The vegetation ecology of

Tasmanian dry closed-forest

by

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Declarations

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Abstract

The subject of this study is a poorly known closed-forest community that occurs as small, disjunct stands in eastern Tasmania. This community has affinities with dry rainforest, a formation that occurs extensively in mainland Australia. There is ongoing debate as to what constitutes Australian rainforest, with most definitions based on the regeneration requirements of the constituent species. A species must be capable of self-replacement in the absence of exogenous disturbance to qualify as a rainforest species. The present study aims to answer the questions:

1. Where does dry closed-forest occur in Tasmania and what environmental factors influence this distribution?

2. How does the floristic composition of this community vary across its range?

3. What are the modes of regeneration of the major tree species of this community and why is *Eucalyptus* absent?

4. What are the conservation management and reservation requirements of the community?

Additionally, an overarching aim concerns whether the study community can be considered rainforest.

To achieve these aims the study: documents the geographic variation of dry closed-forest stands and test the hypothesis that distributional characteristics are related to fire-avoidance by mapping the location and characteristics of stands and measuring variables of the local stand environment; documents the floristic variation of dry closed-forest in relation to environmental variables by conducting a survey of the vascular plant species composition and stand environment; determines if this community requires exogenous disturbance for perpetuation, by studying the spatial arrangement and regeneration characteristics of major canopy species within stands; and investigates why *Eucalyptus* is absent from this community by conducting experiments of the germination and growth of *Eucalyptus* and some comparative dry closed-forest species in a number of soil treatments.

One hundred and eighty three stands were mapped. Stands occupied a number of different topographic and edaphic situations that afford protection from fire. Six floristic sub-communities were differentiated, and a number of environmental variables shown to significantly influence this variation. Floristic similarities were shown to exist between this community and other Australian rainforest and wet-forest communities. Stands not recently disturbed proved to be dominated by self-replacing species, while early-successional stands consisted mainly of species requiring exogenous disturbance for regeneration. There was no significant segregation of individuals either within or between species, however seedlings of bird-dispersed species were clustered around large trees. The germination experiments indicated that limitations on *Eucalyptus* establishment are related to soil properties (particularly damping-off fungi) and competition with dry closed-forest species.

Tasmanian dry closed-forest appears to be a community that has some affinity with rainforest in terms of distribution, floristic composition, structural attributes and regeneration strategy. However, the identification of a number of successional stages of this vegetation type, that require fire for the establishment of a number of key species, brings into question the status of this vegetation as rainforest. This only highlights the challenges present in attempting to define Australian rainforest vegetation.

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Chapter 1 - General Introduction

Australian rainforests

At the broadest level Australian rainforest has been divided into four main sub-formations of tropical rainforest, subtropical rainforest, temperate rainforest and dry rainforest (Baur 1965). It is the last of these sub-formations that is the focus of the present study. Gillison (1987) succinctly refers to dry rainforest as a closed forest formation that has developed in response to a regular seasonal rainfall deficit. In the present study the term dry closed-forest (*sensu* Specht 1970) is used for this community in preference to dry rainforest. The distribution of dry closed-forest in Australia follows a rough arc extending from the southeast corner of the continent, up the east coast and across the north into northwest Western Australia (Figure 1.1). Recently, newly recognised dry closed-forest stands in eastern Victoria have extended this distribution further south (Cameron 1992; Peel 1999). A similar pattern is seen in the distribution of Australian rainforest in general; however, the drought tolerance of dry closed-forest allows it to extend further inland into lower rainfall areas than other rainforests.

Figure 1.1 Potential distribution of dry rainforest in the Australia/ Papua New Guinea (PNG) region based on bioclimate (after Gillison (1987)).

Australian rainforest occurs mainly as disjunct stands, with few relatively large areas. The reduction of a once more extensive rainforest cover to a fragmented distribution has been an ongoing process since Australia broke away from the super-continent Gondwana around 50 million years ago (Hill 1994). The break-up of Gondwana led to the formation of a southern circumpolar current, which caused a cooling of temperatures, and a general reduction in rainfall that also became more erratic. The drier climate favoured an increase in the flammable sclerophyll component of the flora, and led to an increase in the fire frequency, resulting in a decline in rainforest (Hill 1994). Since European settlement of Australia, and associated clearing and burning, the extent of rainforest has been even further reduced, and it is estimated that 30 % of our pre-European rainforest cover has been destroyed (Australian Native Vegetation Assessment 2001). Rainforest now· occupies fire-protected refuges in the fire-dominated Australian landscape (Bowman 2000).

What determines patterns of Australian rainforest distribution?

Discussion of environmental influences on the distribution of Australian rainforest commonly centres on the role of climate, edaphic properties, topography, and fire (Webb & Tracey 1981; Floyd 1989; Bowman 2000). The relative importance of each of these factors in determining rainforest distribution is the subject of conjecture, and it is likely that environmental controls on the distribution of rainforest arise through a complex interrelationship of these factors.

The broad-scale distribution of rainforest is influenced by climate, and in particular by rainfall (Floyd 1989). Climate also influences the occurrence of the basic sub-formations of tropical, subtropical, temperate, and dry rainforest (Baur 1965).

Edaphic properties influence rainforest distribution by supporting rainforest development in those parts of the landscape that have favourable moisture and nutrient levels. For example, gullies often support rainforest because they are a collecting point in the landscape for soil, nutrients, and water. It is possible that the shallow root system of many rainforest trees limits rainforest to edaphically

favourable refuges because of an inability of these trees to survive on less favourable sites during dry periods (Barrett *et al.* 1996).

Rocky sites, either with surrounding cliffs or "rock-mulch", often provided topographic refuge for dry closed-forest. This association is common, and numerous references to it can be found in the literature (Webb & Tracey 1981; Clayton-Greene & Beard 1985; Kirkpatrick *et al.* 1987; Kirkpatrick *et al.* 1988; Ash 1988; Williams 1993; Peel 1999 among others). In addition to its inherent non-flammable properties, rock-mulch also limits grass growth that can fuel fires during the dry season in monsoonal northern Australia (Kirkpatrick *et al.* 1987).

In marginal rainforest areas of eastern Australia rainforest mainly grows on southerly aspects (Fisher 1985; Neyland 1991; Barrett & Ash 1992) and often occur as "arrow-head" scrubs aligned southeast to intercept rain-bearing winds (Webb & Tracey 1981; Fisher 1985). Southerly aspects avoid the worst of desiccating winds and associated fires, and maximise moisture retention. A strong differential in light and water levels exists between north and south aspects. Holland & Steyn (1975) estimated that polar and equatorial facing aspects at the latitude of Tasmania represent a variation in latitude of 20 degrees. Substantial radiation differences, which influence moisture levels, also exist between northern and southern aspects in monsoonal northern Australia during the dry season (Kirkpatrick *et al.* 1988).

