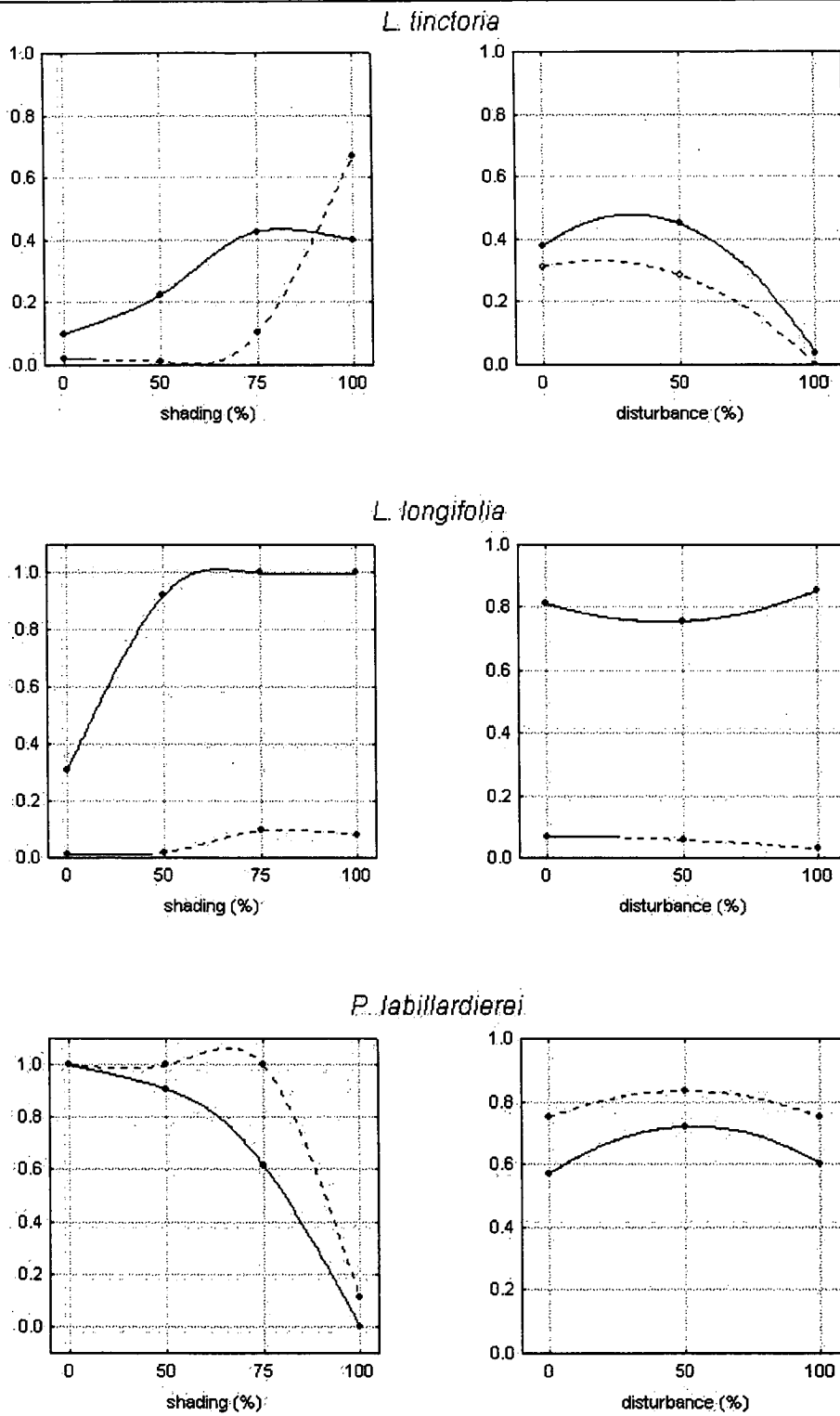


Figure 6.6 The fitted relative physiological performance curves (solid lines) and ecological performance curves (dashed lines) for the three species in response to shading and disturbance.

6.3.5 Chlorophyll fluorescence

In the shading/disturbance matrix *L. longifolia* and *L. tinctoria* experienced moderate photoinhibition in full sun (*L. longifolia*, F_v/F_m sun/shade = 0.69/0.77, *L. tinctoria* F_v/F_m sun/shade = 0.66/0.73) with values significantly ($P < 0.01$) reduced in full sun strips of the matrix. *P. labillardierei* experienced no photoinhibition but, in contrast, displayed significantly ($P < 0.01$) reduced values in the shaded area of the matrix (F_v/F_m sun/shade = 0.77/0.74) (Fig. 6.7b).

In Chapter 5, chlorophyll fluorescence measurements were taken of the three species *L. longifolia*, *L. tinctoria* and *P. gunnii* in a logged coupe and a control area in high altitude *E. delegatensis* forest at Table Mountain and are reproduced in Figure 6.7a. In the field both *L. longifolia* and *L. tinctoria* experienced severe photoinhibition in logged and control areas. F_v/F_m values, however, were further significantly ($P < 0.001$) reduced in the logged coupe compared to the control (*L. longifolia*, F_v/F_m logged/control = 0.53/0.56, *L. tinctoria*, F_v/F_m logged/control = 0.44/0.60). By contrast, the grass *P. gunnii* experienced no photoinhibition ($P > 0.05$) (F_v/F_m logged/control = 0.77/0.79).

6.4 Discussion

6.4.1 The experimental technique

The experiment allowed each species population to expand from their original points of establishment and quickly occupy those areas of the matrix conducive to survival (Campbell and Grime 1992). However, the grass, *Poa labillardierei* exhibited rapid growth and quickly dominated the mixed trays severely reducing the biomass of the

other two species. A *Poa* spp. of small stature, such as *P. gunnii* and *P. rodwayi*, both of which co-exist with the *Lomandra longifolia* and *Lomatia tinctoria* in the grassy understorey of the native forest site at Table Mountain, would perhaps have given a clearer result. Any of these smaller species would reach heights more similar to *L. longifolia* and *L. tinctoria* and would more closely mimic patterns observed in the field. Nevertheless, clear differences in fundamental and realised niches were indicated by the experiment using the selected species.

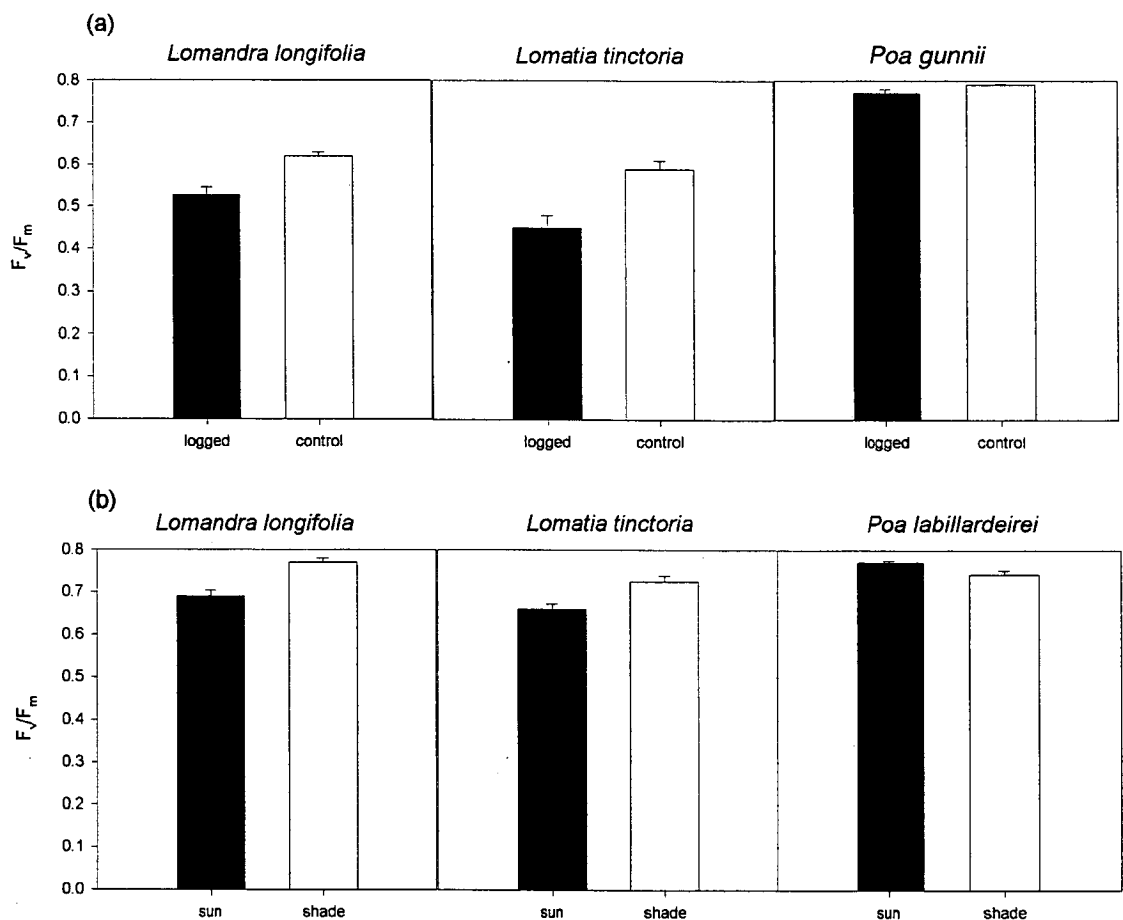


Figure 6.7 Chlorophyll fluorescence measurements (F_v/F_m) for the three species in a) partially logged forest and unlogged control forest (redrawn from chapter 3), b) shading/disturbance tray experiment, sun (0% shading) and shade (50% shade) parts of the matrix. Error bars are standard deviation.

6.4.2 Shading, disturbance and competition

The patterns in vegetative vigour observed across the experimental matrix in the pure stands provide a clear indication that species distributions can be influenced by direct impacts of shading and disturbance. All species were suppressed by the combined effect of high disturbance and high shading with *L. tinctoria* particularly affected by high disturbance and *P. labillardierei* by high shade levels. These two species displayed maximum vigour in the low shade x low disturbance corner of the matrix. *L. longifolia*, however, reached maximum vigour in the mid shade x low disturbance sector of the matrix suggesting a positive requirement for some protection from full sun for this species, even without competition from the other species.

Given that eucalypt forests predominantly regenerate following a disturbance, and noting the observed species patterns in the field, the severe response of *L. tinctoria* to disturbance is surprising. In the logged coupes at Table Mountain, *L. tinctoria* responded rapidly to aboveground foliage damage with the production of shoots from an underground rhizome. This response was limited and slow in the experiment and suggests that the plants had too little underground reserves to respond to aboveground foliage loss. Thus, it appears that the experiment would have benefited from a longer run time. A minimum of six months growth before application of the disturbance gradient would seem more desirable, particularly for the shrub species with slower growth rates than the sedge and grass species.

The ecological optimal response of both *L. tinctoria* and *L. longifolia* shifted with competition to higher shade intensities, whereas that of *P. labillardierei* was unchanged. The greater biomass of *P. labillardierei* in mixed stands suggests that in pure stands this species was self-competing. The reduced stature and vigour of *L. tinctoria* and *L.*

longifolia meant there was increased spacing of individual *P. labillardierei* in mixed stands allowing the capture of more resources than in the pure stands. Given this species negative response to increased shade, individual plants were probably self-shading in pure stands.

The standardisation to the total yield of the most productive species used here provides a consistent and interpretable curve of physiological and ecological response (Austin 1982). The results of this experiment expressing these standardised performances relative to the other species show a general correspondence between the ecological and physiological optimum for each of the species measured here (Fig 6.6). These maxima, however, do not correspond to the absolute yield optima (Fig. 6.5). Regardless of species composition, absolute biomass will show a regular sequence of changes along environmental gradients and may simply reflect the change in carrying capacity with position on the gradient (Austin 1982). The coincidence of ecological and physiological maxima in terms of absolute yield, therefore, is true only for species least affected by competition (Austin 1982, Austin & Austin 1980). In this experiment that is only true for the grass *P. labillardierei* with *L. longifolia* and *L. tinctoria* particularly sensitive to competition. These results, however, are only relevant to this set of species and will be different in other species mixtures as the ecological response curves are complex and sensitive to the species content (Austin 1982, Austin & Austin 1980). The observed physiological and ecological responses provide a good picture of the difference between a species fundamental and realised niche and this is discussed below.

6.4.3 The fundamental and realised niche

The observation that a species performance in monoculture tended to be greater than in mixture led to the distinction of two types of response, a species fundamental and realised niche (Austin *et al.* 1985, Parrish & Bazzaz 1982a, b, Austin 1982, Fresco, 1982, Austin & Austin 1980, Hutchinson 1961, 1957; Ellenberg 1953 in Mueller-Dombois & Ellenberg 1974). The fundamental niche has been variously described as: the occurrence of a species in the absence of competition (Austin 1999), and, the hypervolume defined by environmental dimensions within which a species can survive and reproduce (Hutchinson 1957). The realised niche has been described as: the occurrence of a species after competition and other biotic interactions (Austin 1999); the reduced hypervolume after a species has been excluded from parts of its fundamental niche because of competition and other biotic interactions (Hutchinson 1957); and, that part of the fundamental niche where the species has a competitive advantage (Giller 1984).

It has been assumed in the past that a species response to an environmental gradient was a classical bell shaped Gaussian optimum curve and that the realised niche was a good approximation of the fundamental niche. These assumptions have been criticised, however, and it is now argued that the optimum of the realised niche may differ significantly from the fundamental niche in both position and shape, and that the response is not necessarily symmetric around the range centre (Vetaas, 2002, Austin 1992, 1982). In fact, the realised niche may assume various skewed shapes and even bimodal curves (Fig 6.8) (Austin & Meyers 1996, Austin *et al.* 1990, Austin & Smith 1989, Mueller-Dombois & Ellenberg 1974).

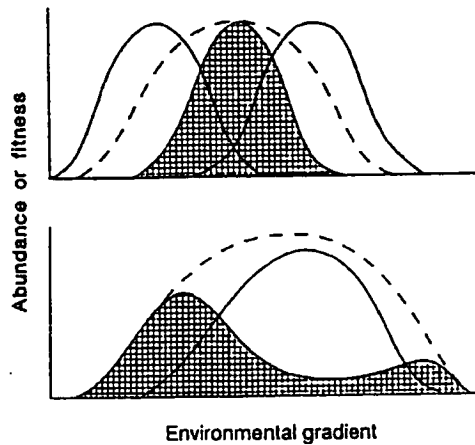


Figure 6.8 Relationship between fundamental and realised niches. Shaded curve represents the realised niche and the broken line the fundamental niche. The upper figure indicates the classical niche theory concept while the lower figure represents the concept where competition may displace a species from the optimal part of its fundamental niche (from Austin 1992).

Several features contribute to the complexity of the shape of the response. The relationship between species occurrence and an environmental factor in the model may be due to a correlation between that environmental factor and a more direct causal environmental variable. For example, direct gradients will show greater partitioning of responses along the gradient due to differential physiological adaptations with the relative performance being determined by plant relative growth rates and ability to form a closed canopy (Austin & Smith 1989). Another feature may be genetic variation within species. Species that have a wide range may have many genetically distinct populations each with a slightly different optimum realised niche (Austin *et al.* 1990).

The recognition of the difference between the realised and the fundamental niche has implications for both spatial and temporal analysis. The realised niche descriptions can be used to study disturbance (such as logging) with a simulation approach: (a) to investigate the sensitivity of simulation models to actual response shapes; and (b) the

descriptions for the full set of species in a region provides a set of predictions against which to compare the community composition generated by the simulation model (Austin *et al.* 1997).

A precise description of the realised niche limits provides a minimum estimate of the fundamental niche. Thus, it can be seen that the optimum of the realised niche may differ significantly from the fundamental niche and this was found here and has been reported by others (Vetaas 2002, Austin 1992, 1982, Austin & Smith 1989). It would appear then that the ecological performance curve could be seen as one dimension of a species realised niche, and is a more appropriate measure of a species ecological response. This is apparent in this experiment where the maxima of the ecological response curves for the three species conform to general impressions of their ecology, particularly in response to logging, and this will be discussed below.

6.4.4 Shading-disturbance-competition in response to logging

The observed responses of the three species in this experiment correspond well with the increased grass/reduced shrub and sedge responses noted after logging in both grassy and shrubby *E. delegatensis* forest. Increased cover of *P. labillardierei* after clearfelling in *E. delegatensis* forest has been correlated with stunted growth of eucalypt regeneration, impeded drainage and reduced air temperature (Ellis 1995, Keenan 1986, Keenan & Candy 1983, Webb *et al.* 1983, Nunez & Sander 1982). These authors also suggested that, rather than being the cause, *P. labillardierei* may just be an indicator of unfavourable conditions. Its rapid growth rate, however, as light levels increase, and the

ability to out compete *L. tinctoria* and *L. longifolia*, suggest it would make a successful competitor to eucalypt saplings. In this study, the majority of logged coupes, in both grassy and shrubby forest, displayed increased cover of a related species *Poa gunnii*.

Concomitantly, the response curves and chlorophyll fluorescence measurements show a requirement for shade for optimal growth of *L. tinctoria* and *L. longifolia* and this is reflected in the general trends of reduced cover of some shrubs and sedges in logged coupes (see Chapter 3 and 4). Recall that both *L. tinctoria* and *L. longifolia* displayed varying degrees of reduced maximal photochemical efficiency in unlogged forest, and this increased in severity in logged coupes. Whether this is due to photodamage or to photoprotection responses (Thiele *et al.* 1998), it still results in reduced growth rates for a large part of the year in these forests and this growth reduction will be exacerbated in the higher light/lower temperature environment of the logged coupe.

There were sites, however, where both species increased in cover after logging, *L. tinctoria* at Clarence Lagoon and *L. longifolia* at Table Mt. These site-specific responses to logging were noted in chapter 3 and 4, and can confound the more general trends. It is suggested that these responses are due to site-specific environmental factors that mediate the photoinhibition and/or competition effects noted above. Possible environmental factors include, the very high rock cover at Clarence Lagoon, increased soil moisture, higher minimum temperatures due to air movement and/or reduced cold air pooling on slopes, and, protection from early morning sunlight in the west facing coupe with increased cover of *L. longifolia* at Table Mountain. Increased rock cover has been correlated with decreased grass cover on the Central Plateau (Fensham & Kirkpatrick 1992), and grass cover has been implicated in thermal inhibition of tree seedlings (Ball

et al. 2002, 1997). The other three factors have been found to reduce the susceptibility of tree seedlings to photoinhibition (Close *et al.* 1999, Ball 1994, Ball *et al.* 1994, 1991).

While competition clearly had an effect in the mixed trays, this result may not be directly transferable to the spatial patterns of the understorey in the field. The plants in the trays are at an early growth phase and the effects of competition have been shown to be highly variable among different life history stages and between different growth forms. For example, graminoids were the superior competitors to dicots at emergence and early growth, but not at the final growth stage (Goldberg *et al.* 2001). In addition, recent studies have found that facilitation is common in situations where competition would be expected to occur, that shrubs can have simultaneously facilitative and inhibitory effects, and that different shrubs have a variety of effects (Facelli & Temby 2002, Goldberg *et al.* 2001). This variability in the nature of competition responses suggests that other environmental variables control the distributions of the understorey communities in these forests. Competition may act primarily through the modulation of environmental variables rather than directly through the availability of resources (Ball *et al.* 2002, 1997, Facelli & Temby 2002, Fowler 2002, Goldberg *et al.* 2001, Egerton *et al.* 2000, Egerton & Wilson 1993, Belsky 1992).

Disturbance operates in a similar fashion, creating short-term trends but not necessarily controlling the understorey distributions. This is because the understorey species in these forests are very resilient to disturbance as eucalypt forests largely regenerate in a disturbance based ecology (Lindenmayer & McCarthy 2002, Peacock *et al.* 1997). In logged forest, *L. longifolia*, *L. tinctoria*, *Leucopogon hookeri* and *Pteridium esculentum* respond rapidly to loss of above ground biomass by vegetative means (see chapter 4). In undisturbed forest, the combination of reduced radiation levels, reduced

diurnal temperature range and increased litter accumulation on the forest floor lead to reduced vigour of the majority of the grasses and *P. esculentum*. A concomitant reduction in the levels of photoinhibition experienced by *L. tinctoria*, *L. longifolia* and *L. hookeri* would also occur. Diversity of grasses, forbs and orchids is kept high, however, in canopy gaps and mediated by fluctuations in soil/air moisture (see Chapter 5). Thus, in unlogged native forest the shrub and sedge species are more able to co-dominate with the grasses, thereby creating the more even pattern of understorey distribution found in the unlogged grassy forest in this study.

7. Effects of plantation establishment on understorey vegetation in *E. delegatensis* R.T. Baker forests of the Central Plateau, Tasmania

7.1 Introduction

The plantation estate in Australia was estimated to cover almost 1.5 million ha in 2000, of which 185,000 ha (12%) occurs in Tasmania (Wood *et al.* 2001). In the past, plantations of *E. delegatensis* and *E. globulus* have performed poorly at sites above 300 m asl in areas such as the Central Plateau (Close *et al.* 2002, Ellis 1995). More recently, a shift to *E. nitens*, a species better able to cope with the combined factors of low temperature and high light (Tibbits 1986), has allowed eucalypt plantations to be established on sites with highly productive soils, to 700m asl (Forestry Tasmania 1999). The primary aim of plantations is, of course, to maximise wood and fibre production, however, plantations can offer biodiversity conservation opportunities by comparison with cleared lands (Borsboom *et al.* 2002, Klomp and Grabham 2002).

This chapter examines two primary questions, 1) does the establishment of higher altitude plantations have an impact on the floristics and structure of the understorey vegetation compared to nearby native forest controls, and 2) are native forest understorey species capable of re-invading ex pasture sites that have been converted to plantations. To do this two plantations were examined, one of 20-year-old *E. delegatensis*, a first rotation ex native forest site, and the other of 4-year-old *E. nitens*, an ex pasture site. Specific questions addressed are; how does plantation establishment

impact on understorey floristics? How do changes, if any, compare/contrast with changes brought about by partial logging in these forests? How does the vegetation structure of plantations compare to partially logged native forest and unlogged forest?