One of the primary restrictors of rainforest distribution in Australia is fire (Bowman 2000). Rainforest is commonly associated with topographic situations that minimise the potential for fire damage. However, rainforest can develop and persist in non-refuge situations provided that the area has a long enough fire-free period. Examples of rainforest expansion in the period since European settlement have been attributed to a cessation of Aboriginal burning (Bowman *et al.* 1990; Harrington & Sanderson 1994; Fensham & Fairfax 1996). However, in some cases it is difficult to separate the effects of changed fire regime and climate change on rainforest expansion (Hopkins *et al.* 1996). In sub-coastal Queensland relatively large areas of dry closed-forest stands occur on edaphically favourable deep basalt soils without topographic fire protection (Webb and Tracey 1981). These stands are surrounded by dry grassy forest and woodland, which produce little fuel for a fire.

Therefore, even though fire in this environment is a common occurrence, the impact upon stands is only minor (Webb and Tracey 1981). The apparent edaphic control on rainforest distribution could partly reflect the underlying necessity for rainforest to avoid fire (Bowman & Fensham 1991). Rainforest growing in gullies and valley bottoms is at less risk from fire damage because fire moves downslope with less intensity than it does upslope. This is probably due to preheating of fuel ahead of the fire when moving upslope, which enhances the rate of spread and intensity of the fire (Unwin *et al.*1985). This excludes most rainforests from occurring upslope of, and contiguous to, pyrophytic (fire-loving) vegetation (Ash 1988).

Floristic composition of Australian dry closed-forests

The floristic composition of dry closed-forest in northern Australia has been investigated in the Northern Territory (Russell-Smith 1991), Western Australia (Kenneally *et al.* 1991), and inland north Queensland (Fensham 1995). Dry closed-forest in monsoonal northern Australia has close floristic affinities with the tropical rainforests of the Palaeotropics (Whitmore 1984; Barlow and Hyland 1988), and it is thought that this rainforest type developed relatively recently from tropical rainforest (Barlow and Hyland 1988). In New South Wales, Floyd (1990) describes the floristic differentiation of dry closed-forest alliances. The most southerly Australian dry closed-forests in southern New South Wales and eastern Victoria have considerable floristic similarities with each other (refer to species lists in Cameron 1992; Keith & Benson 1988; Keith & Bedward 1999). Interestingly, there are a number of genera that are shared between the flora of arid inland regions and the dry closed-forests of Victoria and New South Wales (Cameron 1992). Along with fossil evidence (Kershaw *et al.* 1991), this relationship may be an indication of a past more widespread dry closed-forest distribution, which has contracted as the continent has dried.

Regeneration of rainforest species

The Tasmanian rainforest species definition specifically refers to the ability to perpetuate itself (either vegetatively or from seed) in the absence of fire disturbance within forests dominated by one or more of the rainforest canopy species listed in

the Tasmanian rainforest definition (Jarman & Brown 1983). A more general Australian rainforest species definition is given by Lynch & Neldner (2000), who define rainforest species by their ability to regenerate vegetatively or by seed under the closed canopy of a rainforest or in an area of small-scale disturbance caused by a natural rainforest ecosystem process such as a single tree-fall (Lynch & Neldner 2000). Jarman & Brown (1983) also make note of a group of "dubious rainforest species", so-called because these species occur in the early stages of developing rainforest following disturbance. Although some of these species show the capacity to regenerate beneath a closed canopy, they also commonly regenerate with the aid of fire disturbance.

The regeneration of rainforest species in disturbed areas is often clumped around the base of large trees, not necessarily of the same species. This is most likely to be the result of bird-assisted seed dispersal (Fensham & Butler 2004). Seedling germination beneath bird perches may aid in the regeneration of degraded ex-rainforest areas (Toh *et al.* 1999) and in rainforest establishment in new areas (Fensham & Butler 2004; Kirkpatrick *et al.* 2004). Numerous studies have used spatial analysis techniques to examine the spatial arrangement of plant species in order to answer questions related to regeneration strategies and habitat preference (e.g. Larson & Bliss 1998; Nanami *et al. 1999*; Grau 2000; He & Duncan 2000; McDonald *et al.* 2003; Tirado & Pugnaire 2003). The only study of spatial plant patterns that is specific to Australian dry closed-forest is that of Fensham & Butler (2004).

Is Tasmanian dry closed-forest rainforest?

The Tasmanian dry closed-forest investigated in the current study has not been formally recognised as part of the Tasmanian rainforest estate. According to Jarman & Brown (1983) Tasmanian rainforest refers to forest that is dominated by one or more of *Nothofagus, Atherosperma, Eucryphia, Athrotaxis, Lagarostrobos, Dacrydium, Phyllocladus* and *Diselma*. The oft-cited figure of 70-100% canopy cover for Australian rainforests (Specht 1970) is not inluded in the Tasmanian definition, where communities with a relatively open canopy such as Tasmania's alpine gymnosperm forests are classified as rainforest (Jarman & Brown 1983).

There are numerous Australian rainforest definitions (Webb 1959; Baur 1965; Jarman & Brown 1983; Floyd 1990). However, no overarching rainforest definition has been accepted that encompasses all of the rainforests of Australia. This is due in part to the difficulty of defining part of what is essentially an ecological continuum between fire-dependent and fire-intolerant vegetation (Lynch & Neldner 2000). There has been a continuing debate on the Australian rainforest definition, partly fuelled by the high cultural significance of this vegetation type in Australia (Cameron 1992; Kirkpatrick 1992; Bowman 2001).

A number of dry closed-forest trees are regarded as rainforest species by Jarman & Brown (1983), including *Notelaea ligustrina*, *Pittosporum bicolor*, *Coprosma quadrifida* and *Zieria arborescens*. However, many of the most common trees found in Tasmanian dry closed-forest are on the "doubtful" rainforest species list of Jarman & Brown (1983), presumably because of a wide occurrence that includes vegetation communities that are obviously fire-determined. Kirkpatrick (1992) has suggested that some of these species may be gap-phase regenerators in the absence of fire. Regeneration in small gaps or beneath a closed-canopy is a feature of a number of Tasmanian rainforest trees such as *Phyllocladus asplenifolius* (Read & Hill 1988), *Athrotaxis selaginoides* (Cullen 1987, Cullen 1991), and *Athrotaxis cupressoides* (Cullen & Kirkpatrick 1988). Other rainforest species may use large-scale disturbance events to increase their dominance of stand, as has been suggested for *Sloanea woolsii* in subtropical rainforest (Debski *et al.* 2000).