7.2 Methods

Site description, and the common data analysis techniques of ordination, classification, vector fitting and ANOSIM techniques are described in Chapter 2. Quadrat based data collection techniques mirrored those of the pattern analysis in Chapter 3.

7.2.1 Survey design

Two control sites and three plantations sites were surveyed for the plantation pattern analysis survey at Tarraleah. Two of the plantation sites, 1) within rows and 2) windrows, were in a 20-year-old *E. delegatensis* (dele) plantation established in 1979 in cleared native forest. The third plantation site was in a 4-year-old *E. nitens* (nitens) plantation, established in 1995 on an ex pasture site (Table 1.1).

7.2.2 Data analysis

7.2.2.1 Understorey lifeform groups

Species were grouped into seven vegetation lifeform groups: shrubs, native grasses (ngrass), introduced grasses (igrass), other monocots, native forbs (nforbs), introduced forbs (iforbs) and ferns for the plantation analysis. Tests for significant difference in

mean percentage cover between controls and plantations were carried out using one-way ANOVA and *post-hoc* Tukey test on natural log transformed data.

7.2.2.2 Structural landscape continuum

An attempt was made to place the results of plantation establishment on understorey structure in a context with partially logged native forest. This would enable a comparison to be made of the vegetations structural complexity between the two management regimes. To do this a structural complexity score was derived from the sum of four environmental variables collected at each quadrat including: number of vegetation layers; maximum understorey height; number of eucalypt classes; and the habitat complexity score. Structural complexity was assessed in two ways, first as the mean score for all native forest controls, partially logged coupes and plantations examined in this thesis. Second, as the degree of change between partially logged native forest and plantations, and their adjacent unlogged native forest controls.

7.3 Results

7.3.1 Ordination, classification and vector fitting.

Both plantations were clearly separated from the control forest in the ordination space with the 20-year-old *E. delegatensis* plantation and windrow floristically more similar to the controls than the 4-year-old *E. nitens* plantation (Fig. 7.1 & 7.2). ANOSIM analysis of the three classification defined groups (see Fig. A.4.6, Appendix 4) (controls, 1979

dele plantation, 1995 nitens plantation) was very significant, ($P = 0.000$, best between group statistic = 1.201, real between group statistic = 1.754).

The dominant fitted vectors in the ordination space were *grass cover* (0.94), *habitat complexity* (0.91), *aspect* (0.87), and *altitude* (0.84). The *E. nitens* plantation was associated with increased *grass cover*, *rock cover*, *evenness* and the Shannon-Weiner Diversity Index (H'). Whereas an increase in the *habitat complexity* score, *altitude*, number of *vegetation layers*, *maximum understorey height* and *litter* were associated with the native forest control quadrats. *Altitude* is significant because six of the control quadrats are 30 m higher than the plantation quadrats, *aspect* because the 20-year-old *E. delegatensis* plantation and one control site were on a southerly aspect, whereas the 4-year-old *E. nitens* plantation and the other control site are on a northerly aspect. Table 7.1 confirms that the 4-year-old *E. nitens* plantation differed floristically from both the controls and the *E. delegatensis* plantation, being dominated by a forb/introduced grass group including *Cirsium vulgare*, *Hypochaeris radicata*, *Agrostis capillaris*, and *Anthoxanthum odoratum*. Of 42 species present, 14 (33%) were introduced, with a mean cover of 122%. The 20-year-old *E. delegatensis* plantation displayed high cover of three species not found in control forest, the forbs, *Senecio minimus* and *Cirsium arvense*, and the grass, *Holcus lanatus*. These latter two introduced species still dominated the understorey 20 years after establishment. The 20-year-old *E. delegatensis* plantation displayed a reduced cover, and the *E. nitens* plantation a complete absence of typical wet sclerophyll species common in the adjacent controls. These species included, the trees, *Atherosperma moschatum* and *Nothofagus cunninghamii*, the shrubs, *Olearia argophylla* and *Pimelea drupaceae*, and the ferns, *Dicksonia antarctica*, *Histiopteris incisa* and *Hypolepis rugulosa*.

| | 1979 plant | 1979 wind. | 1995 plant | forest controls |
|----------------------------------|---------------|---------------|---------------|--------------------|
| | 000000 | 000111 | 111111 | 12222222223 |
| | 123456 | 789012 | 345678 | 901234567890 |
| <i>Acacia dealbata</i> | +1++11 | 222222 | r | 111111+11111 |
| <i>Polystichum proliferum</i> | 111211 | 111122 | | 112112112211 |
| <i>Senecio linearifolius</i> | +12112 | 1+2122 | rr | 1+1++ +1 1 |
| <i>Cassinia aculeata</i> | r+1 + 1+1 | r | | +2r+11 11 |
| <i>Uncinia riparia</i> | r r11 | rr11++ | + | ++1111+ +1+r |
| <i>Hydrocotyle hirta</i> | +11++1 | r++++r | 1 + | ++1+rr+111+r |
| <i>Oxalis perennans</i> | +1+r1+ | ++111+ | r++ | r1r +r+++++ |
| <i>Clematis aristata</i> | +r1r+r | +r1+r+ | | r rrr r + r |
| <i>Poaceae</i> | 1+ | ++ | | 1 + r+ + |
| <i>Pimelea drupaceae</i> | + r+ | | | ++++r+rrrr+r |
| <i>Pomaderris apetala</i> | r+ r | +r + | | ++++r |
| <i>Zieria arborescens</i> | + 1 | | r | r++++r+ |
| <i>Acaena novae-zelandiae</i> | 222211 | 1212++ | +12122 | +r11rr r1rr |
| <i>Pteridium esculentum</i> | 212221 | 111112 | 112112 | 22+222+11222 |
| <i>Australopyrum pectinatum</i> | r r+1 | r+11r+ | ++ r 1 | +111+ 1+r+ |
| <i>Geranium potentilloides</i> | 11+rr1 | rr++ r | + + + | rrr+++ rr r |
| <i>Viola hederacea</i> | ++ + | | r 1 | rr + rrrr |
| <i>Galium australe</i> | r r++ | r | r | + r rrr |
| <i>Atherosperma moschatum</i> | | r | | + 111rr+ |
| <i>Nothofagus cunninghamii</i> | | | | 1+ + |
| <i>Urtica incisa</i> | | ++ | | 1+r + |
| <i>Dicksonia antarctica</i> | | 122221 | | 1+ +1222121 |
| <i>Histiopteris incisa</i> | +11 | 11222r | | 11+ 1+ |
| <i>Hypolepis rugulosa</i> | | +111++ | | 11+ 1+ |
| <i>Australina pusilla</i> | | | | + r |
| <i>Carex appressa</i> | + | + + | | r |
| <i>Juncus gregiflorus</i> | r | r + | | r |
| <i>Pittosporum bicolor</i> | | + | | r |
| <i>Hypericum gramineum</i> | + r+ + | | | r |
| <i>Olearia argophylla</i> | | + 1 | | |
| <i>Carex</i> spp | r | | | r |
| <i>Cirsium arvense</i> * | + r+11 | | | |
| <i>Senecio minimus</i> | 111+11 | | r | r |
| <i>Cerastium vulgare</i> * | r | r | | |
| <i>Coprosma quadrifida</i> | | | | r 111 |
| <i>Lagenophora stipitata</i> | | | | r+ |
| <i>Drymophila cyanocarpa</i> | | | | rr |
| <i>Geranium sessiliflorum</i> | | | r | + |
| <i>Acetosella vulgaris</i> * | | | r+r+r1 | |
| <i>Euchiton collinum</i> | | | ++1 r2 | |
| <i>Cirsium vulgare</i> * | | | ++r++1 | r |
| <i>Austrodanthonia pilosa</i> | | | + + 2 | |
| <i>Geranium mollis</i> * | | | 112112 | |
| <i>Taraxacum officinale</i> * | | | 112111 | r |
| <i>Hypochaeris radicata</i> * | + | | 122112 | |
| <i>Linum catharticum</i> | | | 112 +2 | r |
| <i>Ranunculus scapiger</i> | | | r r 1 | |
| <i>Leontodon taraxacoides</i> * | | | rrr r+ | |
| <i>Trifolium</i> spp* | | | r r r+ | |
| <i>Scleranthus biflorus</i> | | | r1 + | |
| <i>Vulpia bromoides</i> * | | | r1 + | |
| <i>Agrostis capillaries</i> * | | | 212112 | +r |
| <i>Anthoxanthum odoratum</i> * | | | 112+12 | r r+r |
| <i>Epilobium sarmentaceum</i> | + | r r r | +11+r2 | |
| <i>Pimelea linifolia</i> | | | r+1+r1 | r rr |
| <i>Gonocarpus serpyllifolius</i> | | | +1 | + |
| <i>Asperula gunnii</i> | | | 112r+1 | 1++r+rrrr + |
| <i>Hypericum japonicum</i> | | | +1rr+2 | rr rr r+rrr |
| <i>Holcus lanatus</i> * | 1r+1++ | | 112222 | r |
| <i>Cerastium glomeratum</i> * | | | r rr | |
| <i>Prunella vulgaris</i> * | | | r r | |
| <i>Solenogyne gunnii</i> | | | r r | |

Table 7.1 Two-way table of species by quadrat for the six classification derived floristic groups and four site groups, 1979 E. delegatensis plantation (quadrats 1-6), 1979 E. delegatensis plantation windrows (quadrats 7-12), 1995 E. nitens plantation (quadrats 13-18) and native forest controls (quadrats 19-30). * denotes introduced species.

The windrow in the 20-year-old dele plantation, however, acted as a refuge for some of these species including *Dicksonia antarctica* (also see raw data in Appendix 1).

7.3.2 Understorey lifeform groups

Six of the seven understorey lifeform groups were significantly different between plantations and adjacent controls (Fig. 7.3). Plantations had less cover of shrubs, monocots and ferns, and an increase in cover of introduced grass, native forbs and introduced forbs compared to the adjacent controls.

7.3.3 Structural landscape continuum

Vegetation structural complexity was high for native forest controls, decreases for shrubby and then grassy partially logged forest, and reaches a minimum with plantations. The degree of structural change from adjacent native forest controls was also highest for plantations (Fig. 7.4).

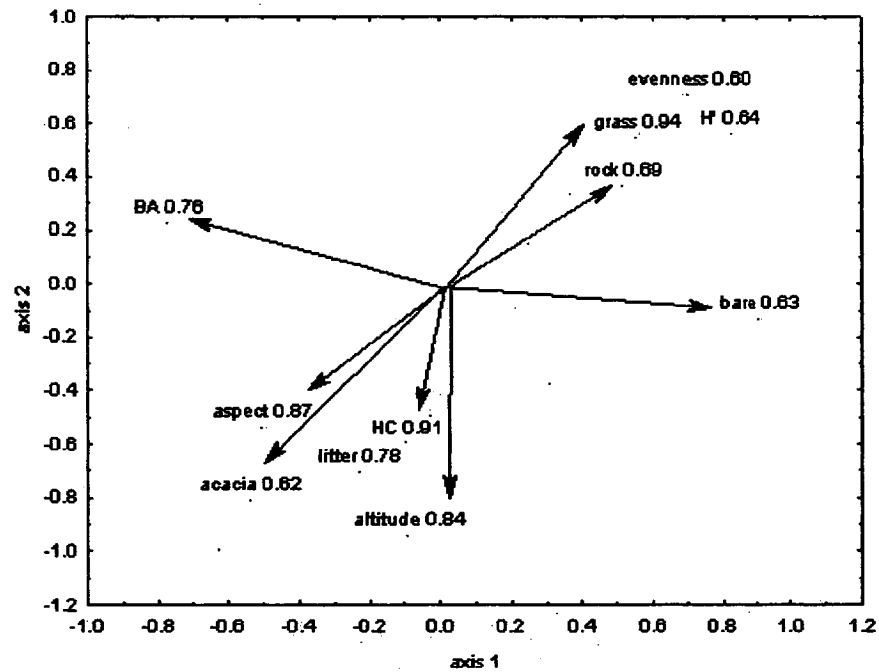
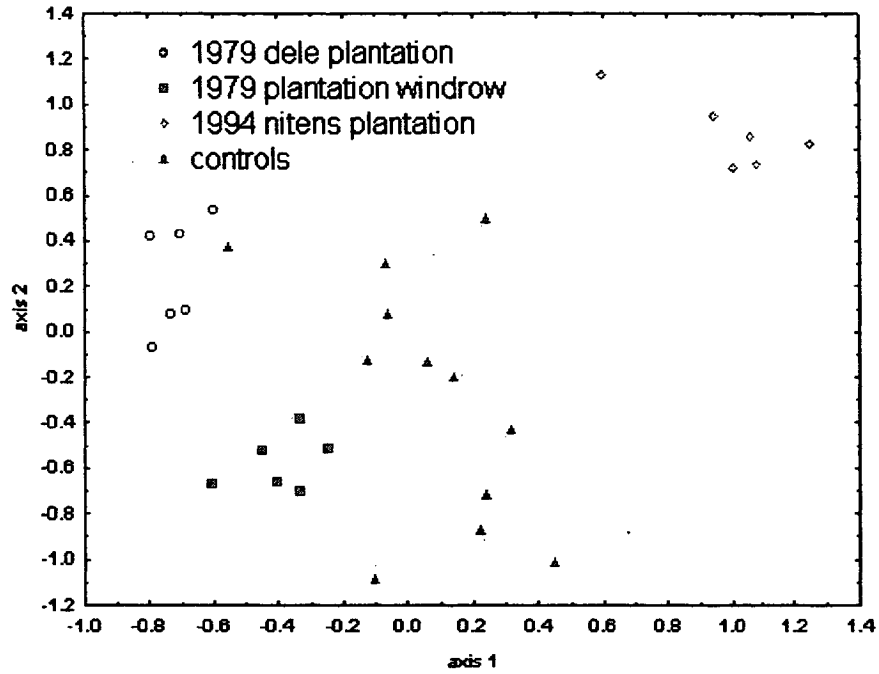


Figure 7.1 SSH ordination (stress = 0.17 in three dimensions) and significant fitted vectors of plantation and control quadrats for axis 1 against axis 2. The number with each vector is the correlation in that direction between the quadrats and the fitted vector.

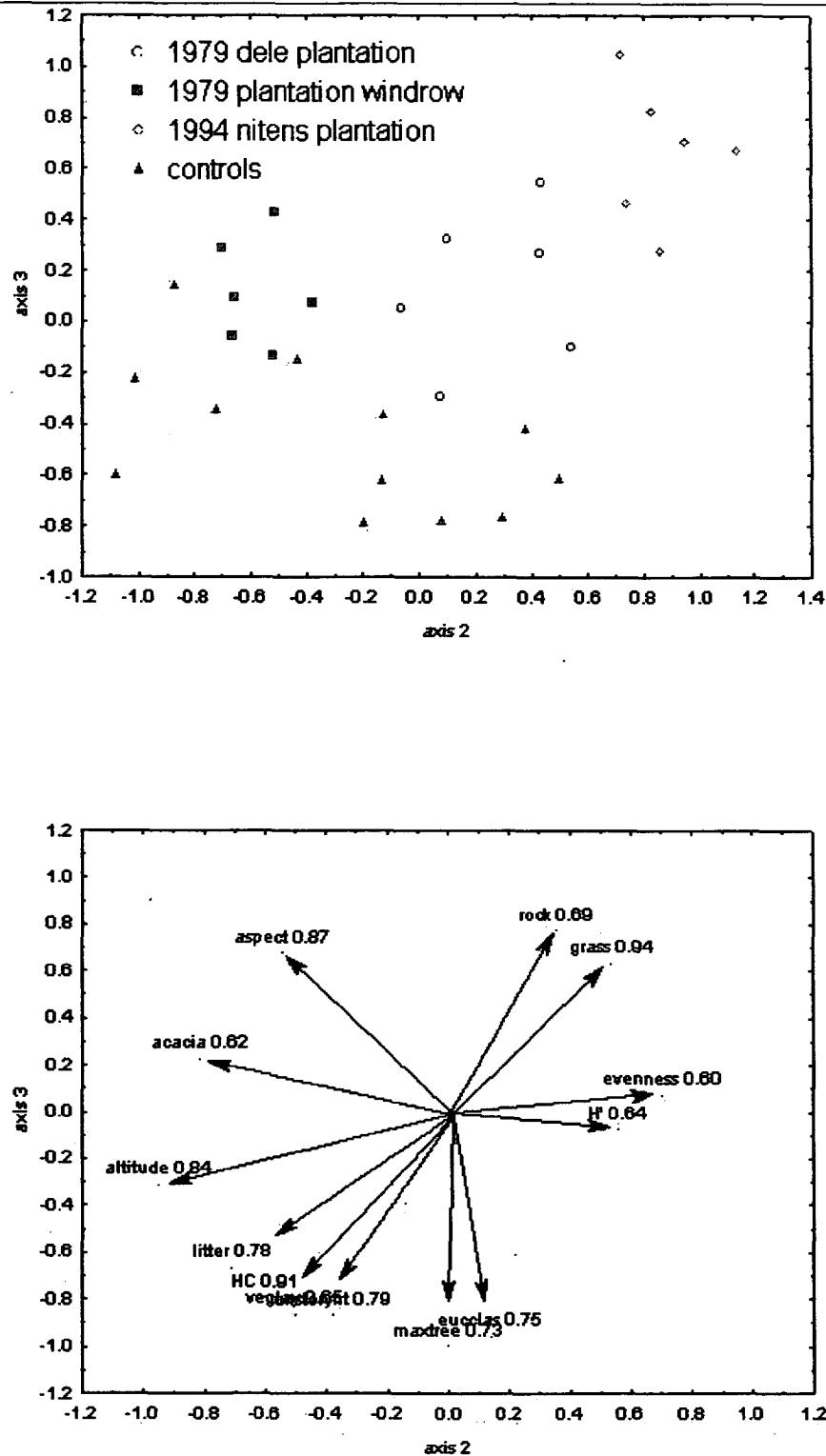


Figure 7.2 SSH ordination (stress = 0.17 in three dimensions) and significant fitted vectors of plantation and control quadrats for axis 2 against axis 3. The number with each vector is the correlation in that direction between the quadrats and the fitted vector.

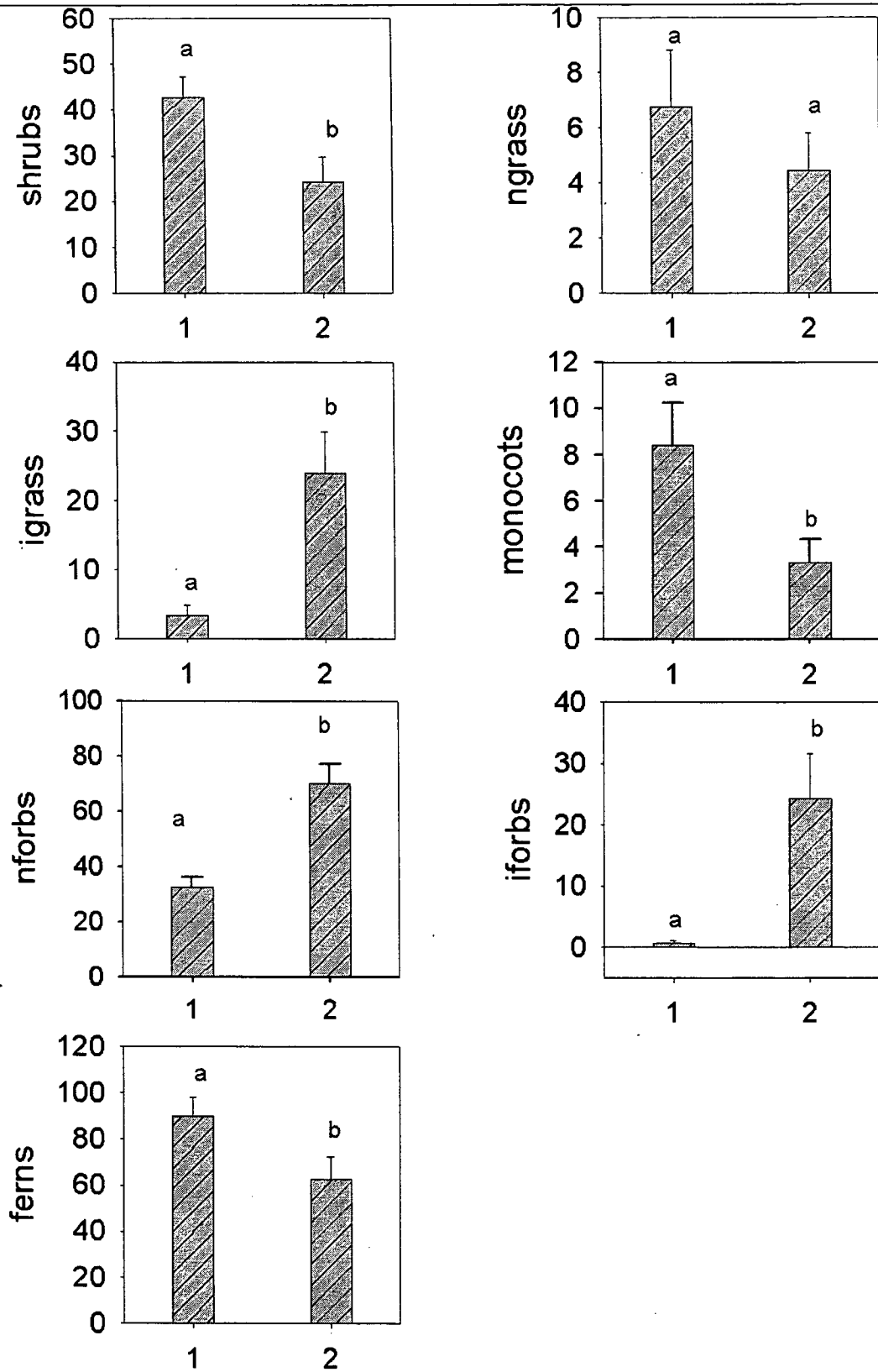


Figure 7.3 Mean percentage cover for seven understory lifeform groups for 1 = control forest, 2 = plantations. Different letters denote significant difference at $P < 0.05$, ANOVA and *post-hoc* Tukey test. Note different percentage scale for each graph. Error bars denote 0.95% confidence limits.