The definition of rainforest species based on the capacity for regeneration in the absence of exogenous disturbance has its own problems. One needs only to read Bowman's (2001) response to Lynch & Neldner's paper, and Neldner and Lynch's (2001) subsequent response, to understand the problems associated with this definition, as many other supposedly non-rainforest tree species also seem to exhibit this quality. There has been a continuing discussion of obstacles to developing a coherent and workable Australian rainforest definition (Kirkpatrick 1992; Bowman 2001). It has been suggested that rainforest should be defined as fire-sensitive forest (Cameron 1992). He noted that even though some other fire-sensitive forests exist in Australia, such as mangrove vegetation or inland communities dominated by *Callitris* and *Allocasuarina*, they would not be

classified as rainforest because they do not meet the floristic and structural specifics of an integrated rainforest definition (Cameron 1992). Previous attempts to define rainforest in terms of variables such as climate, floristic composition, structure and physiognomy (Webb 1959; Baur 1965; Jarman & Brown 1983; Floyd 1990) are regionally significant, but may lack national applicability (Lynch & Neldner 2000). The definition has also been influenced by the forestry debate in southern Australia where the status of "mixed-forest" (a wet forest type with both eucalypts and rainforest trees) is defined inside and outside the rainforest definition depending on differing criteria (Cameron 1992). The separation of rainforest plants into primary and secondary species (in successional terms) was suggested by Cameron (1992), therefore eliminating the need for the so-called "dubious rainforest species" listed in (Jarman & Brown 1983). Secondary species are listed as such because they mainly occur in the early stages of rainforest development following disturbance. These species may exhibit at least some capacity to regenerate in the absence of fire, although they also commonly regenerate in rainforest gaps and margins with the stimulus of fire disturbance.

Absence of *Eucalyptus* from rainforest

One of the primary characteristics of the Australian flora is the dominance of *Eucalyptus* across many different communities of forests and woodlands. However, *Eucalyptus* is not a significant component of rainforest. So why is *Eucalyptus* incapable of also dominating this vegetation type? The answer may relate to controls on the establishment of *Eucalyptus*.

Typical of rainforest vegetation, the dense foliage cover and small-gaps of Tasmanian dry closed-forest generally produces a light-limited environment at ground level. The establishment of *Eucalyptus* species in small gaps can be negatively affected because of low light-levels (Ashton & Chinner 1999). Light-limitations also have a detrimental effect on the development of beneficial mycorrhizal fungi associated with the root system of some *Eucalyptus* species, which translates into a reduction in the growth of plants (Ashton & Turner 1979). In addition, at very low light intensities seedlings of *Eucalyptus* can suffer loss to fungal attack (Ashton & Turner 1979; Withers 1979). This response is not unique

to *Eucalyptus*, and tree species of northern hemisphere woodlands have also been reported to suffer considerable seedling casualties due to the effects of damping-off fungi (Grime 1959; Wardle 1959).

It has been reported that the germination of some *Eucalyptus* species is inhibited when the soil is subjected to water stress (Zohar *et al.* 1975; Bachelard 1985). Moisture stress of establishing *Eucalyptus* individuals may also occur through competition for surface water between *Eucalyptus* and broad-leaved shrubs. Ashton (1976c) reports that thinning of young regenerating *E. regnans* stands is linked to intense root competition with the understorey shrub *Pomaderris aspera*.

In general, fire has a positive effect on the germination and establishment of *Eucalyptus*. A severe fire will set back rainforest vegetation, allowing light to reach the soil, which may lesson the impact of fungal dieback on *Eucalyptus* seedlings in low-light conditions (Ashton & Turner 1979). It is also been documented that heat and smoke of a bushfire positively stimulates the germination of a number of species, including *Eucalyptus* (Roche *et al.* 1997; Tien *et al.* 1999; Lloyd *et al.* 2000, Read *et al.* 2000; Tang *et al.* 2003).

Aims and approaches of this study

The present study investigates a little-known Tasmanian dry closed-forest community that occurs in the drier parts of eastern Tasmania. The primary questions the thesis investigates are:

5. Where does dry closed-forest occur in Tasmania and what environmental factors influence this distribution?

6. How does the floristic composition of this community vary across its range?

7. What are the modes of regeneration of the major tree species of this community and why is *Eucalyptus* absent?

8. What are the conservation management and reservation requirements of the community?

To answer these questions four more specific investigations were undertaken, which make up the 4 substantive chapters of the thesis. The chapters that report these investigations are written as papers, resulting in a minor degree of repetition of material. Question 1 is addressed in Chapter 2, which documents the physical characteristics and distributional properties of stands and identifies environmental factors that may influence the nature of stands and their distribution. Question 2 is addressed in Chapter 3, which investigates the floristic composition of dry closed-forest, and aims to explain regional variation in this composition in terms of environment. Also, the floristic composition of Tasmanian dry closed-forest is compared with some other southern Australian closed-forest communities. Question 3 is addressed in Chapters 4 and 5. Chapter 4 investigates the spatial dynamics of dry closed-forest species and examines whether or not the major species of the community are self-replacing. Chapter 5 tests a number of hypotheses on the causes of *Eucalyptus* absence from dry closed-forest vegetation. These relate to soil properties, competition, and the effects of fire. Question 4 is addressed in Chapter 3, and also in Chapter 6. Chapter 6 is a discussion and synthesis of the findings of Chapters 2-5 in terms of the major questions investigated in the present study. The overarching aim of the thesis is to determine whether the community is rainforest. The outcomes of the investigations of Chapters 3, 4, and 5 are each critical to addressing this aim.

There are a number of reasons why this particular community warrants investigation. Dry closed-forest is a widespread feature of the Australian rainforest estate, but only limited ecological investigation of Tasmanian dry closed-forest has taken place to date (Woolward 1983). If this community can be considered to be rainforest, this will be a considerable extension to the range of this sub-formation in Australia. It is important to recognise the floristic and ecological variation of this community across the State, and the response of the community to fire, in order to adequately conserve and manage a representative assemblage of this vegetation type.