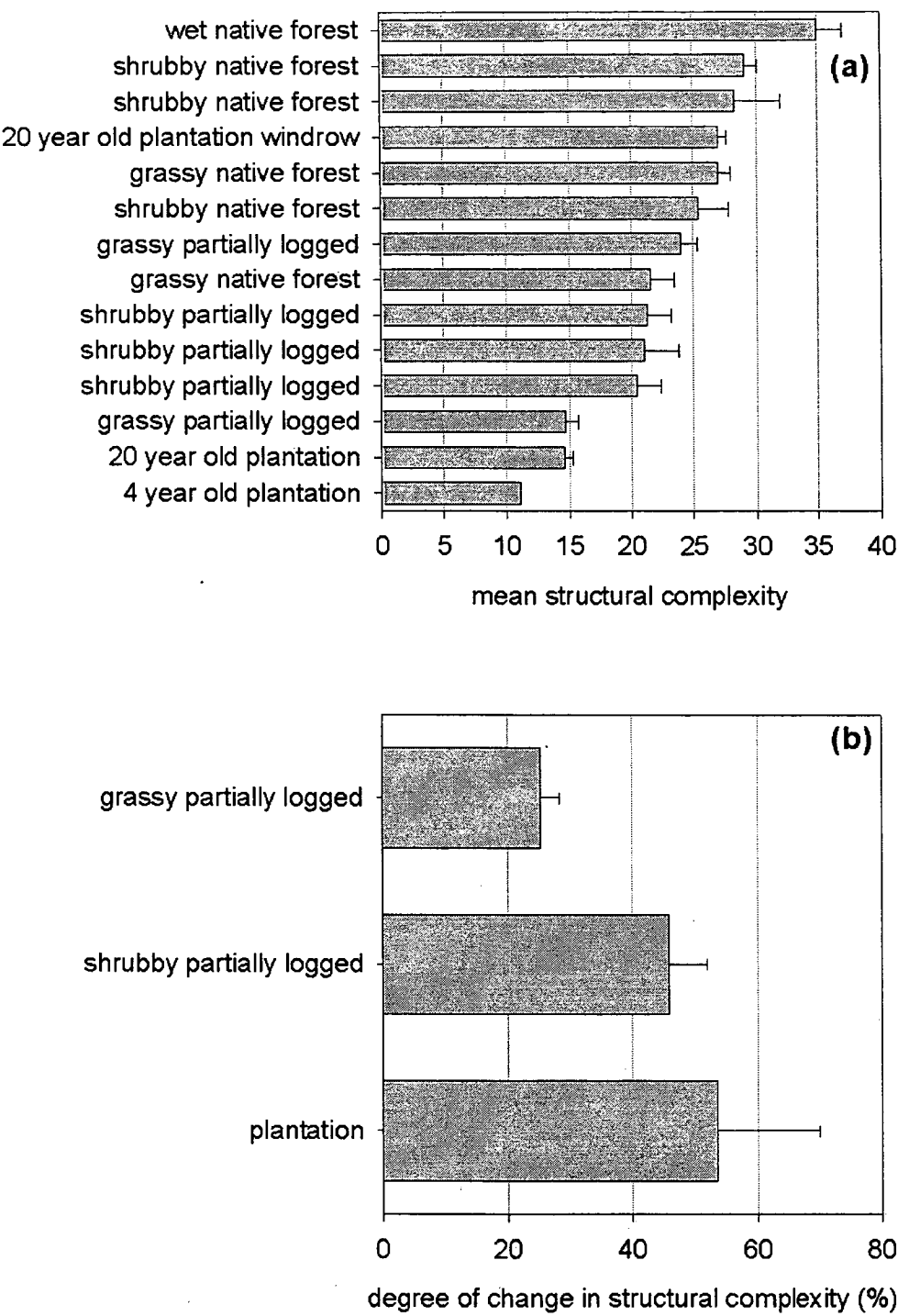


Figure 7.4 (a) Mean (\pm sem) structural complexity score for native forest quadrats, partially logged quadrats, and plantation quadrats. (b) Mean (\pm sem) percentage degree of change in a structural complexity score of grassy and shrubby partially logged native forest, and plantations, from their adjacent control sites.

7.4 Discussion

Partial logging in high altitude *E. delegatensis* forest reduces structural complexity, shrub and monocotyledon cover of the understorey, and increases grass, forb, weed and bare ground cover. These changes to the understorey are exacerbated in magnitude and, probably, duration in plantations. The partial logging of native forest does not result in the loss of species but rather a change in the cover/abundance. Plantation establishment, however, results in significant loss of native species, and the introduction of many weed species.

The understorey of the four years old *E. nitens* plantation is floristically the furthest removed from adjacent control forest. Given the young age of the plantation and that it was an ex pasture site this is understandable. There is little evidence, however, to suggest that native forest species are re-establishing on the site. While many native forb and grass species are present in this plantation only one shrub species, *Pimelea linifolia* was present, and it was not abundant in adjacent control quadrats.

The 20-year-old *E. delegatensis* plantation was closer to adjacent controls in the ordination space, suggesting a reversion to the original floristics, but only in the plantation windrows. The windrow appeared to be a refuge for species common to the site before plantation establishment and was the only part of the plantation where many species were found. Whether these species will now re-establish within the plantation rows remains unknown.

Three factors, however, suggest that a reversion to original floristics is unlikely. First, a rotation time of 20-25 years for pulpwood and 30-35 years for timber (Beadle *pers com* 2003) allows minimal time for natural succession to occur. In addition, increased

diversity has been correlated with increased plantation age (Borsboom *et al.* 2002, Gepp 1976). Second, if plantations are logged and regrown species dependent on these windrow niches may be lost in the second rotation. Third, it has been shown in plantations in Hawaii that abundance of native plants in the understorey decreased with increasing abundance of non-indigenous species (Harrington & Ewel 1997). The last two factors are of particular relevance for the *E. nitens* plantation where the understorey cover is dominated by introduced grasses and forbs. While this situation may change upon canopy closure of the eucalypts, with its consequent reduction in grass and forb cover, it appears unlikely that the native wet sclerophyll species could recolonise a site dominated by introduced species. Other studies have found that species composition in eucalypt forests after disturbance is largely determined by the initial floristics (Ough 2001) and that successive harvesting events result in further change from the original unlogged stands (Lindenmayer *et al.*, 1991a, b). Thus, there may be cumulative long-term effects and the response of species after the first rotation may differ from successive rotations (Lindenmayer, 1999).

7.4.1 Vegetation structure landscape continuum in native forest and plantations

Plantation establishment and repeated harvesting operations in native forest involves considerable simplification of the structural complexity of the vegetation compared to the original forest. This structural simplicity is associated with a reduction in diversity of vertebrate and invertebrate assemblages in plantations (Hobbs *et al.*, 2002). Plantation establishment on ex agricultural land, however, involves an increase in the structural complexity and biodiversity of the site, particularly with the retention of remnant/restored native vegetation patches, retention of logs and stumps, and

windrowing (Fischer & Lindenmayer, 2002, Gibbons & Boak, 2002, Lindenmayer & Munks, 2000).

A plantation continuum ranging from simple agricultural systems to complex native forest systems has been devised by Hobbs *et al.* (2002). This has been modified here by the addition of partially logged native forest (Fig. 7.5). Each land use type (plantation, partially logging, native forest) covers a range of the continuum not a fixed point. This is because within each type of land use there can exist a range of structural complexity from simple to complex i.e. plantation forestry can be more complex (see below) while successive harvests in partially logged native forest can make a system more simple (dotted arrows in Fig. 7.5).

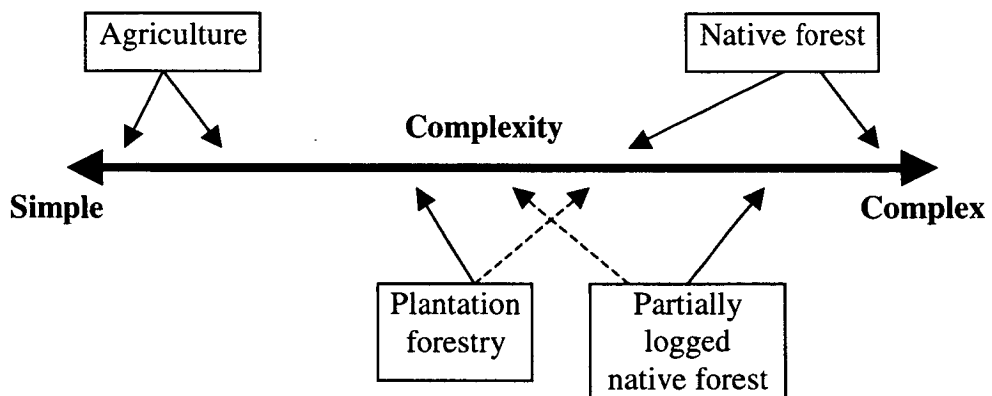


Figure 7.5 The simple-complex structural continuum (redrawn from Hobbs *et al.* 2002) and modified with the addition of partially logged native forest. Dotted arrows indicate increased complexity of complex plantation forestry, and possible decreased complexity of repeat logging in native forest.

Plantation forestry, itself, can also be thought of as a continuum from simple plantation forestry to complex plantation forestry (Kanowski 1997). Simple plantation forestry refers to a narrow and intensive management focus on producing a crop for a limited array of purposes. It is not congruent with the principles of ecological

sustainability and creates similar types of environmental problems that currently afflict agricultural enterprises in many parts of Australia (Hobbs *et al.* 2002, Lindenmayer *et al.* 2002). Complex plantation forestry, while still being a relatively intensive management regime, attempts to include other land uses and values, such as biodiversity conservation, within plantation boundaries. Complex plantation forestry places plantations further to the right on the agriculture-native forest continuum (Fig. 7.5).

Of the two plantations examined in this study, the 1995 *E. nitens* plantation is an example of simple plantation forestry, though it is more structurally complex than the pasture site it replaced, whereas the 1979 *E. delegatensis* plantation is of mid complexity due to the refuge effect of the windrows. The windrows retain elements of the original stand, termed “biological legacies” by Franklin *et al.* 2000, and have important biodiversity conservation value (Bonham *et al.* 2002, Kavanagh & Turner 1994, Friend 1982).

This refuge effect, however, is not expected to survive the next rotation (see above), particularly considering this plantation is small (c 4 ha), it is surrounded by *Pinus radiata* plantation, and the removal of windrows may be carried out in future to control native herbivores (le Mar, 2000). Thus, a second rotation under present management regimes will result in greater floristic change and a further reduction in structural complexity resulting in a shift to a more simple position on the continuum.

Plantation establishment, therefore, can cause either a reduction in structural complexity of a site with a subsequent loss of biodiversity, or an increase in structural complexity of a site, and subsequent gain of biodiversity, depending on the landscape context in which it is used. The replacement of agricultural land with plantation provides increased complexity and subsequent increased diversity. In contrast, the replacement of

native forest with plantation results in a simpler structure than partially logged native forest, and even clearfelled and burned native forest (Ough 2001, Brown 1996, Hickey 1994).

8. General discussion

The first section (8.1) of this chapter summarises the effects of partial logging and plantation establishment on understorey floristics and structure in highland *E. delegatensis* forests uncovered by this research. Following is a discussion on some of the problems encountered in logging impact studies, particularly the increased variability of some community characteristics and how multivariate analyses may provide a better resolution of a disturbance impact drawing on methodological comparisons made in this thesis. A short discussion on ecologically sustainable logging follows.

Section 8.2 discusses the role and importance of cold-induced photoinhibition on the patterning of understorey in the highland forests. Section 8.3 compares disturbance by wildfire and logging and their roles as a structuring factor, and also discusses the results in the light of current ecological theory about community resilience. Section 8.4 provides a general conclusion of the thesis.

8.1 Impacts of partial logging and plantation establishment on highland *E. delegatensis* forests.

8.1.1 General Impacts

8.1.1.1 Partial logging

This study has shown significant effects of partial logging on understorey floristics and structure in both the short and long-term.

The primary short-term (< 2 years) impacts included:

- reductions in the species richness; number of vegetation layers; maximum understorey height; and shrub, forb, grass, orchid, moss and lichen cover,
- increases in soil disturbance and bare ground cover.

Three years after logging:

- some trends had reversed with an increase in the cover of grass, native forbs and weeds;
- other trends persisted such as the greater area of bare ground and the reduced cover of shrubs and orchids.

Five to eight years after logging:

- lowest shrub cover after continuing to decline since logging;
- decreased structural complexity of the forest;
- increased bare ground, weed, and grass cover.

Sixteen and twenty one years after logging in shrubby forest and grassy forest, respectively:

- no recovery of overstorey basal area;
- reduced structural complexity in shrubby forest;
- apparent recovery of structural complexity in grassy forest due to increased grass, sedge, and log cover on the ground and not to any thickening of the tall shrub layer or overstorey canopy;
- shifts in the cover/abundance of dominant species.
- no loss of native species or change in alpha diversity.

8.1.1.2 Plantations

Plantation establishment in native forest resulted in effects that were similar but of much greater magnitude, and probably, of duration than partial logging. Additional changes found in plantations included:

- the loss of many native species.
- the introduction of persistent weed species.

8.1.2 Logging impact studies

Descriptive studies, such as the pattern analysis carried out in Chapter 3, are an essential part of ecological research in order to define the experimental units relevant to the question. This can then be followed with the use of inferential statistics, to determine ecological significance. This procedure was followed in Chapters 3 and 4, and the general agreement between the results of the multivariate analysis, and the replicated, inferential statistical analyses suggests that the general conclusions of the logging impact study are robust. One area of disagreement between the two analyses, however, was in the duration of the logging impact on understorey floristics.

The multivariate analysis techniques of ordination, vector fitting, and permutation tests clearly separated the oldest logged sites from their adjacent unlogged controls and seemed more discriminating of longer-term differences. The multivariate analyses were more sensitive to changes in species patterns following logging and provided a clearer, visual discrimination of quadrats. The univariate analyses of lifeform groups and environmental variables of the space-for-time study, however, suggested that these

variables were approaching the unlogged control values 16-20 years after logging, particularly in the grassy forest.

It is suggested that this spatial agreement and temporal dichotomy in the results arises because of a number of factors, some of which are confounding and are implicit in logging impact studies. These factors have been shown to complicate studies of harvesting impacts and may produce misleading results, particularly when analysed with univariate techniques (Lindenmayer 1999). Some of these factors include:

1. Logged forests contain structural components (i.e. large diameter living and dead trees) remaining from the previous uncut stand. Thus, species responses are more a reflection of forest structure than simply whether a stand was logged or not (Lindenmayer *et al.* 1994, 1991a);
2. There may be cumulative long-term effects of logging and the response of species after the first cut may differ with successive harvests (Lindenmayer *et al.* 1991b), increasing the possibility of local extinctions a long time after disturbance (Tilman *et al.* 1994);
3. Species may differ in response to logging-induced disturbance at different sites, even to the extent of increasing in cover at one site but decreasing in cover at another, as was found in Chapter 4.
4. Within a particular lifeform group, some species may increase in cover whereas others will decrease in cover, negating the chance of detection of any impact for that group.
5. Short term and/or few site studies of logging effects may lack sufficient statistical power to detect impacts that are taking place and will not be able to detect longer-term and landscape scale impacts. Additive or synergistic impacts

that lead to cumulative effects of timber harvesting on forest biota may be difficult to identify even with well-designed, powerful studies.

6. Increased variance in measured variables after disturbance can make any effect difficult to detect.
7. The result may be real with different components of community structure changing at different rates.

Most of these problems may be overcome with the use of well-designed field experiments, such as BACI and beyond BACI designs (Benedetti-Cecchi 2001, Hewitt *et al.* 2001, Underwood, 1993). However, these techniques can be difficult to apply with only the one disturbance event, particularly if the event is not planned.

Two interrelated points arise from the above problems: 1) increased community variability after disturbance may make the detection of any effects difficult; and 2) multivariate analysis techniques may be better able to detect more ecologically significant differences. These two points are discussed below. Factor 7, the problem of different components of the community changing at different rates will be discussed further in light of recent ecological theory in section 8.3.4.3.

8.1.2.1 Community variability as an indicator of disturbance

In the space-for-time and BACI logging impact studies of Chapter 4, an increase in the variability of community pattern, the variance of some environmental variables, and the variance of species cover values were noted after logging induced disturbance. This increase in variability was evident as:

1. the larger error bars of the space-for-time lifeform analysis i.e. greater variance of lifeform percentage covers, particularly grass, monocots, introduced forbs, ferns and orchids in logged quadrats;
2. the wide scatter of the post logging quadrats of the BACI ordination; and
3. increased variability in species covers following logging.

Similar increases in variability following disturbance have been reported for:

- decaying-log resources in Tasmania forests (Meggs 1996);
- spatial patterns of soil moisture in a North American pine plantation (Guo *et al.* 2002); and,
- community patterns and species abundances of benthic marine organisms (Benedetti-Cecchi 2001, Hewitt *et al.* 2001, Glasby 1997, Clarke 1993, Green 1993, Warwick 1993, Underwood 1993, 1991, Warwick & Clarke 1993).

The increased variability in the space-for-time and BACI studies of this thesis is, in part, the result of a number of factors in the post-logging environment:

- post logged quadrats had varying amounts of above ground vegetation removed, ranging from 0 to 100% reduction
- variable spatial species responses, and
- variable temporal species responses.

Similar factors have been reported to explain yearly variation within sites following disturbance in grasslands. These include: 1) the length of time (one to several years) required for species to respond to perturbations (Hirst *et al.* 2003, Belsky 1992,); 2) the interactions of the different species with each other as they respond to different degrees and at different rates (Hirst *et al.* 2003); and 3), the interactions of the species and perturbations with temporally varying environmental factors such as weather and

grazing intensity (Belsky 1992). Factors suggested as leading to increase variability of soil moisture following logging include increased variability of plant root distribution creating corresponding variation in local water uptake rates, and, increased variation in forest floor thickness, enhancing variation in evaporation rates (Guo *et al.* 2002).

It appears that the affects of disturbance will not necessarily be distributed uniformly. Some impacts may have little or no effect on the long-term average numbers in a population, but rather may affect their temporal variation. There may be increased or decreased variability among times of sampling in the disturbed location after the disturbance, and compared with what happens in the controls (Underwood 1993). For example, community variation was found to be greater among fish communities in coral sites subjected to mining than among control sites, in spite of the control sites' greater geographic spread (Clarke 1993).

Statistically, this increased variability would result in: (i) heterogeneity of error variance (higher in the impact area than in the control area); and (ii) a biased error estimate (inflated by impact-caused variation). This variance heterogeneity then, would be both a consequence of disturbance (Underwood 1991), would be evidence of the disturbance impact (Clarke 1993, Green 1993), and would be positively related with the degree of disturbance (Caswell & Cohen 1991).

The high degree of variability intrinsic to most, if not all, ecological systems makes the identification and interpretation of human-induced changes in natural populations complex (Benedetti-Cecchi 2001). The power to detect a particular impact will be decreased where intrinsic variability is large because the size of the effect is small relative to the size of natural, within sample variation (Underwood 1993, Andrew & Mapstone 1987). Conventional univariate ANOVA or *t*-tests may not detect a change

that corresponds to a variance increase. Furthermore, the standard test is invalid if the variance differs substantially between the two groups (Clarke 1993). What this means is that the increased variability among samples with increasing levels of disturbance may preclude the detection of any effect. Impacts occurring on larger spatial and temporal scales exacerbate this problem, and the magnitude of the impact may have to be larger (both in terms of the abundance of individual species and in the number of species) in order for effects to be detected (Hewitt *et al.* 2001).

While a lot of the research on this topic has been exclusively marine, and predominantly involves soft-sediment benthos, the application of these techniques is by no means confined to marine communities. Similar community patterns were detected in the research for this thesis and it is suggested that this increase in community variability itself could be considered as an indication of both, logging, and other human –induced disturbance studies.

8.1.2.2 Multivariate analysis

Considering the above disturbance-induced increase in variability and the subsequent problems of detecting an impact with conventional univariate analyses, it is suggested that multivariate techniques may improve the ability to detect ecologically significant effects. Multivariate techniques have proved particularly useful in human-induced pollution and disturbance studies. They have been shown to:

- be sensitive in their elicitation of community change (Clarke 1993, Warwick 1993, Warwick & Clarke 1993, Warwick & Clarke 1991, Underwood & Peterson 1988),

-
- be robust to a substantial degree of taxonomic aggregation (Clarke 1993, Warwick 1993, Warwick & Clarke 1993, Warwick & Clarke 1991, Underwood & Peterson 1988), and,
 - able to capture better the spatial pattern of understorey vegetation than univariate measures of community, such as richness or cover (Scheller & Mladenoff 2002).

This greater ecological sensitivity of multivariate techniques is because they can integrate both a diversity component and an abundance component. A disturbance impact may result in changes in: 1) the total number of individuals or species present; and/or 2) an increase in the variability among samples due to the presence of different species. Where the latter or both factors dominate, multivariate analysis will show a clear increase in variability with increased levels of perturbation (Warwick & Clarke, 1993).

In a comparative study on diversity and spatial patterning of understorey vegetation between old-growth and managed hardwood forests of North America, differences between the cover of most plant groups were not significant (Scheller & Mladenoff 2002). Spatial patterning of understorey communities, however, was different, with community patch size in old-growth stands exhibiting less variation among stands than for either the managed even-aged or uneven-aged stands. Thus, the fundamental character of the species composition had changed (Scheller & Mladenoff 2002). In this context, spatial patterning of understorey communities was expressed as the mean size of plant communities and the compositional difference between a community and the surrounding matrix of understorey communities, and was quantified with the use of a 'sociogram' (Scheller & Mladenoff 2002, Mistral *et al.* 2000). This sociogram is a

multivariate measure that summarises individual quadrat data to generate information about community patches that are compositionally similar. What they found was that spatial structure was much slower to recover despite the negligible effects on alpha diversity, similar to effects detected in *E. delegatensis* forests for this thesis.

Thus, multivariate analysis techniques may provide a better visualisation of a disturbance impact even when that impact is not detected by common univariate measures. This is particularly important considering that different components of an ecosystem may react to disturbance at different rates or directions (see discussion in 8.3.4.3).

8.1.3 Ecologically sustainable forestry

The major differences in plant species composition, vegetation structure and landscape patchiness between logged forests and wildfire-regenerated forests have been reported in montane ash forests in south-east Australia (Lindenmayer & McCarthy 2002, Lindenmayer *et al.* 2000, Ough 2001). These studies have shown that the disturbance regime of logging is different to the disturbance regime of wildfire in these eucalypt forests, despite previous research that equates the two (Attiwill 1994).

In an effort to conserve biodiversity in multi-use landscapes such as wood production forests, there is now a recognised need for logging induced disturbance to mimic natural forest disturbance regimes as closely as possible. Selective or partial logging has been seen as a way of achieving this as it retains some of the structural components of the previously uncut stand (Lindenmayer & McCarthy 2002, Lindenmayer 1999, Peacock *et al.* 1997). These structural components, or “biological legacies” (Franklin *et al.* 2000),

can be living or dead trees, logging waste, or intact thickets of logging sensitive understorey vegetation. Their retention better mimics the multi-aged forest stands of natural (wildfire) disturbance (Lindenmayer & McCarthy 2002, Ough & Murphy 1998).

Complete congruence between wildfire and logging regimes, however, is not possible, even using partial logging techniques. For example, selective logging does not result in the same structural features as a partial or low intensity burn in Australia (Lindenmayer & McCarthy 2002), and has been found to reduce many of the biological legacies that create patchiness and heterogeneity in old growth forests in North America (Scheller & Mladenoff 2002). Studies from North America comparing clearfelled, selectively logged, and old growth forests have suggested that the impact of selective logging on understorey species was greater than clearfelling (Scheller & Mladenoff 2002, Metzger & Schultz 1984). They found the largest differences in diversity and abundance occurred between old-growth forests and the uneven-aged, managed forests that receive periodic disturbance through selective logging. It was also suggested that vernal species may be more sensitive to selective logging than clearcutting due to more frequent forest floor disturbance and desiccation caused by recurring periods of high radiation (Metzger & Schultz 1981).

Therefore, no matter how closely logging practices mimic 'natural disturbance' regimes, there will never be complete congruence as the disturbance process is fundamentally different (Ough 2001). Logging is a deterministic process unlike the random or stochastic process of wildfire (Lindenmayer & McCarthy 2002, Peacock *et al.* 1997). Inherent stochasticity in natural disturbance events like wildfire means there will be differences in the mean age of forest and spatial characteristics of patches between logged and fire-disturbed landscapes (Seymour & Hunter 1999). Consequently,

in future logging impact studies it will not be adequate to simply determine which types of disturbance has a more or less detrimental effect. The two types of disturbance do not occur in isolation from each other, where logging is carried out the impact is overlaid on a pre-existing wildfire impact. What is required, therefore, is an assessment of their combined effect as both disturbance types, logging (a deterministic one) and wildfire (a stochastic one) are occurring in the landscape at the same time (Lindenmayer & McCarthy 2002, McCarthy & Lindenmayer 1999, Peacock *et al.* 1997).

The research for this thesis followed this premise of a combined assessment of both disturbance types. Thus, the general effects of logging (reduced habitat complexity, shrub and orchid cover, and increased grass, forb and bare ground cover) from Chapters 4 & 5, were primarily caused by an exacerbation of the same environmental factors (litter, light, temperature, and moisture) that were structuring the understorey community in unlogged, wildfire regenerated grassy *E. delegatensis* forest at Table Mountain (Chapters 5 & 6). The only way of accurately determining the future combined effects of both disturbance regimes at this site now is the use of long-term monitoring.

Quantifiable indicators of ecosystem sustainability are one means of monitoring the efficacy of management regimes for maintaining ecosystem patterns within their pre-settlement variability (Peacock 1997, Keddy & Drummond 1996). Many researchers have stressed the importance of on-going monitoring and it is imperative to assess current and future landscape management regimes (Barrett and Davidson 2000), and to better appreciate the significance of past and present disturbance regimes on forest ecosystems (Hewitt *et al.* 2001, Lindenmayer 1999, Margules *et al.* 1998, Rice *et al.* 1998, Peacock *et al.* 1997).

8.2 Role of temperature and photoinhibition in structuring understorey

This study has demonstrated that some of the understorey species in an *E. delegatensis* forest at 730 m asl experienced reductions in maximal photochemical efficiency, as assessed by the F_v/F_m ratio. In the middle of winter, two species, *Lomandra longifolia* and *Lomatia tinctoria*, displayed moderate reductions in maximal photochemical efficiency in undisturbed forest and severe reduction in partially logged forest. Conversely, a third species, the grass *Poa gunnii*, unaffected in the logged forest, and had only a slight reduction in unlogged forest (chapter 5). Similar trends were displayed by *L. longifolia*, *L. tinctoria* and, a related grass, *Poa labillardierei*, in the shading/disturbance experiment carried out at sea level (chapter 6). Reductions in maximal photochemical efficiency of the plants at sea level, however, were not as great as the high altitude forest site. These differences were attributed to species-specific differences in the susceptibility to cold-induced photoinhibition in the higher light/ lower temperature regime of the partially logged forest/shaded experimental tray.

In addition, the distribution of some understorey species in undisturbed forest was positively associated with the more shaded sectors of forest canopy gaps. It was suggested that this distribution was the result of shading from early morning sun, particularly in winter, and a concomitant reduction of the effects of cold-induced photoinhibition (Chapter 5).

For plants that retain and maintain leaves during the winter months, exposure to low temperatures in combination with excessive light can impose a considerable level of stress on the photosynthetic apparatus (Adams *et al.* 1994, Oberhuber & Bauer 1991, Osmond 1981). This can predispose plants to 'photoinhibition', defined as the light dependent loss in photosynthetic functioning of photosystem II (PSII). This is

manifested in whole leaves as a decline in the quantum efficiency of photosynthesis (i.e. mol CO₂ fixed of mol O₂ evolved per mol photons absorbed under limiting light intensities) (Osmond 1994). This reduction can be measured using the technique of chlorophyll fluorescence (see Schreiber & Bilger 1993 for review) through the ratio of variable to maximal fluorescence (F_v/F_m) that has been shown to be 0.78-0.86 at maximal PSII efficiency (Adams *et al.* 1994, Bjorkman & Demmig 1987).

It has been questioned whether photoinhibition itself has any effect on plant production and that it may just represent the photoprotective energy dissipation process when PSII has been down-regulated by other environmental stress factors (Verhoeven *et al.* 1999, 1998, Adams, *et al.* 1994). If this is so, the sustained engagement of a photoprotective process probably occurs in response to restrictions on the utilisation of energy in carbon metabolism. Thus, it is a good indicator that the plant is experiencing stress (Adams *et al.* 1994), typically brought on by low temperature (Warren *et al.* 1998, Hovenden & Warren 1998, Adams & Demmig-Adams 1995).

The changes in the efficiency of PSII as measured by F_v/F_m have been strongly correlated with plant growth where a reduction in F_v/F_m was induced by adverse environmental conditions (Close *et al.* 2002, Holly *et al.* 1994, Long *et al.* 1994, Farage & Long 1991, Koniger & Winter 1991, Baker *et al.* 1989, Aoki 1986). Similarly, the occurrence and severity of cold-induced photoinhibition has been correlated with the regeneration niche that affects the distribution of juvenile trees; this provides a link between early growth and cold-induced photoinhibition in tree seedlings (Ball 1994, Holly *et al.* 1994, Long *et al.* 1994, Ball *et al.* 1991).

It follows that differences between plants in vulnerability to photoinhibition due to inherent differences in the capacity of a plant to use light will manifest itself in growth

(Falls *et al.* 1991), differences in regeneration strategy (Ball *et al.* 1994, Long *et al.* 1994), and play a major role in forest dynamics following disturbance (Ball *et al.* 1994, Whitmore 1992).

The reduction in basal area of the overstorey eucalypts in a partially logged coupe present a very different microclimate to the understorey because plants are suddenly exposed to much longer duration of direct sunlight that is repeated each subsequent day. These conditions exceed the prior environmental history to which the leaves were acclimatised. Moreover, there are other changes in environmental conditions, particularly increased temperature range, leading to lower minimum temperatures (Nunez & Bowman 1986), lower humidity, and water stress resulting from increased evaporative demand, conditions that are conducive to cold-induced photoinhibition. Thus, as suggested before, the short and long-term reductions in shrub cover noted in partially logged coupes and the asymmetry in shrub distribution in unlogged forest, are the result of cold-induced photoinhibition. The author is aware of no references to the phenomenon of cold-induced photoinhibition on the distribution or patterning of understorey species in eucalypt forests of Australia. Reported results typically come from understorey species in northern hemisphere deciduous forests (Verhoeven *et al.* 1998, Adams & Demmig-Adams 1995, Adams *et al.* 1994, Oberhuber & Bauer 1991) or seedlings of overstorey species from Australasia (Close *et al.* 2001, Ball, *et al.* 1994, 1991, Holly *et al.* 1994, Ball 1991). It appears that the understorey species in high altitude *E. delegatensis* forests show a restricted regeneration niche similar to that reported for overstorey tree seedlings (Ball, *et al.* 1994, 1991, Holly *et al.* 1994, Ball 1991). The increased grass cover in partially logged coupes exacerbates this effect by altering the microclimate of plants growing in grass compared to those growing in bare

soil. The lower minimum and higher maximum temperatures over grass lead to thermal inhibition and increased rates of cold-induced photoinhibition of tree seedlings (Ball *et al.* 2002, Ball *et al.* 1997). In partially logged forests, therefore, the understorey is subjected to the combined effects of increased light, reduced minimum temperatures (Nunez & Bowman 1986, Nunez & Sander 1982), and thermal inhibition effect of grass (Ball *et al.* 2002, Ball *et al.* 1997).

The two species *L. longifolia* and *L. tinctoria* displayed reduced maximal photochemical efficiency in the field at Table Mountain in both the logged coupe and the unlogged control, compared to the experimental trays at Cambridge. This suggests that plants at the Table Mountain native forest site experienced a higher level of stress than the plants at Cambridge. This may be due to one or any combination of the following factors:

- the altitude difference (Table Mountain site is at 730m asl, the Cambridge sites at sea level) and concomitant reduction in temperature,
- water stress due to overstorey eucalypts/increased wind speed,
- competitive interactions between the suite of species on the native forest site.

This phenomenon requires further research. Important questions are; are these effects discernible in other forest types? if so, do all species with reduced F_v/F_m ratio show distinct patterns on the ground? and, does cold-induced photoinhibition also lead to reduced overstorey seedling/sapling growth in partially logged forests?

8.3 The role of disturbance in the understorey structure of highland forests

8.3.1 Wildfire

While the large-scale disturbance caused by wildfire is very important in the regeneration of *E. delegatensis*, in the release of the suppressed understorey eucalypts in these forests (Bowman & Kirkpatrick, 1986 a, b), and probably in the structure of the understorey, it may not be that important in the floristic patterning of the understorey. Fire produces a receptive seedbed and increased light levels on the forest floor enhancing eucalypt seed germination, and, typically, does not kill the overstorey eucalypts that rapidly re-establish the forest canopy. Most understorey species also respond rapidly to loss of above ground vegetation, resprouting from protected underground rootstock, as expected given the disturbance-based ecology of eucalypt forests (Lindenmayer & McCarthy 2002, Peacock *et al.* 1997,). Thus, the understorey is not regenerating randomly after fire but originating from the rootstock of plants that were already in favourable locations on the forest floor. These favourable locations will be determined by the optimal light, temperature and litter penetration regimes of each particular species. Even the two forest types examined for this thesis, grassy and shrubby, appear to be the result of site specific factors such as rock cover, topography and watertable height rather than time since fire (Fensham & Kirkpatrick 1992).

Fire, however, does provide regeneration opportunities for seed dispersed forbs and some grasses through the initiation of fine-scale disturbance such as the exposure of mineral seedbed. In the absence of fire, the fine-scale disturbance of treefall will also maintain long-term diversity of the understorey (Okland 2000), increasing the spatial

heterogeneity of the forest floor, creating openings for understorey establishment with increased light levels, increasing the variation in microtopography and soil moisture upon opening of the litter cover and mineral soil exposure (Peterson *et al.* 1990, Schaetzl *et al.* 1989, Beatty 1984, Troedsson & Lyford 1973), and enhancing nutrient availability (Windsor 2000, Hobbs & Hueneke 1996, Pare *et al.* 1993, Mladenoff 1987). The small scale of the canopy gaps developing after treefall also provides the benefits of the increased irradiance without the disadvantages of a concomitant reduction in minimum temperatures (see Chapter 5).

The understorey is, therefore, very resilient to disturbance that results in a rapid recovery of the overstorey canopy (as happens with epicormic bud development of the overstorey eucalypts after wildfire), and the understorey will tend to follow the same understorey trajectory and return to a quasi-stable state until the next fire.

8.3.2 Partial Logging

Logging induced disturbance in the short term appears to create the same large and fine-scale disturbances on the forest floor as fire, providing regeneration niches for light dependent seed dispersers, and allowing the rapid recovery of vegetative species. This is misleading, however, as the use of heavy, ground-based vehicles during the logging operation change the fundamental nature of the disturbance. The use of tracked vehicles, in particular causes stripping of the original vegetation and exposure of mineral soil. These modified site conditions, soil compaction, altered hydrology, and changes in the availability of propagules lead to a different direction of succession (see Hirst *et al.* 2003 for review).

In the longer-term, wildfire and disturbance by logging, differ in the persistence of the much reduced canopy of the overstorey eucalypts in a partially logged coupe. This reduction in basal area of the overstorey eucalypts after partial logging, and the apparent lack of recovery for at least 20 years, presents the understorey with a very different microclimate. The initial rapid recovery of the understorey, therefore, is slowed, or even reversed, by the altered light and temperature regimes of the forest floor. The understorey is subjected to increased irradiance, increased temperature range leading to lower minimum temperatures, lower humidity, and greater water stress resulting from increased evaporative demand. In addition, the thermal inhibition effect of the increased grass cover predisposes susceptible species to cold-induced photoinhibition (Ball *et al.* 2002, Ball *et al.* 1997).

Reduced F_v/F_m values in winter for some shrub and sedge understorey species in unlogged native forest show that plant function is constrained by environmental stress. There is also direct evidence that plants favour lower light levels during stressful periods and higher light levels during favourable conditions (Egerton *et al.* 2000, Ball 1994, Ball *et al.* 1991). The more open canopy of the logged forest, therefore, exposes the understorey to increased irradiance at a time when plants would actually benefit from a reduction in irradiance, increasing plant stress in an already stressful environment.

In the introduction it was mentioned that *E. delegatensis* forests are of particular interest as they occur within the climatic range of subalpine grasslands. The boundary between forest and grassland is dynamic (Fensham & Kirkpatrick 1992), and quite unstable following opening of the overstorey canopy, particularly in grassy forests (Keenan & Candy 1983, Webb *et al.* 1983). The typical structure of these forests after logging is that retained trees tend to be in variable sized clumps scattered throughout the

coupe. It has been observed that the trees in some clumps respond with an increased growth increment to the opening of the canopy (Battaglia & Wilson 1990), whereas trees in other clumps exhibit the condition of 'growth check' (Battaglia *pers com* 2003). It appears, therefore, that there may be a minimum size for the viability of these clumps and below this size there may be shifts in a range of environmental factors that are sufficient to alter conditions at the regeneration site so that secondary succession occurs along a different path. The result will be a decrease in the stability of these disequilibrium communities, possibly causing a flip from a forest to a grassland system. Trees will then be inhibited from invading the site by occupation of other species, particularly *Poa* spp., and conditions become increasingly unfavourable for eucalypts (Forestry Tasmania 2001, Ellis & Pennington 1992, Fensham & Kirkpatrick 1992, Keenan & Candy 1983, Webb *et al.* 1983).

It appears, then, that there is a spatial, a temporal, and a stochastic factor involved in the unpredictable onset of 'growth check' and the expansion of grass in these forests following logging. Some logged coupes will revert to forest whereas others will become grassland, causing shifts in the forest/grassland boundaries. While the vagaries of climate and disturbance over time cannot be controlled, logging codes of practice that retain a greater percentage of the original forest basal area (retained forest basal area of all partially logged coupes at Table Mountain was lower than the prescribed $12 \text{ m}^2 \text{ ha}^{-1}$) and/or the maintenance of a predetermined minimal clump size in logged forest, particularly in forest with a grassy understorey, may cause a significant shift in the probability that succession will result in a forest system rather than grassland one. The determination of an ideal retained basal area and/or minimal clump size requires further research.

8.3.3 Effect of disturbance on community structure and ecosystem stability

Recent debate of community dynamics has centred on whether there is convergence or divergence of community structure following disturbance and evidence of both has been reported (Samuels & Drake 1997, Wilson & Whittaker 1995, Wilson *et al.* 1995, Wilson *et al.* 1994, Nilsson & Wilson 1991, McCune & Allen 1985). The differing views of community dynamics have led to four different concepts of community stability (Samuels & Drake 1997):

- a) Single stable point: given sufficient time, communities under the same conditions will converge to a common, persistent, environmentally determined state leading to a high degree of convergence.
- b) Multiple stable states: convergence to one of a number of alternative stable states leading to low degree of convergence.
- c) Attractor or cycle: Communities move through a repeating (or at least finite) series of stages. At any one point in time, the communities may appear very similar or very different leading to varying/low degree of convergence;
- d) Random or chaotic trajectories: Communities move through a series of apparently unrelated states, and each community is driven by its own history, leading to varying/low degree of convergence.

The information needed to assess convergence depends on the nature of the community dynamics. A truly stable, equilibrium community can be defined by its state at a single point in time, whereas a nonequilibrium system requires a time series (Samuel & Drake, 1997).

In the context of the results of this thesis, if the prelogging community is considered to be the environmentally-derived endpoint, convergence to it after logging would seem the most desirable outcome suggesting a return to original floristics and structure, and reflecting the point a) above. There is more evidence, however, that historical differences and intrinsic indeterminism will lead to long-term community divergence. The presence of multiple stable states and transitions among them have been described in a range of ecological systems (see Gunderson 2000 and Samuels & Drake 1997 for reviews) reflecting that a combination of b) multiple stable states, and d) chaotic trajectories, is in operation.

Determination of impact and successional endpoints will be complicated when different components of an ecological system display different trends. Recall from section 8.1.2 that the lifeform group analysis suggested convergence with prelogged values, whereas the species cover/abundance data did not. The two measures are different components within a hierarchy of community structure. This hierarchy can be defined into three broad groups: 1) community properties, such as species richness or diversity; 2) guild or other species groupings; and 3) species properties, such as presence/absence, abundance and cover (Samuels & Drake, 1997). As seen in this thesis measurements in one scale of the hierarchy (lifeform groups) do not correspond to results in another (species cover/abundance). This difference in the rate of change between different components of a community has been reported by others with convergence predominantly found at coarse structural levels (e.g. guilds), and divergence at the finer levels of scale such as species composition (Inouye & Tilman 1995, Wilson & Roxburgh 1994, Lawton *et al.* 1993). This suggests that the dichotomy in results is real and not an artefact of the analyses.

The different results within different scales of the community make it hard to predict the endpoint from logging induced disturbance, i.e. is the community converging to prelogged values or diverging to a slightly altered, or a massively altered endpoint. Given the evidence for the very formidable effects of chance and site history on community structure (Hirst *et al.* 2003, Ricklefs & Schulter 1993, Drake 1990, Chesson & Warner 1981, Sale 1977) it would seem likely that once a forest has been partially-logged it will follow an alternative community trajectory to that followed after wildfire disturbance reflecting the existence of multiple semi-stable states in these forest systems.

Further support for an altered trajectory of community structure for these highland forest ecosystems following logging, and the presence of multiple stable states and transitions among them, come from the theory of ecological resilience and resistance in response to disturbance (for a full review see Gunderson 2000). Ecological resilience (also called ecological stability) refers to the time period required for a vegetation to return to its pre-disturbance state, and ecological resistance is the ability of a system to resist change when subjected to disturbance (Hirst *et al.* 2003, Gunderson 2000, Loreau & Behera 1999).

This is best visualised with the 'ball and cup heuristic of system stability' (Gunderson 2000, Carpenter & Cottingham 1997) in Fig. 8.1. In ecological terms, ecological systems (the balls) can exist in different equilibrium states (the cups). Resistance is defined by the slope of the cup, and resilience represented by the breadth of the cup. Disturbance shakes the ball in its cup but the system will return to its original equilibrium state. If the disturbance event is great enough, however, the system will be pushed into a new mode of functioning with a new equilibrium state (Hirst *et al.* 2003) or one of a multiple of stable states (Samuels & Drake 1997).

Eucalypt forest ecosystems such as studied in this thesis show both high ecological resilience and high ecological resistance to disturbance. The increased variability of community measures following logging may be a reflection of high ecological resistance, making the biological impact lower with the provision of refuge islands, soil moisture variation etc. creating the small scale heterogeneity that is important for the maintenance of biodiversity in these forests. In terms of the ecological stability of highland forests, therefore, these essentially disequilibrium communities, would appear extremely stable in relation to the majority of wildfire disturbance events.