Chapter 2 - The nature and distribution of Tasmanian dry closed-forest stands

Abstract

The distribution of dry closed-forest in Tasmania was mapped from aerial photographs. An investigation of the physical characteristics and environment relations of these stands was undertaken. The hypothesis was tested that stands receive protection from fire by the nature of the adjacent northwest topography. One hundred and eighty three stands were identified. The majority of stands were small in size and occured in gullies. Rainfall is relatively low compared to temperate rainforest sites. Variation in physical characteristics of stands was consistently associated with the height of the surrounding topography, for both gully and non-gully dry closed-forest stands. The location of stands was also associated with the height of surrounding land, as well as with its slope and aspect. Dry closed-forest stands occur primarily on southern aspects and where the surrounding slopes are higher and steeper than comparable adjacent sites that do not support this community. These results support the hypothesis that stands receive topographic protection from fire.

Introduction

There is no standard definition for Australian dry closed-forest. The term dry closed-forest (*sensu* Specht 1970) is used in this paper to refer to a number of rainforest formations "that normally reflect a marked response to seasonal variability" (Gillison 1987). Dry closed-forests are known regionally as monsoon rainforest in the tropical north of Australia, softwood scrub and vine thicket in sub-coastal Queensland and New South Wales, and dry rainforest or vine forest generally east of the Great Dividing Range in Queensland, New South Wales and Victoria. Despite having a broad distribution from the tropics to the temperate areas of Australia, most dry closed-forest stands exhibit some climatic, edaphic and topographic similarities. On mainland Australia, dry closed-forest stands are commonly located in fire-protected niches associated with gullies, cliffs, gorges and rock scree (Webb & Tracey 1981; Clayton-Greene & Beard 1985; Kirkpatrick *et al.* 1987; Kirkpatrick *et al.* 1988; Ash 1988; Williams 1993; Peel 1999).

The distribution of rainforest is controlled by the interplay of a number of factors including moisture, topography, and fire regime (Bowman 2000). Australian rainforests are restricted to relatively small refuges in the landscape that are under favourable influence from the controlling factors on distribution. Webb & Tracey (1981) describe four different situations that provide refuge for rainforest in Australia. Three of these refuge types are commonly occupied by dry closed-forest. These are "small, often narrow edaphic isolates", "small, relatively dry topographical isolates", and "topographic, edaphic, climatic isolates", which are a combination of the other types.

"Small, often narrow edaphic isolates" (Webb & Tracey 1981) are locations that can support rainforest because of favourable edaphic conditions. Situations include along streams, on small soaks where the water-table lies close to the surface, on red earths in undulating terrain, in the lee of coastal dune systems, and at the head of gullies in coastal hills (known as "arrow-head scrub"). Soils of edaphic refuges are usually deep, well drained. Gully sites are enriched with nutrients and water by virtue of the funnelling effect of local topography. In the case of coastal dunes, nutrient enrichment occurs through the breakdown of seashells (Webb & Tracey

1981). In southern New South Wales, the restriction of rainforests to edaphically favourable sites may be related to the shallow root system of many of the regions rainforest trees, which are inadequate to meet moisture demands during drought (Barrett *et al.* 1996).

Additionally, the role of fire in apparent edaphic-based distribution patterns must be considered. In northern Queensland, rainforest is rarely found upslope of pyrophytic vegetation (Ash 1988). Apart from the deep soil and accumulation of nutrients that are features of gully situations, rainforest in a gully is also topographically protected from fire. An advancing fire front moves uphill more rapidly than downhill and hence the potential for impact on rainforest boundaries is generally greater for rainforest occurring uphill of pyrophytic vegetation (Ash 1988). The increased intensity and rate of spread of a fire burning uphill is primarily related to the preheating of fuel (Unwin *et al.*1985). On the south coast of New South Wales the potential for intense fires is relatively high, and rainforest in restricted to small isolates in valley bottoms and on southern slopes. Rainforest distribution in gullies and valley bottoms is explained by Barrett & Ash (1992) to be partly the result of plant physiological responses to light, water and nutrients, but also influenced by differences in fire frequency and intensity across varying topographies. Bowman (1992) found that dry monsoon forest soils have higher but not significantly different water contents than the surrounding soils of the eucalypt savanna, which further supports the suggestion that moisture levels are not the primary determinant of dry closed-forest distribution patterns. Any difference most likely reflects changes in the microclimate rather than an edaphic discontinuity at the community boundary (Bowman & Fensham 1991; Bowman 1992).

"Small, relatively dry topographical isolates" (Webb & Tracey 1981) are rainforest refuges composed primarily of rocky situations. Dry closed-forest occurrence on rocky ground appears to be primarily a strategy for fire avoidance rather than for any edaphic benefit. It has been suggested by Kirkpatrick *et al.* (1988) that the catchment effect of rocky ground can be offset by shallow soil formation, resulting in low soil moisture levels, particularly in the upper reaches of a catchment where extensive areas of bedrock are exposed. In lower parts of a catchment where weathered rock accumulates, such as on scree slopes, the capacity for soil water

retention improves, as fissures between rocks aid in the funnelling and accumulation of water and organic material. Rocky ground also inhibits the establishment of grasses that can be a major source of fuel for fires during the dry season (Kirkpatrick *et al.* 1987). Typically dry closed-forest has an open understorey with low fuel loads. Williams (1993) describes dry closed-forest of the Manning River valley in northern New South Wales as having a very open understorey devoid of any ground cover, often consisting of bare earth or "rock-mulch".

At non-rocky stands the dense canopy of a dry closed-forest stand usually discourages grass growth and hence produces low fuel loads with little potential for carrying a ground fire. However, repeated burning can kill trees, open up the canopy and enable the infiltration of grasses. The high-fuel load of grasses increases the likelihood of further fires, thus aiding the further degradation of a stand (Bowman 1991). Dry closed-forest can persist and even expand at non-topographically protected situations provided that the fire-frequency is kept to a minimum. An example of this is the apparent expansion of dry closed-forest clumps on Holocene coastal grasslands at Cobourg Peninsula in the Northern Territory. This expansion is thought to be the result of removing a former fire management regime based on regular firing of the grasslands (Bowman *et al.* 1990a).

"Topographic, edaphic, climatic isolates" (Webb & Tracey 1981) are a refuge type that combine features of the other refuge types. Examples occur in low rainfall areas of sub coastal Queensland on relatively moist hills or mountains, with typically deep and fertile basalt soils. In drier areas, extensive areas of rainforest occur on red earths without topographic fire protection. These patches are surrounded by dry grassy forest or woodland that produces little fuel, and although fires in this environment are frequent they are of low intensity (Webb & Tracey 1981).