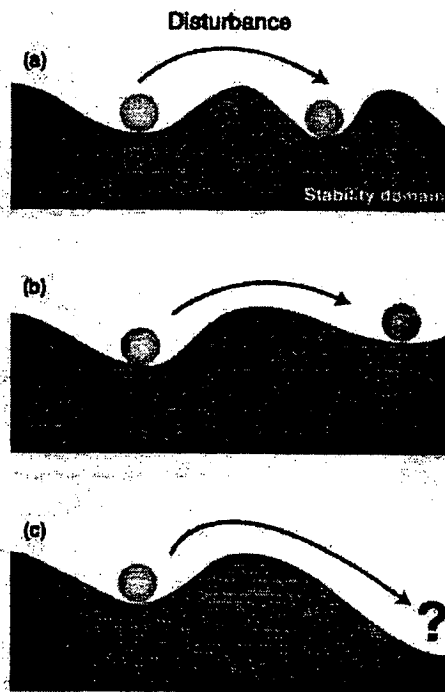


Figure 8.1 The ball and cup heuristic of system stability redrawn from Hirst *et al.* (2003) and Gunderson (2000). Steeper cup sides represent greater resistance against disturbance or stress, and a shorter distance between cup floor and lip indicates greater resilience. (a) Shows disturbance resulting in a stability domain with greater resistance and resilience than original stability domain. (b) new stability domain with less resistance and resilience. (c) Resilience and resistance of post-disturbance stability domain difficult to predict.

Resistance to disturbance, however, is not an additive function and the successive trajectory following more acute or repeated disturbance events will be less predictable.

The determination of what is a more acute disturbance will also vary with site and ecosystem type. A single disturbance intensity that may only 'rattle the ball in its cup' at one site, may shift it to a less stable domain at another site (Fig. 8.1b), or even flip the ball to an unpredictable state at a third site (Fig. 8.1c). A repeat disturbance on the first site may also result in an unpredictable endpoint (Fig. 8.1c).

E. delegatensis forest/subalpine grassland boundaries are a dynamic system subject to an array of forces. Site history is important in determining the future direction of community structure, logging-induced disturbance is highly variable, there is a high probability of repeat disturbance events, the unpredictable onset of 'growth check' on canopy opening, and the imposition of an additional disturbance regime on top of the existing wildfire disturbance regime. It is unsurprising that partially-logged forests differ from wildfire-regenerated forests. In the best case scenario, an altered stable forest state will be reached, in the worst case, the stability of the forest ecosystem may be reduced enough to flip to a grassland ecosystem with all the concomitant problems of tree reestablishment and the loss of both productivity and diversity. There is evidence that this has occurred as a result of past logging practices (Forestry Tasmania 2001, Keenan & Candy 1983, Webb *et al.* 1983) but also in response to extreme natural occurrences such as frosts (Davidson & Reid 1987, Calder 1850).

8.4 General conclusions

Examinations of the impacts of partial logging in *E. delegatensis* forests have revealed significant and long-term effects on the species composition and vegetation structure of the understorey. While understorey species in these forests are extraordinarily resilient to disturbance, the altered regime of partial logging has now been imposed on to the

original disturbance regime of wildfire causing possible cumulative changes in the regeneration of these forests. Examination of the causal environmental factors of the primary logging impacts has enabled the development of an understanding of the key ecological processes that control the spatial patterning of the understorey in these forests including light, temperature, air and soil moisture, litter and initial floristics. In particular, the importance of cold-induced photoinhibition has been highlighted in creating patterns in the understorey vegetation of both logged and unlogged native forest.

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Appendix 1. Pattern analysis raw data.

Frequency of occurrence (number of quadrats a species was recorded in) and mean percentage cover for all vascular plants recorded in control and logged quadrats for the five site/forest types, and for control and plantation quadrats at Tarraleah.

| Species | Frequency of occurrence (% of quadrats) | | Mean percentage cover | |
|-------------------------------------|--|--------|-----------------------|--------|
| | Control | Logged | Control | Logged |
| Table Mountain grassy forest | | | | |
| <i>Acacia dealbata</i> | 92 | 92 | 12.0 | 6.7 |
| <i>Acacia melanoxylon</i> | 17 | 17 | 26.3 | 7.8 |
| <i>Acaena novae-zelandiae</i> | 67 | 100 | 3.9 | 8.8 |
| <i>Acaena echinata</i> | 50 | 33 | 1.0 | 1.0 |
| <i>Acianthus</i> spp | 17 | 0 | 1.0 | 0.0 |
| <i>Ajuga australis</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Arthropodium milleflorum</i> | 17 | 58 | 1.0 | 1.0 |
| <i>Asplenium flabellifolium</i> | 8 | 8 | 1.0 | 1.0 |
| <i>Austrofestuca hookeriana</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Blechnum penna-marina</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Brachyscome decipiens</i> | 25 | 8 | 1.0 | 1.0 |
| <i>Brachyscome spathulata</i> | 17 | 33 | 1.0 | 1.0 |
| <i>Caladenia alpina</i> | 33 | 0 | 1.8 | 0.0 |
| <i>Cardamine</i> spp | 8 | 8 | 1.0 | 1.0 |
| <i>Carex</i> spp | 0 | 8 | 0.0 | 1.0 |
| <i>Carex breviculmis</i> | 17 | 0 | 1.0 | 0.0 |
| <i>Carex raleighii</i> | 17 | 0 | 1.0 | 0.0 |
| <i>Cassinia aculeata</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Chiloglottis gunnii</i> | 25 | 8 | 2.0 | 1.0 |
| <i>Cirsium vulgare</i> * | 0 | 83 | 0.0 | 1.3 |
| <i>Comesperma volubile</i> | 0 | 17 | 0.0 | 1.0 |
| <i>Cotula</i> spp | 0 | 8 | 0.0 | 1.0 |
| <i>Craspedia glauca</i> | 17 | 8 | 1.0 | 1.0 |
| <i>Cyathodes parvifolia</i> | 58 | 83 | 5.1 | 7.6 |
| <i>Dianella tasmanica</i> | 42 | 17 | 4.4 | 1.0 |
| <i>Dichelachne micrantha</i> | 50 | 0 | 2.5 | 0.0 |
| <i>Dichelachne rara</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Dichondra repens</i> | 8 | 0 | 4.0 | 0.0 |
| <i>Diplarrena moraea</i> | 8 | 33 | 1.0 | 1.0 |
| <i>Drosera peltata</i> | 17 | 8 | 1.0 | 1.0 |
| <i>Drymophila cyanocarpa</i> | 67 | 58 | 1.0 | 1.0 |
| <i>Epilobium sarmentaceum</i> | 8 | 75 | 1.0 | 1.7 |
| <i>Gahnia grandis</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Galium australe</i> | 92 | 25 | 1.3 | 1.0 |
| <i>Geranium sessiliflorum</i> | 83 | 92 | 1.6 | 1.3 |
| <i>Euchiton collinum</i> | 33 | 50 | 0.9 | 2.0 |
| <i>Gonocarpus serpyllifolius</i> | 100 | 100 | 4.3 | 2.3 |
| <i>Gonocarpus tetragynus</i> | 8 | 8 | 1.0 | 1.0 |
| <i>Helichrysum scorpioides</i> | 50 | 50 | 0.8 | 1.0 |
| <i>Hydrocotyle hirta</i> | 100 | 92 | 7.6 | 9.7 |
| <i>Hypericum gramineum</i> | 0 | 25 | 0.0 | 1.0 |

| Species | Frequency of occurrence (%) of quadrats) | | Mean percentage cover | |
|-------------------------------------|---|--------|-----------------------|--------|
| | Control | Logged | Control | Logged |
| Table Mountain grassy forest | | | | |
| <i>Hypericum japonicum</i> | 100 | 67 | 1.3 | 1.0 |
| <i>Hypochaeris glabra</i> * | 8 | 0 | 1.0 | 0.0 |
| <i>Hypochaeris radicata</i> * | 25 | 75 | 0.8 | 1.3 |
| <i>Juncus</i> spp | 0 | 8 | 0.0 | 1.0 |
| <i>Juncus astreptus</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Juncus gregiflorus</i> | 17 | 0 | 2.5 | 0.0 |
| <i>Lagenophora stipitata</i> | 92 | 75 | 1.0 | 1.7 |
| <i>Leontodon taraxacoides</i> * | 0 | 25 | 0.0 | 5.7 |
| <i>Leptospermum lanigerum</i> | 0 | 25 | 0.0 | 6.7 |
| <i>Leucopogon hookeri</i> | 100 | 92 | 21.6 | 4.9 |
| <i>Lomandra longifolia</i> | 83 | 58 | 11.8 | 50.1 |
| <i>Lomatia tinctoria</i> | 83 | 100 | 12.9 | 12.9 |
| <i>Luzula</i> spp | 42 | 75 | 0.9 | 1.0 |
| <i>Microseris scapigera</i> | 33 | 0 | 0.9 | 0.0 |
| <i>Myosotis australis</i> | 0 | 17 | 0.0 | 1.0 |
| <i>Neopaxia australis</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Olearia phlogopappa</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Olearia viscosa</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Oreomyrrhis eriopoda</i> | 0 | 25 | 0.0 | 1.0 |
| <i>Oxalis perennans</i> | 25 | 42 | 1.0 | 1.0 |
| <i>Pimelea drupaceae</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Pimelea humilis</i> | 8 | 8 | 1.0 | 1.0 |
| <i>Plantago antarctica</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Plantago glabrata</i> | 33 | 0 | 1.0 | 0.0 |
| <i>Plantago hispida</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Plantago paradoxa</i> | 0 | 8 | 0.0 | 4.0 |
| <i>Plantago tasmanica</i> | 0 | 8 | 0.0 | 1.0 |
| Poaceae spp | 58 | 92 | 1.0 | 6.4 |
| <i>Poa gunnii</i> | 100 | 100 | 24.4 | 25.3 |
| <i>Poa rodwayi</i> | 67 | 50 | 9.1 | 7.2 |
| <i>Poranthera microphylla</i> | 50 | 75 | 1.0 | 1.0 |
| <i>Pratia pedunculata</i> | 75 | 92 | 1.0 | 3.8 |
| <i>Pteridium esculentum</i> | 100 | 92 | 12.3 | 5.5 |
| <i>Pterostylis</i> spp | 67 | 0 | 1.0 | 0.0 |
| <i>Pultenaea juniperina</i> | 33 | 83 | 0.9 | 9.5 |
| <i>Ranunculus muricatus</i> * | 0 | 8 | 0.0 | 1.0 |
| <i>Ranunculus scapiger</i> | 92 | 92 | 0.9 | 1.3 |
| <i>Scleranthus biflorus</i> | 25 | 8 | 6.7 | 1.0 |
| <i>Senecio gunnii</i> | 25 | 50 | 1.0 | 1.0 |
| <i>Stylidium graminifolium</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Taraxacum officinale</i> * | 0 | 25 | 0.0 | 1.0 |
| <i>Veronica calycina</i> | 75 | 50 | 1.0 | 1.0 |
| <i>Veronica gracilis</i> | 42 | 17 | 1.0 | 1.0 |
| <i>Viola betonicifolia</i> | 58 | 17 | 1.0 | 1.0 |
| <i>Viola hederacea</i> | 100 | 67 | 3.0 | 1.8 |
| <i>Vulpia megalura</i> * | 25 | 0 | 2.0 | 0.0 |
| <i>Wahlenbergia</i> spp | 75 | 83 | 1.0 | 1.0 |

| Species | Frequency of occurrence (%) of quadrats) | | Mean percentage cover | |
|--------------------------------------|---|--------|-----------------------|--------|
| | Control | Logged | Control | Logged |
| Table Mountain shrubby forest | | | | |
| <i>Acacia dealbata</i> | 92 | 50 | 12.1 | 7.2 |
| <i>Acaena novae-zelandiae</i> | 100 | 100 | 10.0 | 10.9 |
| <i>Acianthus</i> spp | 0 | 8 | 0.0 | 1.0 |
| <i>Anodopetalum biglandulosum</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Aristotelia peduncularis</i> | 0 | 8 | 0.0 | 0.5 |
| <i>Arthropodium milleflorum</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Asperula gunnii</i> | 17 | 0 | 1.0 | 0.0 |
| <i>Asplenium flabellifolium</i> | 8 | 33 | 1.0 | 1.0 |
| <i>Australina pusilla</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Australopyrum pectinatum</i> | 25 | 0 | 4.0 | 0.0 |
| <i>Bedfordia salicina</i> | 33 | 0 | 12.3 | 0.0 |
| <i>Brachyscome spathulata</i> | 25 | 17 | 1.0 | 1.0 |
| <i>Caladenia alpina</i> | 25 | 17 | 1.0 | 1.0 |
| <i>Cardamine</i> spp | 17 | 8 | 1.0 | 1.0 |
| <i>Chiloglottis gunnii</i> | 17 | 25 | 1.0 | 2.0 |
| <i>Cirsium vulgare</i> * | 0 | 33 | 0.0 | 0.9 |
| <i>Coprosma hirtella</i> | 8 | 8 | 0.5 | 1.0 |
| <i>Coprosma quadrifida</i> | 8 | 42 | 1.0 | 2.8 |
| <i>Craspedia glauca</i> | 0 | 17 | 0.0 | 2.5 |
| <i>Cyathodes glauca</i> | 67 | 42 | 3.9 | 3.4 |
| <i>Cyathodes parvifolia</i> | 100 | 100 | 42.0 | 27.2 |
| <i>Deyeuxia monticola</i> | 17 | 0 | 1.0 | 0.0 |
| <i>Dianella tasmanica</i> | 17 | 17 | 8.0 | 8.0 |
| <i>Dichelachne micrantha</i> | 17 | 0 | 1.0 | 0.0 |
| <i>Diplarrena moraea</i> | 8 | 25 | 0.5 | 0.8 |
| <i>Dryophila cyanocarpa</i> | 25 | 42 | 1.0 | 1.0 |
| <i>Epilobium sarmentaceum</i> | 50 | 83 | 1.0 | 2.4 |
| <i>Galium australe</i> | 75 | 33 | 1.0 | 1.0 |
| <i>Geranium potentilloides</i> | 25 | 33 | 1.0 | 1.0 |
| <i>Geranium sessiliflorum</i> | 92 | 92 | 1.3 | 1.8 |
| <i>Euchiton collinum</i> | 50 | 8 | 1.0 | 1.0 |
| <i>Gonocarpus serpyllifolius</i> | 67 | 33 | 2.1 | 1.0 |
| <i>Gonocarpus tetragynus</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Helichrysum scorpioides</i> | 33 | 33 | 1.0 | 1.0 |
| <i>Helichrysum thyrsoideum</i> | 0 | 42 | 0.0 | 5.6 |
| <i>Hydrocotyle hirta</i> | 92 | 83 | 4.9 | 1.6 |
| <i>Hypericum gramineum</i> | 25 | 8 | 1.0 | 1.0 |
| <i>Hypericum japonicum</i> | 67 | 50 | 1.0 | 1.0 |
| <i>Hypochaeris glabra</i> * | 8 | 0 | 1.0 | 0.0 |
| <i>Hypochaeris radicata</i> * | 17 | 0 | 0.8 | 0.0 |
| <i>Lagenophora stipitata</i> | 92 | 67 | 1.5 | 1.4 |
| <i>Leontodon taraxacoides</i> * | 0 | 25 | 0.0 | 1.0 |
| <i>Leptospermum lanigerum</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Leucopogon hookeri</i> | 58 | 17 | 1.4 | 2.5 |
| <i>Lomandra longifolia</i> | 17 | 8 | 1.0 | 4.0 |
| <i>Lomatia tinctoria</i> | 83 | 92 | 11.8 | 6.2 |
| <i>Luzula</i> spp | 33 | 58 | 1.0 | 1.0 |

| Species | Frequency of occurrence (% of quadrats) | | Mean percentage cover | |
|--------------------------------------|--|--------|-----------------------|--------|
| | Control | Logged | Control | Logged |
| Table Mountain shrubby forest | | | | |
| <i>Microseris scapigera</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Myosotis australis</i> | 8 | 8 | 1.0 | 1.0 |
| <i>Olearia argophylla</i> | 0 | 8 | 0.0 | 15.0 |
| <i>Olearia phlogopappa</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Olearia viscosa</i> | 33 | 8 | 29.0 | 4.0 |
| <i>Oreomyrrhis eriopoda</i> | 17 | 0 | 1.0 | 0.0 |
| <i>Oxalis perennans</i> | 25 | 17 | 1.0 | 1.0 |
| <i>Pimelea drupaceae</i> | 8 | 0 | 1.0 | 0.0 |
| Poaceae spp | 67 | 67 | 6.3 | 3.1 |
| <i>Poa gunnii</i> | 67 | 92 | 9.1 | 5.1 |
| <i>Poa rodwayi</i> | 58 | 33 | 5.9 | 1.8 |
| <i>Polystichum proliferum</i> | 42 | 33 | 23.4 | 6.8 |
| <i>Poranthera microphylla</i> | 50 | 33 | 1.5 | 1.0 |
| <i>Pratia pedunculata</i> | 50 | 58 | 1.0 | 1.0 |
| <i>Pteridium esculentum</i> | 58 | 83 | 13.5 | 14.6 |
| <i>Pterostylis</i> spp | 0 | 8 | 0.0 | 1.0 |
| <i>Pultenaea juniperina</i> | 75 | 92 | 25.1 | 14.1 |
| <i>Ranunculus scapiger</i> | 50 | 67 | 1.0 | 1.0 |
| <i>Richea procera</i> | 17 | 0 | 4.0 | 0.0 |
| <i>Scleranthus biflorus</i> | 17 | 8 | 2.5 | 1.0 |
| <i>Senecio gunnii</i> | 75 | 33 | 1.0 | 1.0 |
| <i>Senecio linearifolius</i> | 0 | 42 | 0.0 | 7.8 |
| <i>Stellaria multiflora</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Stylidium graminifolium</i> | 33 | 8 | 5.3 | 1.0 |
| <i>Taraxacum officinale</i> * | 0 | 8 | 0.0 | 1.0 |
| <i>Tasmannia lanceolata</i> | 17 | 17 | 1.0 | 4.0 |
| <i>Uncinia compacta</i> | 25 | 0 | 1.0 | 0.0 |
| <i>Urtica incisa</i> | 17 | 17 | 4.0 | 1.0 |
| <i>Veronica calycina</i> | 67 | 83 | 1.0 | 1.0 |
| <i>Veronica gracilis</i> | 8 | 0 | 1.0 | 0.0 |
| <i>Viola betonicifolia</i> | 33 | 33 | 1.0 | 1.0 |
| <i>Viola hederacea</i> | 67 | 25 | 1.0 | 1.0 |
| <i>Wahlenbergia</i> spp | 50 | 25 | 1.0 | 1.0 |
| Glenmark shrubby forest | | | | |
| <i>Acacia dealbata</i> | 33 | 73 | 19.3 | 8.8 |
| <i>Acacia verniciflua</i> | 67 | 9 | 26.3 | 4.0 |
| <i>Acaena novae-zelandiae</i> | 50 | 100 | 2.0 | 21.7 |
| <i>Acianthus</i> spp | 17 | 0 | 1.0 | 0.0 |
| <i>Asperula conferta</i> | 83 | 18 | 1.6 | 2.5 |
| <i>Asperula gunnii</i> | 0 | 64 | 0.0 | 3.4 |
| <i>Asplenium flabellifolium</i> | 17 | 0 | 1.0 | 0.0 |
| <i>Australopyrum pectinatum</i> | 0 | 45 | 0.0 | 3.8 |
| <i>Bedfordia salicina</i> | 0 | 18 | 0.0 | 4.0 |
| <i>Blechnum watsii</i> | 0 | 9 | 0.0 | 4.0 |
| <i>Carex</i> spp | 0 | 9 | 0.0 | 1.0 |
| <i>Cirsium vulgare</i> * | 0 | 36 | 0.0 | 2.5 |
| <i>Comesperma volubile</i> | 17 | 0 | 1.0 | 0.0 |

| Species | Frequency of occurrence (% of quadrats) | | Mean percentage cover | |
|----------------------------------|--|--------|-----------------------|--------|
| | Control | Logged | Control | Logged |
| Glenmark shrubby forest | | | | |
| <i>Coprosma hirtella</i> | 0 | 9 | 0.0 | 4.0 |
| <i>Cyathodes parvifolia</i> | 100 | 100 | 18.3 | 20.4 |
| <i>Austrodanthonia pilosa</i> | 0 | 9 | 0.0 | 1.0 |
| <i>Deyeuxia monticola</i> | 33 | 55 | 2.5 | 6.7 |
| <i>Dianella tasmanica</i> | 17 | 0 | 1.0 | 0.0 |
| <i>Dichelachne micrantha</i> | 0 | 9 | 0.0 | 4.0 |
| <i>Dicksonia antarctica</i> | 17 | 18 | 1.0 | 8.0 |
| <i>Dryophila cyanocarpa</i> | 83 | 64 | 1.0 | 1.0 |
| <i>Echinopogon ovatus</i> | 0 | 18 | 0.0 | 1.0 |
| <i>Ehrharta stipoides</i> | 0 | 9 | 0.0 | 1.0 |
| <i>Epilobium sarmentaceum</i> | 0 | 36 | 0.0 | 1.8 |
| <i>Galium australe</i> | 83 | 73 | 1.0 | 2.5 |
| <i>Geranium potentilloides</i> | 33 | 73 | 1.0 | 1.4 |
| <i>Geranium sessiliflorum</i> | 50 | 45 | 1.0 | 5.0 |
| <i>Euchiton collinum</i> | 0 | 36 | 0.0 | 1.0 |
| <i>Gonocarpus serpyllifolius</i> | 0 | 45 | 0.0 | 3.8 |
| <i>Gonocarpus teucrioides</i> | 0 | 27 | 0.0 | 2.0 |
| <i>Helichrysum scorpioides</i> | 50 | 36 | 2.0 | 1.0 |
| <i>Hydrocotyle hirta</i> | 100 | 73 | 7.2 | 11.5 |
| <i>Hypericum japonicum</i> | 0 | 55 | 0.0 | 1.0 |
| <i>Lagenophora stipitata</i> | 100 | 82 | 1.0 | 1.7 |
| <i>Leucopogon hookeri</i> | 0 | 55 | 0.0 | 4.3 |
| <i>Lomatia tinctoria</i> | 67 | 45 | 12.3 | 24.5 |
| <i>Luzula</i> spp | 0 | 27 | 0.0 | 1.0 |
| <i>Lycopodium australianum</i> | 0 | 18 | 0.0 | 1.0 |
| <i>Notolea ligustrina</i> | 67 | 9 | 6.0 | 1.0 |
| <i>Olearia phlogopappa</i> | 33 | 0 | 2.5 | 0.0 |
| <i>Olearia viscosa</i> | 100 | 18 | 19.3 | 9.5 |
| <i>Oxalis perennans</i> | 33 | 27 | 1.0 | 2.0 |
| <i>Pimelea drupaceae</i> | 100 | 55 | 3.8 | 0.9 |
| <i>Poaceae</i> spp | 33 | 45 | 2.5 | 19.5 |
| <i>Poa gunnii</i> | 17 | 91 | 1.0 | 18.1 |
| <i>Poa rodwayi</i> | 0 | 36 | 0.0 | 5.3 |
| <i>Poa tenera</i> * | 33 | 36 | 2.5 | 17.9 |
| <i>Poa pratensis</i> * | 0 | 27 | 0.0 | 6.7 |
| <i>Polystichum proliferum</i> | 67 | 82 | 8.0 | 7.3 |
| <i>Poranthera microphylla</i> | 17 | 36 | 1.0 | 1.8 |
| <i>Pteridium esculentum</i> | 83 | 64 | 35.8 | 34.6 |
| <i>Pterostylis</i> spp | 50 | 9 | 0.8 | 0.5 |
| <i>Pultenaea juniperina</i> | 67 | 91 | 31.9 | 26.3 |
| <i>Ranunculus scapiger</i> | 33 | 18 | 1.0 | 0.8 |
| <i>Scleranthus biflorus</i> | 0 | 36 | 0.0 | 1.0 |
| <i>Senecio minimus</i> | 0 | 36 | 0.0 | 3.3 |
| <i>Tasmannia lanceolata</i> | 0 | 18 | 0.0 | 0.8 |
| <i>Uncinia elegans</i> | 0 | 36 | 0.0 | 1.0 |
| <i>Veronica notabilis</i> | 0 | 27 | 0.0 | 1.0 |
| <i>Veronica calycina</i> | 17 | 9 | 1.0 | 1.0 |
| <i>Viola hederacea</i> | 33 | 73 | 1.0 | 2.1 |

| Species | Frequency of occurrence (% of quadrats) | | Mean percentage cover | |
|---------------------------------------|--|--------|-----------------------|--------|
| | Control | Logged | Control | Logged |
| Glenmark shrubby forest | | | | |
| <i>Vulpia megalura</i> * | 0 | 9 | 0.0 | 1.0 |
| Clarence Lagoon shrubby forest | | | | |
| <i>Acacia dealbata</i> | 0 | 8 | 0.0 | 0.5 |
| <i>Acaena novae-zelandiae</i> | 0 | 50 | 0.0 | 1.5 |
| <i>Aristotelia peduncularis</i> | 20 | 25 | 1.0 | 1.0 |
| <i>Arthropodium milleflorum</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Asperula conferta</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Asperula gunnii</i> | 0 | 25 | 0.0 | 1.0 |
| <i>Asplenium flabellifolium</i> | 80 | 0 | 1.8 | 0.0 |
| <i>Bedfordia linearis</i> | 100 | 92 | 24.0 | 12.5 |
| <i>Billardierei longiflora</i> | 40 | 25 | 1.0 | 1.0 |
| <i>Blechnum</i> spp | 0 | 17 | 0.0 | 1.0 |
| <i>Cardamine</i> spp | 40 | 0 | 0.5 | 0.0 |
| <i>Coprosma hirtella</i> | 60 | 42 | 2.0 | 1.6 |
| <i>Coprosma quadrifida</i> | 60 | 17 | 2.0 | 1.0 |
| <i>Crassula sieberana</i> | 20 | 0 | 1.0 | 0.0 |
| <i>Cyathodes parvifolia</i> | 80 | 100 | 3.3 | 5.6 |
| <i>Deyeuxia monticola</i> | 40 | 0 | 2.5 | 0.0 |
| <i>Dianella tasmanica</i> | 40 | 42 | 2.5 | 3.4 |
| <i>Diplarrena latifolia</i> | 100 | 100 | 6.2 | 11.1 |
| <i>Dryophila cyanocarpa</i> | 60 | 100 | 1.0 | 2.0 |
| <i>Euchiton imbricola</i> | 20 | 0 | 1.0 | 0.0 |
| <i>Galium australe</i> | 80 | 33 | 1.0 | 1.0 |
| <i>Geranium sessiliflorum</i> | 60 | 58 | 1.0 | 1.0 |
| <i>Euchiton collinum</i> | 0 | 25 | 0.0 | 1.0 |
| <i>Goodenia lanata</i> | 20 | 58 | 1.0 | 1.0 |
| <i>Gonocarpus serpyllifolius</i> | 20 | 25 | 1.0 | 1.0 |
| <i>Gonocarpus teucrioides</i> | 40 | 0 | 1.0 | 0.0 |
| <i>Hakea lissosperma</i> | 60 | 50 | 2.0 | 4.8 |
| <i>Helichrysum scorpioides</i> | 80 | 92 | 1.0 | 1.5 |
| <i>Helichrysum thyrsoideum</i> | 0 | 8 | 0.0 | 15.0 |
| <i>Hydrocotyle hirta</i> | 20 | 42 | 1.0 | 1.0 |
| <i>Hypericum japonicum</i> | 0 | 17 | 0.0 | 1.0 |
| <i>Hypochaeris radicata</i> * | 0 | 25 | 0.0 | 1.0 |
| <i>Lagenophora stipitata</i> | 0 | 50 | 0.0 | 1.0 |
| <i>Leucopogon hookeri</i> | 0 | 17 | 0.0 | 2.5 |
| <i>Lomatia tinctoria</i> | 100 | 100 | 12.8 | 16.9 |
| <i>Luzula</i> spp | 40 | 17 | 1.0 | 0.8 |
| <i>Notolea ligustrina</i> | 100 | 58 | 4.0 | 1.9 |
| <i>Olearia erubescens</i> | 100 | 92 | 1.0 | 1.0 |
| <i>Olearia phlogopappa</i> | 20 | 50 | 1.0 | 2.0 |
| <i>Olearia viscosa</i> | 60 | 67 | 1.0 | 2.1 |
| Orchidaceae | 80 | 75 | 2.5 | 1.0 |
| <i>Oreomyrrhis eriopoda</i> | 0 | 17 | 0.0 | 1.0 |
| <i>Pimelea nivea</i> | 60 | 58 | 1.0 | 1.0 |
| <i>Pittosporum bicolour</i> | 20 | 8 | 1.0 | 1.0 |
| Poaceae spp | 20 | 0 | 1.0 | 0.0 |

| Species | Frequency of occurrence (% of quadrats) | | Mean percentage cover | |
|---------------------------------------|--|--------|-----------------------|--------|
| | Control | Logged | Control | Logged |
| Clarence Lagoon shrubby forest | | | | |
| <i>Poa gunnii</i> | 60 | 100 | 3.0 | 10.4 |
| <i>Poranthera microphylla</i> | 60 | 67 | 1.0 | 1.0 |
| <i>Pteridium esculentum</i> | 0 | 25 | 0.0 | 4.0 |
| <i>Pultenaea juniperina</i> | 100 | 100 | 42.5 | 30.0 |
| <i>Ranunculus scapiger</i> | 0 | 25 | 0.0 | 1.0 |
| <i>Senecio lautus</i> | 20 | 0 | 0.5 | 0.0 |
| <i>Senecio linearifolius</i> | 60 | 92 | 1.0 | 2.1 |
| <i>Stellaria multiflora</i> | 0 | 8 | 0.0 | 1.0 |
| <i>Stylidium graminifolium</i> | 0 | 25 | 0.0 | 1.0 |
| <i>Tasmannia lanceolata</i> | 80 | 75 | 1.8 | 1.0 |
| <i>Veronica notabilis</i> | 20 | 17 | 1.0 | 1.0 |
| <i>Viola hederacea</i> | 0 | 25 | 0.0 | 0.8 |
| Mt Franklin grassy forest | | | | |
| <i>Acaena novae-zelandiae</i> | 100 | 100 | 2.0 | 3.0 |
| <i>Asplenium flabellifolium</i> | 0 | 17 | 0.0 | 1.0 |
| <i>Bossiaea riparia</i> | 0 | 17 | 0.0 | 1.0 |
| <i>Brachyscome spathulata</i> | 33 | 17 | 1.0 | 0.5 |
| <i>Callistemon viridiflorus</i> | 33 | 0 | 9.5 | 0.0 |
| <i>Coprosma quadrifida</i> | 67 | 17 | 1.8 | 1.0 |
| <i>Cotula</i> spp | 0 | 17 | 0.0 | 1.0 |
| <i>Craspedia glauca</i> | 0 | 33 | 0.0 | 1.0 |
| <i>Crassula sieberana</i> | 17 | 0 | 1.0 | 0.0 |
| <i>Cyathodes parvifolia</i> | 100 | 100 | 46.3 | 32.8 |
| <i>Deyeuxia monticola</i> | 50 | 17 | 4.0 | 1.0 |
| <i>Diplarrena moraea</i> | 67 | 67 | 0.9 | 1.0 |
| <i>Dryophila cyanocarpa</i> | 17 | 17 | 1.0 | 1.0 |
| <i>Epilobium sarmentaceum</i> | 0 | 33 | 0.0 | 4.0 |
| <i>Euphrasia collina</i> | 33 | 0 | 2.3 | 0.0 |
| <i>Galium australe</i> | 33 | 83 | 1.0 | 1.0 |
| <i>Geranium molle</i> * | 0 | 100 | 0.0 | 1.5 |
| <i>Geranium sessiliflorum</i> | 50 | 0 | 1.0 | 0.0 |
| <i>Euchiton collinum</i> | 17 | 83 | 1.0 | 1.6 |
| <i>Gonocarpus serpyllifolius</i> | 100 | 100 | 1.0 | 2.0 |
| <i>Hakea lissosperma</i> | 67 | 0 | 6.0 | 0.0 |
| <i>Helichrysum scorpioides</i> | 67 | 33 | 1.0 | 1.0 |
| <i>Hydrocotyle hirta</i> | 50 | 100 | 1.0 | 2.5 |
| <i>Hypericum japonicum</i> | 33 | 100 | 1.0 | 1.0 |
| <i>Hypochaeris radicata</i> * | 33 | 33 | 0.5 | 1.0 |
| <i>Leucopogon hookeri</i> | 100 | 100 | 2.5 | 13.2 |
| <i>Lomatia tinctoria</i> | 100 | 33 | 7.7 | 4.0 |
| <i>Luzula</i> spp | 0 | 83 | 0.0 | 1.0 |
| <i>Microseris scapigera</i> | 33 | 0 | 1.0 | 0.0 |
| <i>Olearia erubescens</i> | 100 | 33 | 1.5 | 1.0 |
| Orchidaceae | 83 | 83 | 1.5 | 0.9 |
| <i>Oreomyrrhis eriopoda</i> | 0 | 33 | 0.0 | 1.0 |
| <i>Pittosporum bicolour</i> | 17 | 0 | 0.5 | 0.0 |
| <i>Plantago</i> spp | 17 | 50 | 1.0 | 1.0 |

| Species | Frequency of occurrence (% of quadrats) | | Mean percentage cover | |
|--------------------------------|---|--------|-----------------------|--------|
| | Control | Logged | Control | Logged |
| Mt Franklin grassy forest | | | | |
| <i>Poa gunnii</i> | 100 | 100 | 11.3 | 54.2 |
| <i>Polystichum proliferum</i> | 0 | 17 | 0.0 | 0.5 |
| <i>Poranthera microphylla</i> | 50 | 50 | 1.0 | 1.0 |
| <i>Pultenaea gunnii</i> | 100 | 0 | 11.3 | 0.0 |
| <i>Pultenaea juniperina</i> | 67 | 0 | 6.0 | 0.0 |
| <i>Ranunculus scapiger</i> | 17 | 100 | 1.0 | 2.0 |
| <i>Senecio gunnii</i> | 17 | 83 | 1.0 | 1.0 |
| <i>Stellaria multiflora</i> | 17 | 0 | 1.0 | 0.0 |
| <i>Stylidium graminifolium</i> | 33 | 0 | 1.0 | 0.0 |
| <i>Taraxacum officinale</i> * | 0 | 17 | 0.0 | 1.0 |
| <i>Veronica calycina</i> | 83 | 100 | 1.0 | 3.0 |
| <i>Veronica gracilis</i> | 0 | 17 | 0.0 | 0.5 |
| <i>Viola hederacea</i> | 50 | 67 | 2.0 | 1.8 |
| <i>Wahlenbergia</i> spp | 50 | 17 | 1.0 | 1.0 |

| Species | Control | 1979 plant | 1995 plant | Control | 1979 plant | 1995 plant |
|---------------------------------|---------|------------|------------|---------|------------|------------|
| Tarraleah plantations | | | | | | |
| <i>Acacia dealbata</i> | 100 | 100 | 17 | 17.8 | 25.6 | 1.0 |
| <i>Acaena novae-zelandiae</i> | 83 | 100 | 100 | 5.5 | 27.7 | 16.9 |
| <i>Acetosella vulgaris</i> * | 0 | | 100 | 0.0 | 0.0 | 2.5 |
| <i>Agrostis capillaris</i> * | 17 | 0 | 100 | 2.5 | 0.0 | 18.8 |
| <i>Agrostis stolonifera</i> * | 0 | 8 | 0 | 0.0 | 15.0 | 0 |
| <i>Anthoxanthum odoratum</i> * | 33 | 0 | 100 | 1.8 | 0.0 | 13.2 |
| <i>Aquilegia</i> spp * | 0 | 8 | 0 | 0.0 | 1.0 | 0.0 |
| <i>Asperula conferta</i> | 0 | 8 | 0 | 0.0 | 1.0 | 0.0 |
| <i>Asperula gunnii</i> | 83 | 0 | 100 | 3.6 | 0.0 | 9.0 |
| <i>Atherosperma moschatum</i> | 58 | 8 | 0 | 7.9 | 1.0 | 0.0 |
| <i>Australina pusilla</i> | 17 | 0 | 0 | 2.5 | 0.0 | 0.0 |
| <i>Australopyrum pectinatum</i> | 75 | 83 | 67 | 8.6 | 2.5 | 3.3 |
| <i>Carex</i> spp | 8 | 8 | 0 | 1.0 | 1.0 | 0.0 |
| <i>Carex appressa</i> | 8 | 25 | 0 | 1.0 | 3.0 | 0.0 |
| <i>Cassinia aculeata</i> | 67 | 58 | 17 | 13.3 | 7.9 | 1.0 |
| <i>Cerastium glomeratum</i> * | 0 | 0 | 50 | 0.0 | 0 | 1.0 |
| <i>Cerastium vulgare</i> * | 0 | 17 | 0 | 0.0 | 0.8 | 0.0 |
| <i>Cirsium arvense</i> * | 0 | 75 | 0 | 0.0 | 3.7 | 0.0 |
| <i>Cirsium vulgare</i> * | 8 | 0 | 100 | 1.0 | 0.0 | 3.5 |
| <i>Clematis aristata</i> | 58 | 100 | 0 | 1.4 | 3.1 | 0.0 |
| <i>Coprosma quadrifida</i> | 33 | 0 | 0 | 11.5 | 0.0 | 0.0 |
| <i>Austrodanthonia pilosa</i> | 0 | 0 | 50 | 0.0 | 0.0 | 7.7 |
| <i>Deyeuxia densa</i> | 8 | 0 | 0 | 4.0 | 0.0 | 0.0 |
| <i>Deyeuxia monticola</i> | 0 | 0 | 17 | 0.0 | 0.0 | 4.0 |
| <i>Dianella tasmanica</i> | 0 | 8 | 0 | 0.0 | 15.0 | 0.0 |
| <i>Dicksonia antarctica</i> | 83 | 75 | 0 | 26.8 | 21.0 | 0.0 |
| <i>Dryophila cyanocarpa</i> | 17 | 0 | 0 | 1.0 | 0.0 | 0.0 |
| <i>Epilobium sarmentaceum</i> | 0 | 33 | 100 | 0.0 | 1.6 | 7.2 |
| <i>Gahnia grandis</i> | 0 | 8 | 0 | 0.0 | 0.5 | 0.0 |
| <i>Galium australe</i> | 42 | 42 | 17 | 1.6 | 1.0 | 1.0 |
| <i>Geranium molle</i> * | 0 | 0 | 100 | 0.0 | 0.0 | 15.0 |

| Species | Frequency of occurrence (% of quadrats) | | | Mean percentage cover | | |
|----------------------------------|---|------------|------------|-----------------------|------------|------------|
| | Control | 1979 plant | 1995 plant | Control | 1979 plant | 1995 plant |
| Tarraleah plantations | | | | | | |
| <i>Geranium potentilloides</i> | 75 | 92 | 50 | 2.0 | 4.0 | 3.0 |
| <i>Geranium sessiliflorum</i> | 8 | 0 | 17 | 4.0 | 0.0 | 1.0 |
| <i>Euchiton collinum</i> | 0 | 0 | 83 | 0.0 | 0.0 | 5.6 |
| <i>Gonocarpus serpyllifolius</i> | 8 | 0 | 33 | 4.0 | 0.0 | 4.0 |
| <i>Gonocarpus tetragynus</i> | 0 | 0 | 17 | 0.0 | 0.0 | 1.0 |
| <i>Histiopteris incisa</i> | 42 | 75 | 0 | 10.6 | 19.8 | 0.0 |
| <i>Holcus lanatus</i> * | 8 | 100 | 100 | 1.0 | 4.6 | 22.5 |
| <i>Hydrocotyle hirta</i> | 100 | 100 | 33 | 6.9 | 4.6 | 2.5 |
| <i>Hypericum gramineum</i> | 8 | 25 | 0 | 1.0 | 1.0 | 0.0 |
| <i>Hypericum japonicum</i> | 75 | 0 | 100 | 1.3 | 0.0 | 6.7 |
| <i>Hypochaeris radicata</i> * | 0 | 8 | 100 | 0.0 | 4.0 | 18.8 |
| <i>Hypolepis rugulosa</i> | 42 | 50 | 0 | 10.6 | 9.5 | 0.0 |
| <i>Juncus gregiflorus</i> | 8 | 25 | 0 | 1.0 | 1.7 | 0.0 |
| <i>Juncus pallidus</i> | 0 | 8 | 0 | 0.0 | 0.5 | 0.0 |
| <i>Lagenophora stipitata</i> | 17 | 0 | 0 | 2.5 | 0.0 | 0.0 |
| <i>Leontodon taraxacoides</i> * | 0 | 0 | 83 | 0.0 | 0.0 | 1.0 |
| <i>Linum catharticum</i> * | 8 | 0 | 83 | 1.0 | 0.0 | 12.8 |
| <i>Nothofagus cunninghamii</i> | 25 | 0 | 0 | 7.7 | 0.0 | 0.0 |
| <i>Olearia argophylla</i> | 0 | 17 | 0 | 0.0 | 9.5 | 0.0 |
| <i>Oreomyrrhis eriopoda</i> | 0 | 0 | 17 | 0.0 | 0.0 | 1.0 |
| <i>Oxalis perennans</i> | 83 | 100 | 50 | 4.2 | 7.2 | 2.0 |
| <i>Pimelea drupaceae</i> | 92 | 25 | 0 | 2.6 | 1.8 | 0.0 |
| <i>Pimelea linifolia</i> | 25 | 0 | 100 | 1.0 | 0.0 | 3.0 |
| <i>Pittosporum bicolor</i> | 8 | 8 | 0 | 1.0 | 4.0 | 0.0 |
| Poaceae spp | 42 | 33 | 0 | 5.6 | 6.8 | 0.0 |
| <i>Polystichum proliferum</i> | 100 | 100 | 0 | 24.4 | 22.5 | 0.0 |
| <i>Pomaderris apetala</i> | 42 | 50 | 0 | 3.4 | 2.4 | 0.0 |
| <i>Poranthera microphylla</i> | 8 | 0 | 0 | 1.0 | 0.0 | 0.0 |
| <i>Pratia pedunculata</i> | 0 | 0 | 17 | 0.0 | 0.0 | 1.0 |
| <i>Prunella vulgaris</i> * | 0 | 8 | 33 | 8.0 | 1.0 | 1.0 |
| <i>Pteridium esculentum</i> | 100 | 100 | 100 | 34.4 | 28.4 | 15.0 |
| <i>Ranunculus scapiger</i> | 0 | 0 | 50 | 0.0 | 0.0 | 2.0 |
| <i>Scleranthus biflorus</i> | 0 | 0 | 50 | 0.0 | 0.0 | 2.0 |
| <i>Senecio linearifolius</i> | 67 | 100 | 33 | 9.5 | 22.5 | 1.0 |
| <i>Senecio minimus</i> | 8 | 100 | 17 | 1.0 | 7.4 | 1.0 |
| <i>Solenogyne gunnii</i> | 0 | 0 | 33 | 0.0 | 0.0 | 1.0 |
| <i>Taraxacum officinale</i> * | 8 | 0 | 100 | 1.0 | 0.0 | 13.2 |
| <i>Tasmannia lanceolata</i> | 8 | 0 | 0 | 1.0 | 0.0 | 0.0 |
| <i>Trifolium</i> spp* | 0 | 0 | 67 | 0.0 | 0.0 | 1.0 |
| <i>Uncinia riparia</i> | 92 | 83 | 17 | 8.7 | 2.8 | 1.0 |
| <i>Urtica incisa</i> | 33 | 17 | 0 | 6.0 | 1.0 | 0.0 |
| <i>Veronica gracilis</i> | 0 | 0 | 17 | 0.0 | 0.0 | 1.0 |
| <i>Viola hederacea</i> | 58 | 25 | 33 | 1.4 | 2.0 | 2.5 |
| <i>Vulpia bromoides</i> * | 0 | 0 | 50 | 0.0 | 0.0 | 3.0 |
| <i>Zieria arborescens</i> | 50 | 17 | 17 | 3.0 | 3.0 | 0.5 |