Dry closed-forest stands can occur in areas that receive an annual average rainfall of only 600 mm (Webb & Tracey 1981). In some topographic situations, rainforest can supplement low rainfall with other sources of moisture. For example, climatically marginal subtropical rainforest growing at the crest of the Liverpool

Ranges in New South Wales supplements rainfall by fog stripping (Fisher 1985). The stands are situated at the head of gullies that have aspects that are exposed to moist southeasterly winds and low cloud.

Dry closed-forest stands commonly occur on nutrient-rich soils in eastern Australia, and are often associated with basalt flows (Ash 1988; Williams *et al.* 1984). However, in the Northern Territory this community occurs widely on soils of lower nutrient status, such as those derived from sedimentary rocks (Russell-Smith 1991). Bowman *et al.* (1990b) argue that monsoon forest has more fertile soils than those of the surrounding vegetation communities because efficient nutrient cycling and gradual accretion, this being enhanced where soil moisture is higher. Fire is also discouraged in vegetation growing on moist soils. Repeated fires reduce soil fertility (Jackson 1968; Bowman & Minchin 1987) and therefore monsoon forest in relatively moist, fire-protected sites avoid nutrient loss.

Rainforest growing in a marginal environment seems to favour an aspect between south and east (Fisher 1985; Neyland 1991; Barrett & Ash 1992). Under such circumstances stands commonly occur in the upper reaches of streams as "arrow-head" scrubs (Webb & Tracey 1981; Fisher 1985). Where rainforest grows on a steep southerly slope, additional fire protection from a watercourse on the lower side of the stand is common (Neyland 1991). This aspect preference may be a consequence of the differences in moisure and light that exist between southern and northern aspects. Holland & Steyn (1975) estimated that polar and equatorial facing aspects at the latitude of Tasmania represent a variation in latitude of 20 degrees. Substantial radiation differences exist between southern and northern aspects in the summer dry temperate climate zone of southern Australia (Kirkpatrick & Nunez 1980) and in monsoonal northern Australia during the dry season (Kirkpatrick *et al.* 1988).

Numerous studies on Australian rainforests have been conducted that address a limited suite of the factors that may influence rainforest distribution. However, there are few synthetic studies that have looked at the influence of all of these factors on rainforest distribution (see Bowman 2000 for a comprehensive review of these factors). The present study investigates the influence that a broad range of

environmental factors may have on the distribution of Tasmanian dry closed-forest.

This aims are to:

- document the physical characteristics of Tasmanian dry closed-forest stands

- document the distributional properties of stands

- identify environmental factors that may influence their physical nature and distribution.

The hypothesis was tested that stands are afforded protection from fires coming from the northwest. A significantly greater height or slope of land to the NW compared to the heights and slopes of land in other directions would provide support for this hypothesis.

In the present study, the stand properties of area and length were identified for analysis against stand environmental variables. Logically we can assume that stand area is a measure of site suitability, with larger dry closed-forest stands occurring where the environment is most suitable. Generally, riparian dry closed-forest stands have a greater length dimension compared to other stand shapes. Therefore, identifying which environmental variables most strongly influence stand length should tell us what environmental controls exist relating to the formation of riparian dry closed-forest stands.

Methods

One hundred and eighty three stands were examined. These are located in the eastern half of Tasmania and extend from Flinders Island to near Dover in the south of the state (Figure 2.1). A facies of the community that is the by-product of disturbance of wet eucalypt forest (Harris & Kitchener 2005) exists in the northwest and west of the state and is mapped in the TASVEG mapping program of the Tasmanian Department of Primary Industries, Water, & Environment within the mapping units *Notelaea- Pomaderris- Beyeria* forest (NNP) or Broad-leaf Scrub (BSR) (Harris & Kitchener 2005). These northwest stands were not included in the present study because, although the species composition is similar to eastern dry closed-forest, they are essentially a successional stage in the regeneration of wet eucalypt forest following fire disturbance.
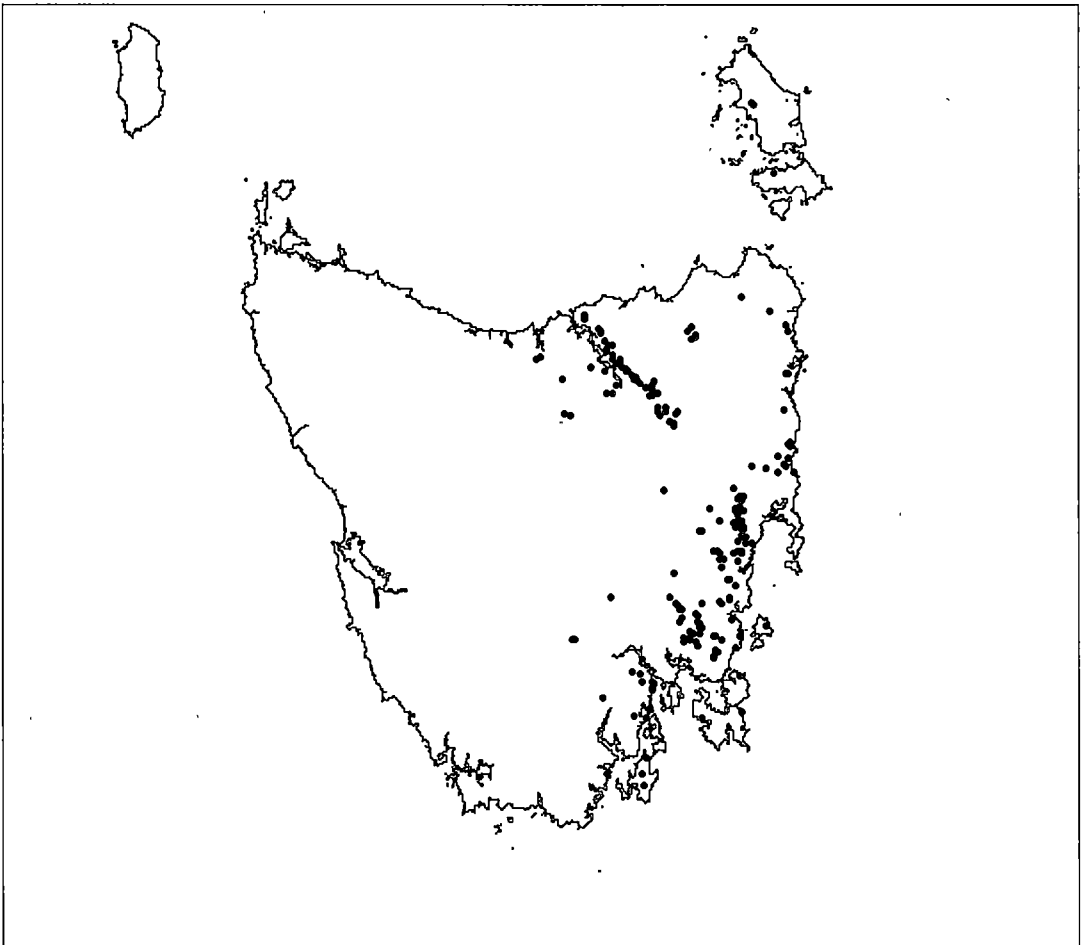
Figure 2.1 Location of 183 dry closed-forest stands mapped in the present study.