Appendix 2 BACI study raw data

Frequency of occurrence (Freq) (number of times a species was recorded in) and mean percentage cover (% Cover) for all vascular plants recorded in quadrats at the three sampling times Prelog, Postlog 1 and Postlog 2, for the BACI study at Table Mountain

| Species Logged quadrats | Prelog | | Postlog 1 | | Postlog 2 | |
|----------------------------------|--------|---------|-----------|---------|-----------|---------|
| | Freq | % Cover | Freq | % Cover | Freq | % Cover |
| <i>Acacia dealbata</i> | 24 | 2.6 | 18 | 1.4 | 29 | 1.6 |
| <i>Acacia melanoxylon</i> | 14 | 1.6 | 6 | 0.7 | 13 | 0.6 |
| <i>Acaena novae-zelandiae</i> | 8 | 0.1 | 5 | 0.0 | 12 | 0.1 |
| <i>Acaena echinata</i> | 1 | 0.0 | 0 | 0.0 | 1 | 0.0 |
| <i>Acrotriche serrulata</i> | 1 | 0.0 | 3 | 0.1 | 3 | 0.1 |
| <i>Ajuga australis</i> | 8 | 0.4 | 11 | 0.4 | 13 | 0.5 |
| <i>Arthropodium milleflorum</i> | 24 | 0.3 | 12 | 0.1 | 11 | 0.0 |
| <i>Austrofestuca hookeriana</i> | 3 | 0.8 | 2 | 0.5 | 3 | 0.2 |
| <i>Bossiaea prostrata</i> | 7 | 0.2 | 4 | 0.1 | 4 | 0.1 |
| <i>Bossiaea riparia</i> | 1 | 0.1 | 1 | 0.1 | 1 | 0.1 |
| <i>Brachyscome decipiens</i> | 21 | 0.4 | 3 | 0.0 | 17 | 0.2 |
| <i>Brachyscome spathulata</i> | 8 | 0.1 | 8 | 0.1 | 6 | 0.0 |
| <i>Cardamine</i> spp | 2 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Carex breviculmis</i> | 2 | 0.0 | 0 | 0.0 | 3 | 0.0 |
| <i>Celmisia</i> spp. | 1 | 0.0 | 0 | 0.0 | 1 | 0.0 |
| <i>Cerastium glomeratum</i> * | 1 | 0.0 | 1 | 0.0 | 1 | 0.0 |
| <i>Cirsium arvense</i> | 0 | 0.0 | 0 | 0.0 | 1 | 0.0 |
| <i>Cirsium vulgare</i> * | 0 | 0.0 | 3 | 0.0 | 14 | 0.3 |
| <i>Comesperma volubile</i> | 1 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Coprosma quadrifida</i> | 1 | 0.0 | 0 | 0.0 | 1 | 0.0 |
| <i>Cotula alpina</i> | 1 | 0.0 | 0 | 0.0 | 1 | 0.0 |
| <i>Craspedia glauca</i> | 8 | 0.1 | 1 | 0.0 | 3 | 0.0 |
| <i>Crassula sieberana</i> | 1 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Cyathodes juniperina</i> | 0 | 0.0 | 0 | 0.0 | 1 | 0.0 |
| <i>Cyathodes parvifolia</i> | 17 | 0.6 | 5 | 0.2 | 7 | 0.2 |
| <i>Dianella tasmanica</i> | 6 | 0.4 | 4 | 0.3 | 7 | 0.3 |
| <i>Dichondra repens</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Diplarrena moraea</i> | 15 | 0.2 | 8 | 0.1 | 12 | 0.1 |
| <i>Drosera peltata</i> | 9 | 0.2 | 0 | 0.0 | 0 | 0.0 |
| <i>Dryophila cyanocarpa</i> | 16 | 0.2 | 9 | 0.1 | 3 | 0.0 |
| <i>Epacris impressa</i> | 1 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Epilobium sarmentaceum</i> | 3 | 0.0 | 1 | 0.0 | 3 | 0.0 |
| <i>Galium australe</i> | 19 | 0.3 | 10 | 0.1 | 7 | 0.1 |
| <i>Geranium potentilloides</i> | 1 | 0.0 | 4 | 0.0 | 0 | 0.0 |
| <i>Geranium sessiliflorum</i> | 40 | 0.7 | 12 | 0.1 | 44 | 0.6 |
| <i>Glycine</i> spp. | 0 | 0.0 | 0 | 0.0 | 2 | 0.0 |
| <i>Gnaphalium collinum</i> | 16 | 0.4 | 6 | 0.1 | 20 | 0.5 |
| <i>Gonocarpus serpyllifolius</i> | 72 | 2.5 | 53 | 1.4 | 57 | 1.4 |
| <i>Hakea lissosperma</i> | 0 | 0.0 | 1 | 0.0 | 1 | 0.0 |
| <i>Helichrysum scorpioides</i> | 17 | 0.3 | 9 | 0.1 | 10 | 0.1 |
| <i>Hydrocotyle hirta</i> | 73 | 3.4 | 54 | 1.6 | 65 | 2.3 |

| Species | Prelog | | Postlog 1 | | Postlog 2 | |
|---------------------------------|--------|---------|-----------|---------|-----------|---------|
| Logged quadrats | Freq | % Cover | Freq | % Cover | Freq | % Cover |
| <i>Hypericum gramineum</i> | 23 | 0.4 | 13 | 0.2 | 9 | 0.1 |
| <i>Hypericum japonicum</i> | 57 | 1.0 | 35 | 0.4 | 40 | 0.7 |
| <i>Hypochaeris radicata</i> * | 12 | 0.1 | 7 | 0.0 | 4 | 0.1 |
| <i>Juncus gregiflorus</i> | 8 | 0.4 | 7 | 0.4 | 12 | 0.3 |
| <i>Lagenophora stipitata</i> | 69 | 1.9 | 32 | 0.3 | 37 | 0.5 |
| <i>Leontodon taraxacoides</i> * | 1 | 0.0 | 0 | 0.0 | 1 | 0.0 |
| <i>Leucopogon hookeri</i> | 82 | 13.6 | 62 | 8.4 | 65 | 6.8 |
| <i>Leucopogon stuartii</i> | 20 | 0.4 | 17 | 0.3 | 21 | 0.4 |
| <i>Linum marginale</i> | 0 | 0.0 | 1 | 0.0 | 1 | 0.0 |
| <i>Lomandra longifolia</i> | 65 | 11.3 | 68 | 8.6 | 69 | 7.3 |
| <i>Lomatia tinctoria</i> | 82 | 12.8 | 72 | 8.9 | 78 | 8.0 |
| <i>Luzula</i> spp | 28 | 0.3 | 6 | 0.0 | 29 | 0.4 |
| <i>Neopaxia australis</i> | 1 | 0.0 | 0 | 0.0 | 1 | 0.0 |
| <i>Olearia phlogopappa</i> | 1 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Olearia viscosa</i> | 7 | 0.8 | 8 | 0.4 | 9 | 0.5 |
| <i>Ophioglossum lusitanicum</i> | 1 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| Orchidaceae | 54 | 2.5 | 15 | 0.1 | 23 | 0.4 |
| <i>Oreomyrrhis eriopoda</i> | 5 | 0.1 | 2 | 0.0 | 3 | 0.0 |
| <i>Oxalis perennans</i> | 5 | 0.1 | 4 | 0.1 | 4 | 0.1 |
| <i>Pimelea humilis</i> | 17 | 0.4 | 17 | 0.3 | 18 | 0.2 |
| <i>Plantago glabrata</i> | 13 | 0.4 | 13 | 0.1 | 15 | 0.1 |
| <i>Plantago paradoxa</i> | 1 | 0.0 | 0 | 0.0 | 1 | 0.0 |
| Poaceae spp | 52 | 2.2 | 38 | 1.0 | 79 | 3.1 |
| <i>Poa gunnii</i> | 89 | 22.3 | 74 | 15.9 | 80 | 10.6 |
| <i>Poa rodwayi</i> | 67 | 8.1 | 51 | 3.1 | 64 | 4.9 |
| <i>Poranthera microphylla</i> | 21 | 0.3 | 9 | 0.1 | 24 | 0.2 |
| <i>Pratia pedunculata</i> | 37 | 1.0 | 17 | 0.3 | 28 | 0.5 |
| <i>Pteridium esculentum</i> | 59 | 7.8 | 47 | 4.3 | 62 | 7.5 |
| <i>Pultenaea juniperina</i> | 3 | 0.1 | 4 | 0.1 | 4 | 0.1 |
| <i>Ranunculus lappaceus</i> | 7 | 0.1 | 3 | 0.0 | 4 | 0.0 |
| <i>Ranunculus scapiger</i> | 22 | 0.4 | 15 | 0.1 | 22 | 0.4 |
| <i>Scleranthus biflorus</i> | 2 | 0.1 | 3 | 0.1 | 4 | 0.1 |
| <i>Senecio gunnii</i> | 21 | 0.3 | 4 | 0.1 | 11 | 0.1 |
| <i>Solenogyne gunnii</i> | 5 | 0.1 | 3 | 0.0 | 7 | 0.1 |
| <i>Stackhousia monogyna</i> | 1 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Stylidium graminifolium</i> | 2 | 0.0 | 1 | 0.0 | 2 | 0.0 |
| <i>Taraxacum officinale</i> * | 10 | 0.1 | 1 | 0.0 | 3 | 0.0 |
| <i>Veronica calycina</i> | 34 | 0.7 | 19 | 0.2 | 19 | 0.2 |
| <i>Veronica gracilis</i> | 11 | 0.2 | 4 | 0.0 | 3 | 0.0 |
| <i>Viola betonicifolia</i> | 22 | 0.4 | 22 | 0.3 | 14 | 0.1 |
| <i>Viola hederacea</i> | 51 | 2.6 | 35 | 0.9 | 44 | 1.7 |
| <i>Wahlenbergia</i> spp | 64 | 1.7 | 24 | 0.2 | 42 | 0.9 |
| All Poaceae | 99 | 32.6 | 90 | 20.0 | 94 | 18.6 |

| Species | Prelog | | Postlog 1 | | Postlog 2 | |
|-------------------------------|--------|---------|-----------|---------|-----------|---------|
| Control quadrats | Freq | % Cover | Freq | % Cover | Freq | % Cover |
| <i>Acacia dealbata</i> | 74 | 10.0 | 74 | 9.0 | 74 | 9.1 |
| <i>Acacia melanoxylon</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Acaena novae-zelandiae</i> | 3 | 0.0 | 3 | 0.0 | 12 | 0.1 |
| <i>Acaena echinata</i> | 9 | 0.2 | 6 | 0.1 | 0 | 0.0 |
| <i>Acrotriche serrulata</i> | 0 | 0.0 | 6 | 0.1 | 0 | 0.0 |

| Species Control quadrats | Prelog | | Postlog 1 | | Postlog 2 | |
|----------------------------------|--------|---------|-----------|---------|-----------|---------|
| | Freq | % Cover | Freq | % Cover | Freq | % Cover |
| <i>Ajuga australis</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Arthropodium milleflorum</i> | 12 | 0.1 | 0 | 0.0 | 0 | 0.0 |
| <i>Austrofestuca hookeriana</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Bossiaea prostrata</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Bossiaea riparia</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Brachyscome decipiens</i> | 9 | 0.1 | 0 | 0.0 | 3 | 0.0 |
| <i>Brachyscome spathulata</i> | 0 | 0.0 | 3 | 0.0 | 0 | 0.0 |
| <i>Cardamine</i> spp | 0 | 0.0 | 0 | 0.0 | 3 | 0.0 |
| <i>Carex breviculmis</i> | 0 | 0.0 | 0 | 0.0 | 3 | 0.0 |
| <i>Celmisia</i> spp. | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Cerastium glomeratum</i> * | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Cirsium arvense</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Cirsium vulgare</i> * | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Comesperma volubile</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Coprosma quadrifida</i> | 0 | 0.0 | 0 | 0.0 | 3 | 0.0 |
| <i>Cotula alpina</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Craspedia glauca</i> | 3 | 0.0 | 0 | 0.0 | 3 | 0.0 |
| <i>Crassula sieberana</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Cyathodes juniperina</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Cyathodes parvifolia</i> | 3 | 0.1 | 3 | 0.0 | 12 | 0.4 |
| <i>Dianella tasmanica</i> | 6 | 0.1 | 12 | 2.0 | 15 | 1.3 |
| <i>Dichondra repens</i> | 3 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Diplarrena moraea</i> | 6 | 0.1 | 3 | 0.0 | 6 | 0.0 |
| <i>Drosera peltata</i> | 12 | 0.1 | 0 | 0.0 | 0 | 0.0 |
| <i>Dryophila cyanocarpa</i> | 62 | 1.1 | 68 | 1.7 | 65 | 1.4 |
| <i>Epacris impressa</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Epilobium sarmentaceum</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Galium australe</i> | 56 | 0.8 | 35 | 0.5 | 44 | 0.6 |
| <i>Geranium potentilloides</i> | 15 | 0.3 | 12 | 0.1 | 12 | 0.1 |
| <i>Geranium sessiliflorum</i> | 71 | 1.3 | 59 | 0.8 | 79 | 1.1 |
| <i>Glycine</i> spp. | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Gnaphalium collinum</i> | 3 | 0.1 | 0 | 0.0 | 3 | 0.0 |
| <i>Gonocarpus serpyllifolius</i> | 71 | 2.0 | 59 | 1.7 | 68 | 1.9 |
| <i>Hakea lissosperma</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Helichrysum scorpioides</i> | 3 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Hydrocotyle hirta</i> | 88 | 3.1 | 65 | 1.7 | 76 | 2.0 |
| <i>Hypericum gramineum</i> | 26 | 0.4 | 3 | 0.0 | 12 | 0.1 |
| <i>Hypericum japonicum</i> | 79 | 1.2 | 68 | 0.7 | 62 | 0.9 |
| <i>Hypochaeris radicata</i> * | 18 | 0.1 | 6 | 0.0 | 6 | 0.0 |
| <i>Juncus gregiflorus</i> | 6 | 0.1 | 0 | 0.0 | 3 | 0.0 |
| <i>Lagenophora stipitata</i> | 76 | 1.8 | 53 | 0.9 | 65 | 0.7 |
| <i>Neopaxia australis</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Olearia phlogopappa</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Olearia viscosa</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Ophioglossum lusitanicum</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| Orchidaceae | 56 | 2.7 | 15 | 0.2 | 35 | 1.4 |
| <i>Oreomyrrhis eriopoda</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Oxalis perennans</i> | 3 | 0.1 | 9 | 0.1 | 6 | 0.1 |
| <i>Pimelea humilis</i> | 6 | 0.1 | 0 | 0.0 | 6 | 0.1 |
| <i>Plantago glabrata</i> | 3 | 0.1 | 3 | 0.0 | 3 | 0.0 |

| Species | Prelog | | Postlog 1 | | Postlog 2 | |
|--------------------------------|--------|---------|-----------|---------|-----------|---------|
| | Freq | % Cover | Freq | % Cover | Freq | % Cover |
| Control quadrats | | | | | | |
| <i>Plantago paradoxa</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| Poaceae spp | 59 | 1.5 | 3 | 0.0 | 85 | 2.4 |
| <i>Poa gunnii</i> | 53 | 5.6 | 68 | 18.6 | 50 | 4.5 |
| <i>Poa rodwayi</i> | 97 | 33.7 | 91 | 16.1 | 100 | 16.7 |
| <i>Poranthera microphylla</i> | 24 | 0.2 | 9 | 0.1 | 18 | 0.2 |
| <i>Pratia pedunculata</i> | 53 | 0.6 | 32 | 0.5 | 44 | 0.7 |
| <i>Pteridium esculentum</i> | 85 | 9.7 | 85 | 9.6 | 91 | 4.0 |
| <i>Pultenaea juniperina</i> | 3 | 0.1 | 6 | 0.1 | 0 | 0.0 |
| <i>Ranunculus lappaceus</i> | 0 | 0.0 | 0 | 0.0 | 3 | 0.0 |
| <i>Ranunculus scapiger</i> | 15 | 0.3 | 9 | 0.2 | 18 | 0.5 |
| <i>Scleranthus biflorus</i> | 9 | 0.1 | 6 | 0.1 | 6 | 0.2 |
| <i>Senecio gunnii</i> | 6 | 0.0 | 3 | 0.0 | 0 | 0.0 |
| <i>Solenogyne gunnii</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Stackhousia monogyna</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Stylidium graminifolium</i> | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| <i>Taraxacum officinale</i> * | 21 | 0.2 | 0 | 0.0 | 3 | 0.0 |
| <i>Veronica calycina</i> | 15 | 0.2 | 21 | 0.2 | 18 | 0.2 |
| <i>Veronica gracilis</i> | 6 | 0.1 | 9 | 0.1 | 9 | 0.1 |
| <i>Viola betonicifolia</i> | 24 | 0.2 | 21 | 0.3 | 21 | 0.1 |
| <i>Viola hederacea</i> | 79 | 4.9 | 68 | 2.2 | 88 | 3.4 |
| <i>Wahlenbergia</i> spp | 65 | 1.9 | 47 | 0.6 | 65 | 1.7 |
| All Poaceae | 100 | 40.8 | 100 | 34.7 | 100 | 23.7 |

Appendix 3 Halo study raw data

Frequency of occurrence (Frequency) (number of times a species was recorded in) and mean percentage cover (Mean % cover) for all vascular plants recorded in quadrats of the trunk ring, the canopy edge ring and forest gaps , in unlogged native grassy forest for the Halo study at Table Mountain.

| species | Frequency | | | Mean % cover | | |
|----------------------------------|-----------|--------|-----|--------------|--------|------|
| | trunk | canopy | gap | trunk | canopy | gap |
| <i>Acacia dealbata</i> | 25 | 40 | 26 | 2.5 | 5.3 | 3.3 |
| <i>Acacia melanoxylon</i> | 13 | 10 | 7 | 1.0 | 0.9 | 1.6 |
| <i>Acaena novae-zelandiae</i> | 3 | 0 | 14 | 0.0 | 0.0 | 0.3 |
| <i>Acianthus</i> spp | 12 | 20 | 24 | 0.6 | 0.5 | 1.1 |
| <i>Ajuga australis</i> | 2 | 2 | 14 | 0.1 | 0.3 | 0.8 |
| <i>Arthropodium milleflorum</i> | 7 | 27 | 27 | 0.1 | 0.3 | 0.5 |
| <i>Bossiaea prostrata</i> | 2 | 7 | 9 | 0.0 | 0.2 | 0.3 |
| <i>Brachyscome decipiens</i> | 12 | 12 | 23 | 0.2 | 0.3 | 0.6 |
| <i>Brachyscome spathulata</i> | 0 | 8 | 10 | 0.0 | 0.1 | 0.2 |
| <i>Caladenia alpina</i> | 3 | 8 | 11 | 0.0 | 0.1 | 0.1 |
| <i>Chiloglottis gunnii</i> | 13 | 12 | 20 | 0.4 | 0.5 | 1.2 |
| <i>Craspedia glauca</i> | 5 | 7 | 7 | 0.0 | 0.1 | 0.1 |
| <i>Cyathodes parvifolia</i> | 12 | 12 | 16 | 0.3 | 0.2 | 0.7 |
| <i>Dianella tasmanica</i> | 7 | 5 | 3 | 0.1 | 0.5 | 0.3 |
| <i>Dichelachne</i> spp | 20 | 12 | 6 | 0.8 | 0.6 | 0.3 |
| <i>Diplarrena moraea</i> | 10 | 15 | 11 | 0.1 | 0.3 | 0.2 |
| <i>Drosera peltata</i> | 2 | 10 | 13 | 0.0 | 0.1 | 0.4 |
| <i>Dryophila cyanocarpa</i> | 22 | 28 | 17 | 0.3 | 0.4 | 0.4 |
| <i>Galium australe</i> | 18 | 23 | 31 | 0.2 | 0.4 | 0.5 |
| <i>Geranium sessiliflorum</i> | 22 | 35 | 63 | 0.3 | 0.5 | 1.8 |
| <i>Euchiton collinum</i> | 5 | 7 | 26 | 0.1 | 0.3 | 0.6 |
| <i>Gonocarpus serpyllifolius</i> | 58 | 70 | 74 | 1.7 | 2.4 | 3.1 |
| <i>Helichrysum scorpioides</i> | 8 | 23 | 11 | 0.1 | 0.4 | 0.3 |
| <i>Hydrocotyle hirta</i> | 65 | 82 | 73 | 2.3 | 3.1 | 4.9 |
| <i>Hypericum gramineum</i> | 13 | 22 | 27 | 0.2 | 0.3 | 0.6 |
| <i>Hypericum japonicum</i> | 38 | 67 | 66 | 0.6 | 1.4 | 1.3 |
| <i>Hypochaeris radicata</i> * | 5 | 8 | 16 | 0.0 | 0.1 | 0.2 |
| <i>Lagenophora stipitata</i> | 52 | 77 | 67 | 1.4 | 2.1 | 2.0 |
| <i>Leucopogon hookeri</i> | 73 | 82 | 77 | 9.8 | 14.3 | 16.7 |
| <i>Leucopogon stuartii</i> | 15 | 17 | 21 | 0.3 | 0.2 | 0.6 |
| <i>Lomandra longifolia</i> | 72 | 72 | 54 | 12.7 | 12.7 | 12.0 |
| <i>Lomatia tinctoria</i> | 80 | 85 | 76 | 12.5 | 13.5 | 14.6 |
| <i>Luzula</i> spp | 15 | 32 | 30 | 0.1 | 0.4 | 0.5 |

| species | Frequency Mean % cover | | species | Frequency Mean % cover | | species |
|-------------------------------|------------------------|--------|---------|------------------------|--------|---------|
| | trunk | canopy | | trunk | canopy | |
| <i>Olearia viscosa</i> | 3 | 7 | 7 | 0.1 | 0.3 | 1.6 |
| Orchidaceae | 5 | 3 | 10 | 0.0 | 0.0 | 0.3 |
| <i>Pimelea humilis</i> | 20 | 17 | 6 | 0.5 | 0.4 | 0.1 |
| <i>Plantago glabrata</i> | 5 | 8 | 19 | 0.1 | 0.2 | 0.8 |
| Poaceae spp | 23 | 37 | 44 | 0.7 | 1.2 | 2.2 |
| <i>Poa gunnii</i> | 67 | 90 | 76 | 13.1 | 20.7 | 23.7 |
| <i>Poa rodwayi</i> | 72 | 77 | 57 | 10.3 | 13.1 | 14.5 |
| <i>Poranthera microphylla</i> | 12 | 25 | 24 | 0.2 | 0.3 | 0.4 |
| <i>Pratia pedunculata</i> | 37 | 47 | 29 | 1.0 | 1.2 | 0.7 |
| <i>Pteridium esculentum</i> | 62 | 58 | 56 | 9.0 | 8.1 | 8.0 |
| <i>Pterostylis</i> spp | 15 | 30 | 27 | 0.3 | 0.7 | 1.0 |
| <i>Ranunculus scapiger</i> | 8 | 15 | 30 | 0.1 | 0.2 | 0.9 |
| <i>Senecio gunnii</i> | 13 | 25 | 13 | 0.1 | 0.5 | 0.2 |
| <i>Taraxacum officinale</i> * | 3 | 15 | 16 | 0.0 | 0.1 | 0.2 |
| <i>Veronica calycina</i> | 23 | 30 | 33 | 0.6 | 0.6 | 0.7 |
| <i>Veronica gracilis</i> | 5 | 8 | 16 | 0.1 | 0.1 | 0.2 |
| <i>Viola betonicifolia</i> | 20 | 23 | 24 | 0.3 | 0.3 | 0.5 |
| <i>Viola hederacea</i> | 33 | 50 | 69 | 1.1 | 3.1 | 4.3 |
| <i>Wahlenbergia</i> spp | 50 | 53 | 76 | 1.3 | 1.2 | 2.7 |