Vegetation dominated by *Callitris* and *Allocasuarina* occurs on parts of the east coast of Tasmania. There is some evidence of continuous regeneration in these species (Kirkpatrick 1989, Bowman 2001), which gives them potential rainforest species status. Despite this, the relatively open canopy of these communities (considerably less than the 70-100% projective foliage level suggested by Specht (1970) for closed-forest communities) excluded them from the present study. In aerial photograph interpretation, dry closed-forest was readily discriminated from eucalypt forest by having a dark green colour and uniformly-textured closed-canopy. The community could potentially be confused with temperate rainforest. Unlike dry closed-forest, in aerial photographs the canopy of temperate rainforest is uneven, often with obvious conical emergent trees of *Atherosperma moschatum* (Sassafras). Field verification revealed that a small number of the dry closed-forest stands identified from aerial photographs were in fact *Acacia melanoxylon* (Blackwood) forest or *Melaleuca* scrub. These stands were excluded from analysis. The possibility remains that a few of the stands included in the analysis are not dry closed-forest, as not all mapped stands could be verified on the ground.

The physical characteristics of stands

Several measurements were made of stand characteristics (Table 2.1). These variables were stand area, length, length from highest elevation to middle, length from lowest elevation to middle, width, and stand altitudinal range. The measurement of stand area refers to the area occupied by a stand when viewed vertically from above. The surface area of stands would be considerably larger than this figure on steep slopes. The centre of the stand was identified as the point where the width and length axes intersect. Stand length was measured along the axis that crosses the contours, and stand width was measured perpendicular to this axis.

Table 2.1 Abbreviations and details of measurements, both raw and derived, of local stand environment used in this study

Variable Abbreviation	height rs	height ls	height NW	height mr	dis pro top
Full Variable description	*Height of land on right side of gully (m)*	*Height of land on left side of gully (m)*	*Height of land in NW direction (m)*	*Height of land of main protective ridge (non-gully only) (m)*	*Distance between left and right side protective features (m)*

Variable Abbreviation	diff heights	slope rs	slope ls	slope NW	slope mr
Full Variable description	*Difference in heights of protective features (max height - average heights) (m)*	*Slope on right side of gully (°)*	*Slope on left side of gully (°)*	*Slope in NW direction (°)*	*Slope of main protective ridge (non-gully only) (m)*

Variable Abbreviation	nor	eas	alt	asp	anpr
Full Variable description	*northing*	*easting*	*Stand altitude (m)*	*Aspect relating to moisture gradient (scale of 0 – 180 where 0 is SE and 180 is NW)*	*Mean annual precipitation (mm)*

Variable Abbreviation	drqpr	maxtempwaqu	mintempcoqu		
Full Variable description	*Mean precipitation of the driest quarter (mm)*	*Mean maximum temperature of the warmest quarter (°C)*	*Mean minimum temperature of the coldest quarter (°C)*		

Stand aspect was the aspect that the majority of the stand faces. It was measured on a scale from 0 (favourable = SE) to 180 (poor = NW). In Tasmania, destructive fire-fronts are driven by hot summer winds blowing from the NW. This is the most fire-prone aspect and therefore the scale is based around NW being an unfavourable aspect for dry closed-forest development and the opposite aspect of SE being the most favourable aspect for dry closed-forest development.

Figures 2.2 and 2.3 display how height measurements were made for gully and non-gully situations respectively. The area of investigation was designated to include all land within 1 km of a stand. This area is sufficient to include the vast majority of land that has an influence on the distributional characteristics of dry closed-forest stands. The intersection point of the length and width axes was used to mark the

core of a stand and from this point the height and slope of surrounding land was measured. Height was measured either to the highest point on the topographic feature or to where there was a break in slope, defined as a slope of less than 12.5 degrees. Measurements made of height and slope for gully situations were: height of the topographic feature on the left side of the gully (facing downstream), height of the topographic feature on the right side of the gully, and height of the protective ridge or peak in a northwest direction. This height is defined as the highest point in that segment of aspect between 300 and 330 degrees. For stands occurring in non-gully situations such as beneath a cliff, the left and right side measurements were not suitable. Instead, along with the height of the protective ridge or peak in a northwest direction, the height of the main protective ridge was measured. For each measurement of height the associated slope was determined using the following trigonometric formula:

$$\theta = \left(\frac{e}{d}\right) Tan^{-1}$$

where e is the difference in elevation between the height of the particular topography and the centre of the stand and d is the distance from the top of the topographic feature and the centre of the stand.
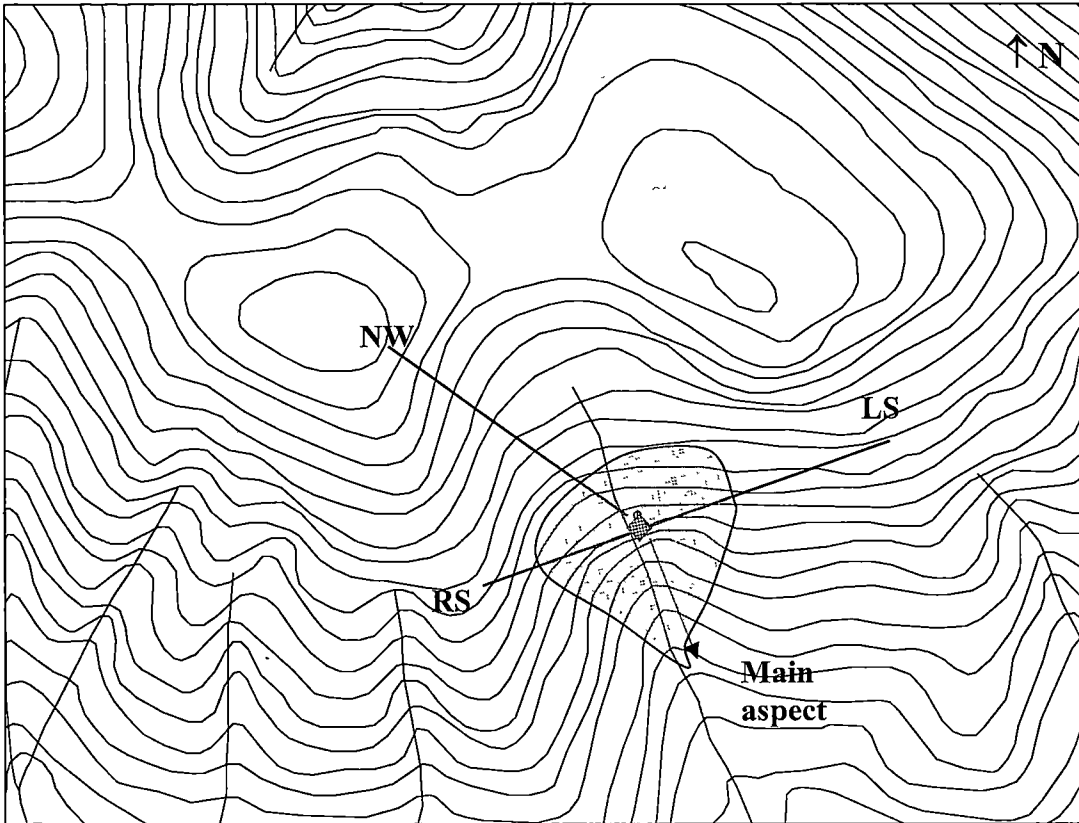
Figure 2.2 Measurements for dry closed-forest stands occurring in gully situations.
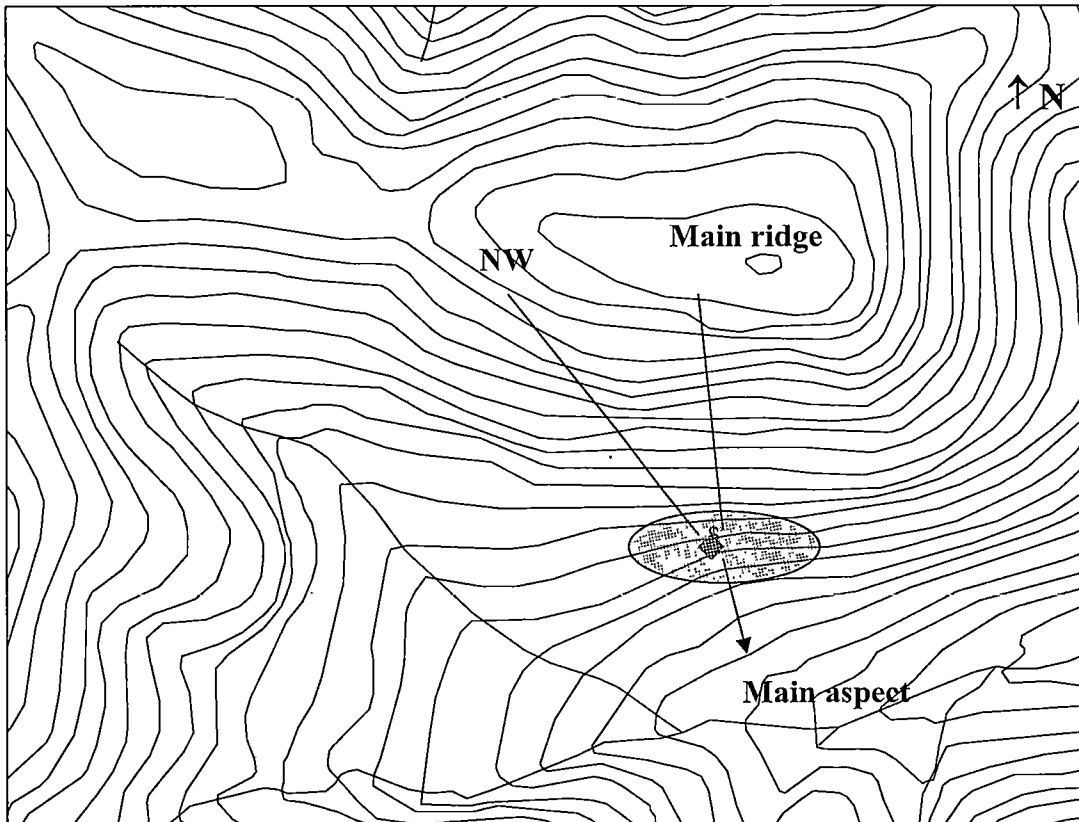
Figure 2.3 Measurements for dry closed-forest stands occurring in non-gully situations.

A measure "evenness of protection" was derived from the original height measurements. Evenness of protection is a measure of the height discrepancy between the highest point in the land that surrounds a gully stand and the other height measurements. This purpose of this measure is to identify stands with poor protection in any of the three directions. Each stand was assigned to one of: typical gully; deep gully; steep slope with a southern aspect; riparian; beneath cliffs; and miscellaneous. A deep gully was discriminated from a typical gully by having none of the height measurements of the surrounding land less than 50 m.

Testing the 'stands are protected from fire by NW topography' hypothesis

Paired t-tests were performed for each combination of height measurements (left side/right side, left side/NW direction, right side/NW direction) and for each combination of slope measurements (left side/right side, left side/NW direction, right side/NW direction). Distributions were examined and paired t-tests of significant differences among heights and slopes were performed in MINITAB version 14 statistical software. The null hypothesis is accepted in all analyses if $p > 0.05$.

Influences on the physical nature of stands

This section of the study aimed to identify stand environmental variables that may influence the physical nature of dry closed-forest stands. Statistical analysis of all data was performed using MINITAB version 14 statistical software. Correlations between stand environmental variables were examined to eliminate any redundant variables. For gully dry closed-forest stands multiple regressions were performed of stand area against stand environmental variables and stand length against stand environmental variables. For non-gully stands a multiple stepwise was performed of only stand area against stand environmental variables. Riparian patches only occur in gully situations and therefore stand length regression analysis was not applicable. All data were tested for normality and appropriately transformed before analysis. The default settings of MINITAB were used for the regression procedure, which is a forward and backward method with a cut-off alpha-value of 0.15. Individual linear relationships were also examined between stand physical variables

and stand environmental variables.