Appendix 4 Classification dendrograms

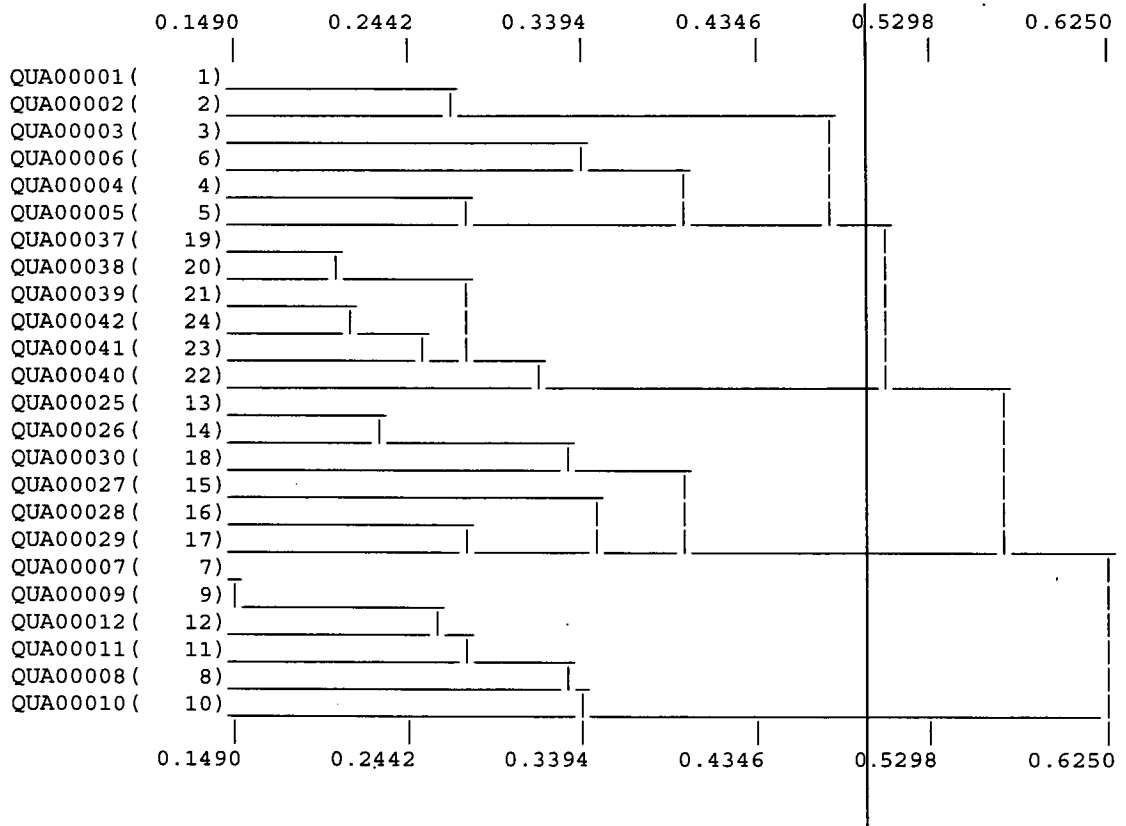


Figure A4.1 Site classification dendrogram of the 24 quadrats of Table Mtn grassy forest showing cut-off line defining four groups. Group 1 of quadrats 1-6 = control forest; group 2 of quadrats 37-42 = control forest; group 3 of quadrats 25-30 = logged coupe 1996; group 4 of quadrats 7-12 = logged coupe 1992.

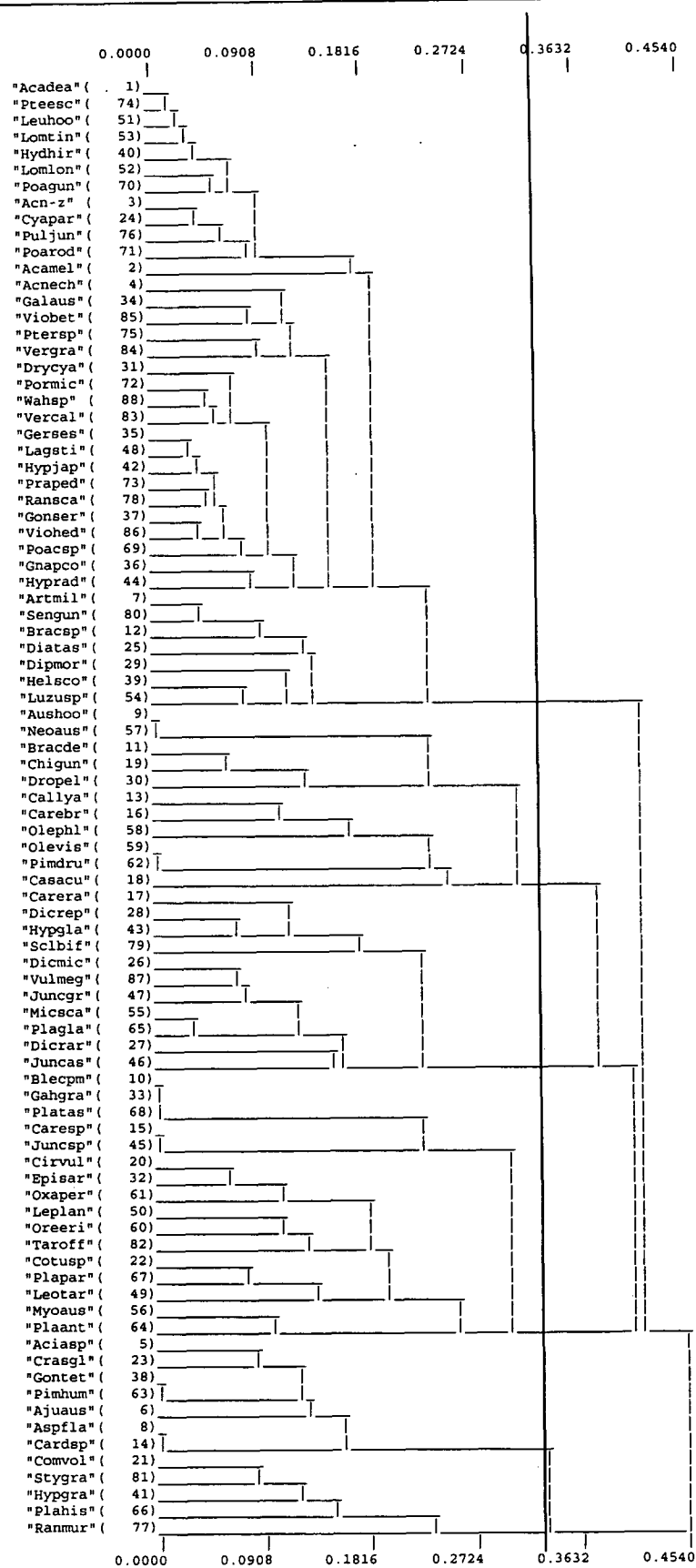


Figure A4.2
Classification
dendrogram of the 88
species found in Table
Mtn grassy forest. Cut-
off line shows the six
groups displayed in the
two-way table of
Chapter 3 (Table 3.2).

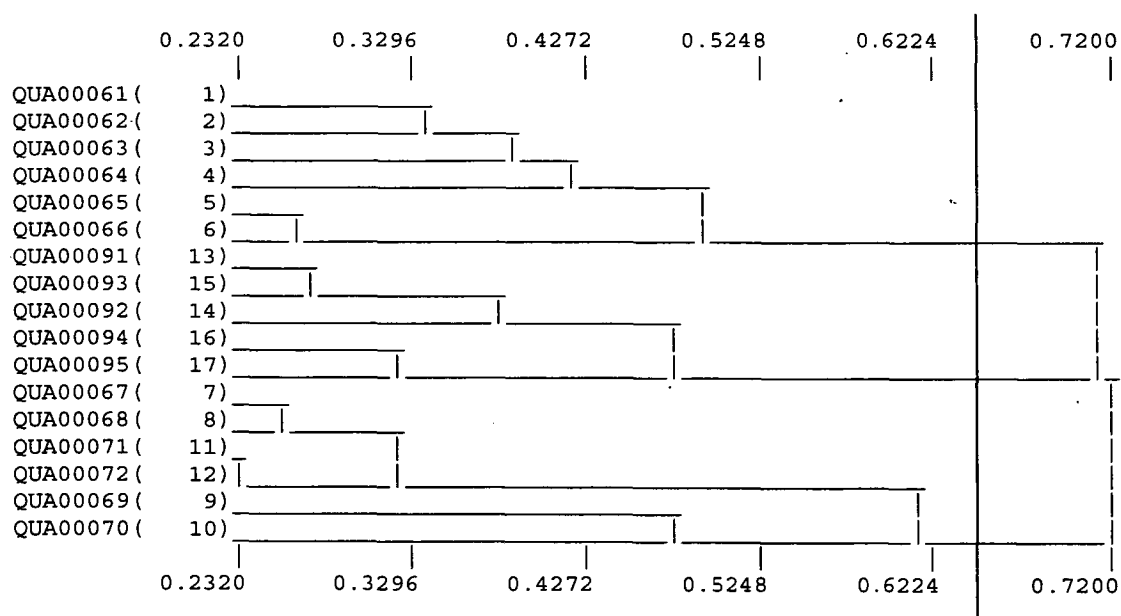


Figure A4.3 Site classification dendrogram of the 17 quadrats of Glenmark shrubby forest showing cut-off line defining three groups. Group 1 of quadrats 61-66 = logged coupe 1995; group 2 of quadrats 91-95 = logged coupe 1993/94; group 3 of quadrats 67-72 = control forest.

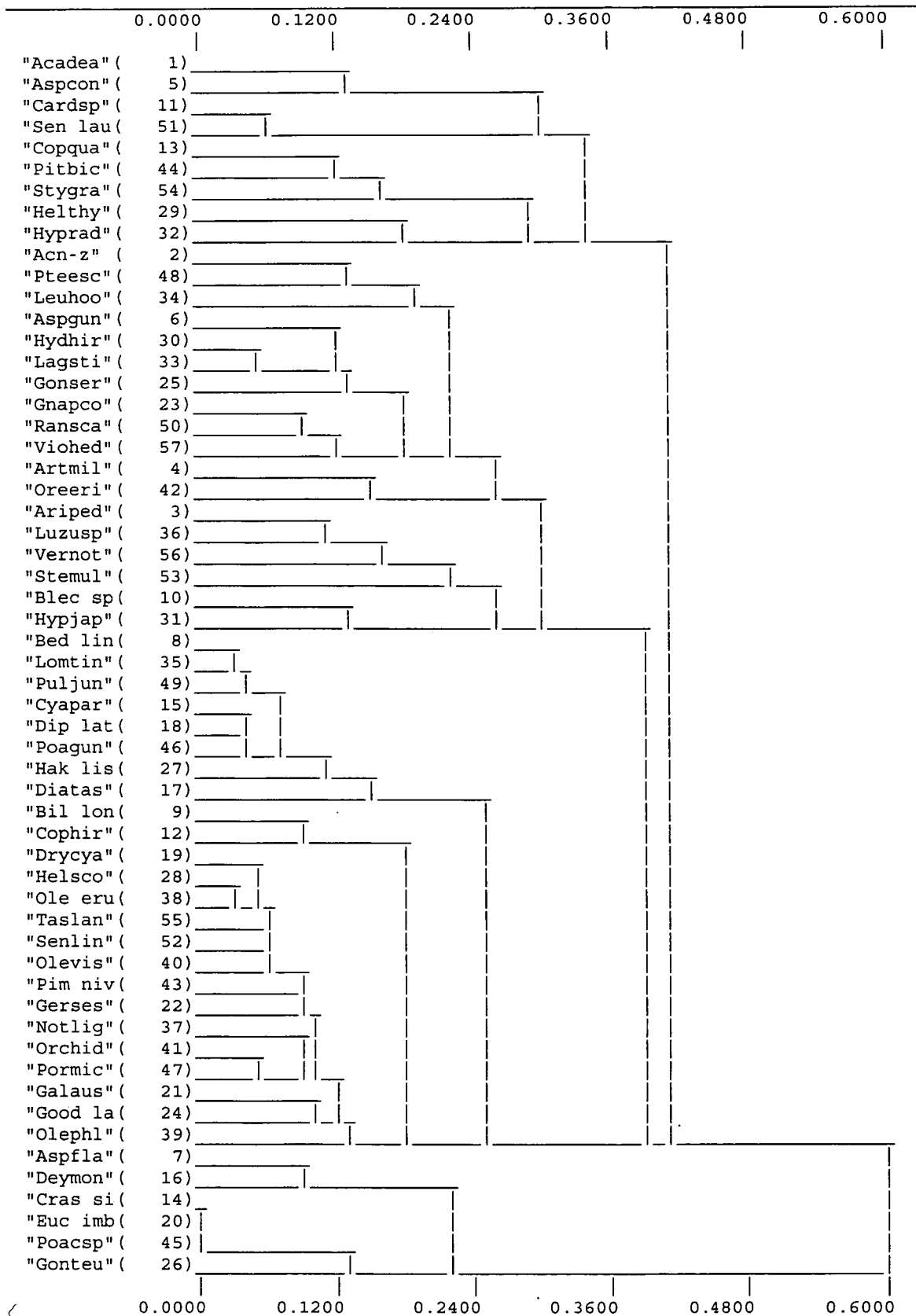


Figure A4.4 Classification dendrogram of the 57 species of Clarence Lagoon shrubby forest. Ten species groups were defined for two-way table (Table 3.4).

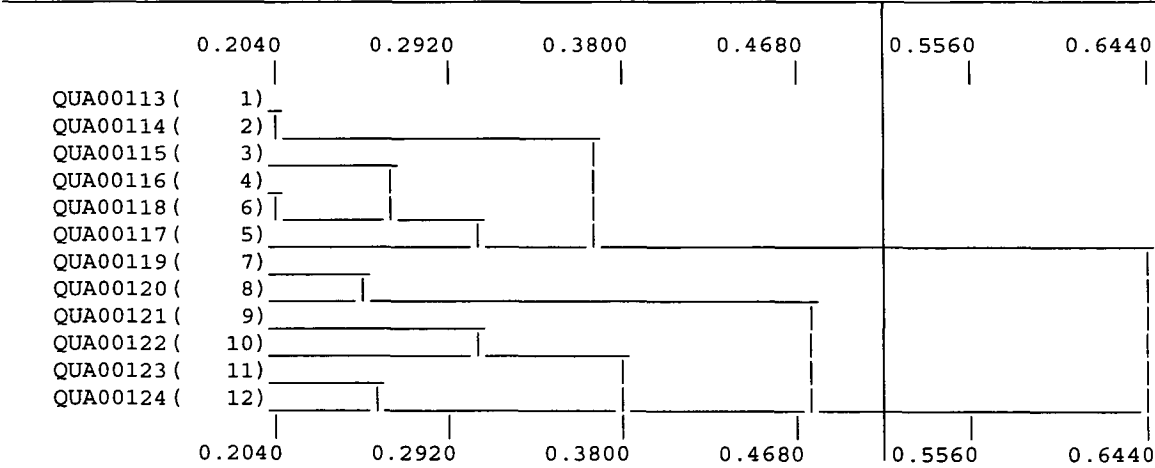


Figure A4.5 Site classification dendrogram of the 12 quadrats of Mt Franklin grassy forest showing cut-off line defining two groups. Group 1, quadrats 113-118 = logged coupe 1977/78; Group 2, quadrats 119-124 = control forest.

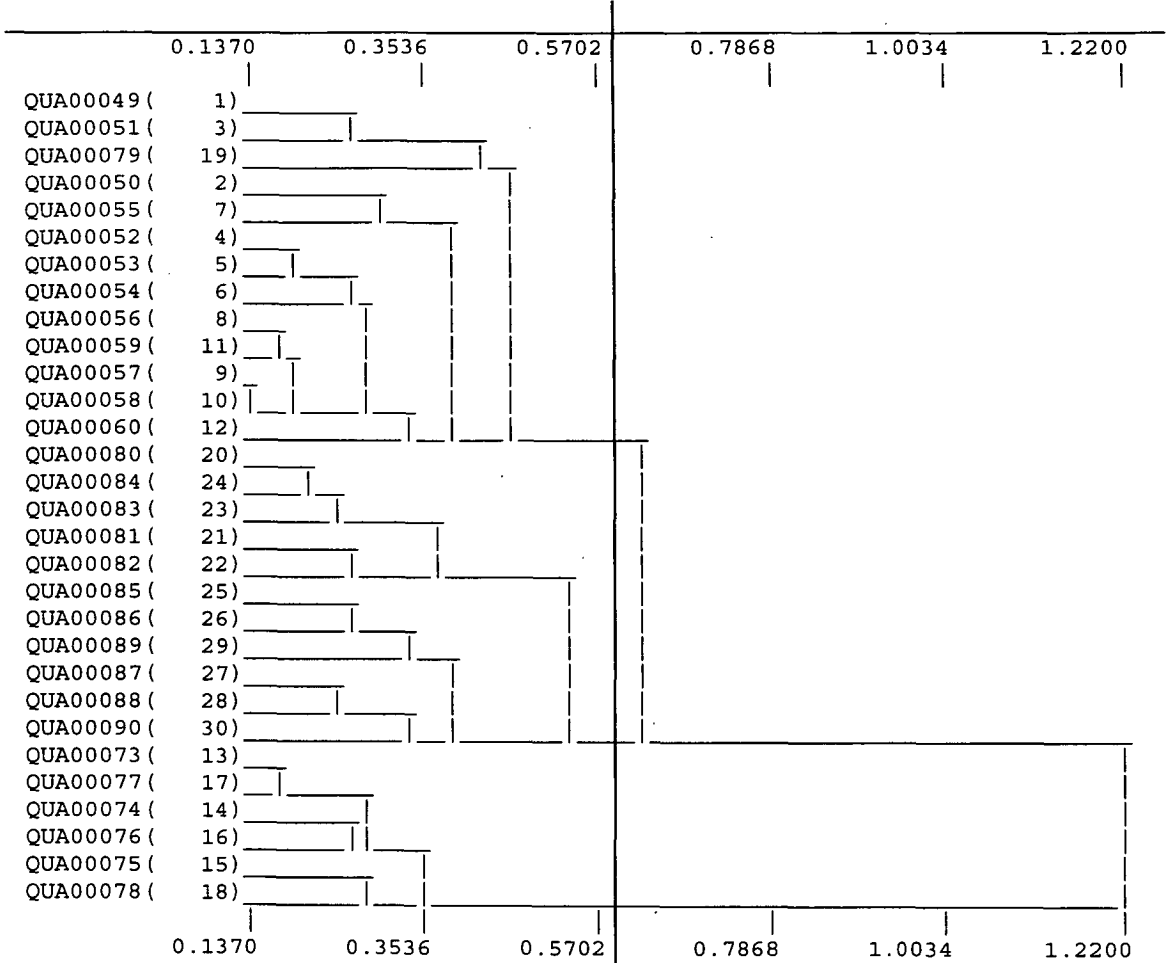


Figure A4.6 Site classification dendrogram of the Tarraleah plantations showing cut-off line defining three groups. Group 1, quadrats 49-60 = 1979 *E. delegatensis* plantation; Group 2, quadrats 80-90 = control forest; Group 3, quadrats 73-78 = 1994 *E. nitens* plantation.