Influences on the location of stands

A subset of dry closed-forest locations was selected from the 185 dry closed-forest localities mapped. These were for the purpose of matching with adjacent locations not supporting dry closed-forest. The selection was based on how easy and confidently a paired location could be identified for a particular dry closed-forest site. If a matched pair was difficult to assign the dry closed-forest site was excluded from the subset. The location of the paired site for a particular dry closed-forest locality was selected according to the following procedure:

Within 1 km radius of the location of the dry closed-forest locality;

- All similar geomorphic situations were identified

- The location with the most similar aspect was selected

- For gully stands, it was also necessary to position the paired site to match the specific location of the dry closed-forest stand within its geomorphic situation. This was achieved by measuring the average slope of the watercourse on which the dry closed-forest stand occurs and to then position the matched site where the equivalent slope occurs in the matched geomorphic situation.

The variables measured were aspect relating to moisture gradient (scale of 0 – 180 where 0 is SE and 180 is NW), height of the main protective ridge (upslope of stand; non-gully stands only), height of the right side of gully (gully stands only), height of the left side of gully (gully stands only), height in NW direction, slope of main protective ridge (non-gully only), slope of right side of gully (gully stands only), slope of left side of gully (gully stands only), and slope in NW direction. Paired t-tests of differences in these variables between dry closed-forest sites and matched sites were performed in MINITAB version 14 statistical software. Slopes were measured according to the method detailed previously in this chapter under the "physical characteristics of stands" subsection.

Results

The physical nature of stands
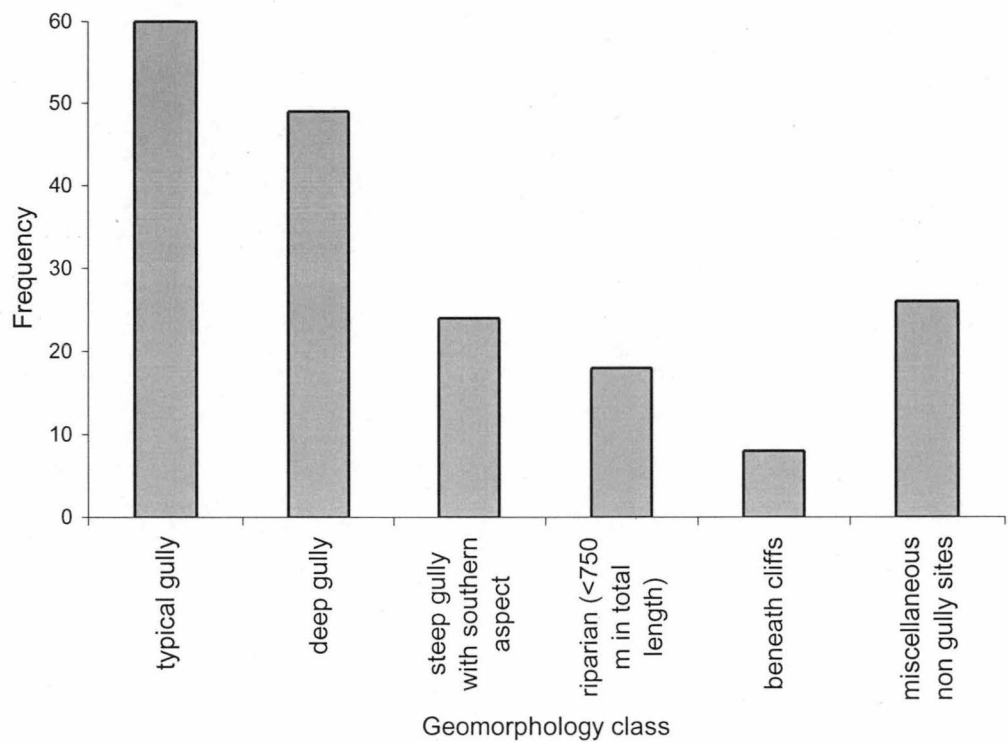
Figure 2.4 Frequency of the geomorphological situations of Tasmanian dry closed-forest stands (N = 183).

Of the dry closed-forest stands mapped, 82% occur in gully situations (gully, deep gully, steep gully with S aspect, and riparian), while a relatively small number of stands occur in non-gully situations including beneath cliffs, on flat benches on the side of mountains, and across a steep south or southeast-facing slope (Figure 2.4, Plates 2.1- 2.5).
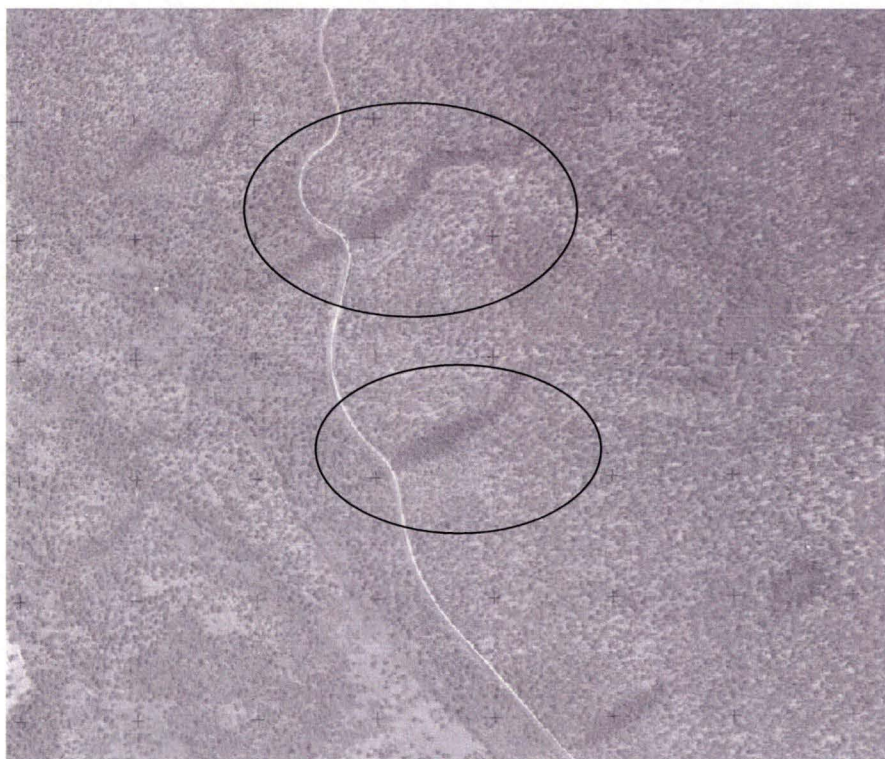
Plate 2.1 Typical gully dry closed-forest (eastern side of Tamar River).

Plate 2.2 Dry closed-forest in a deep gully (Truganini Reserve, near Hobart).
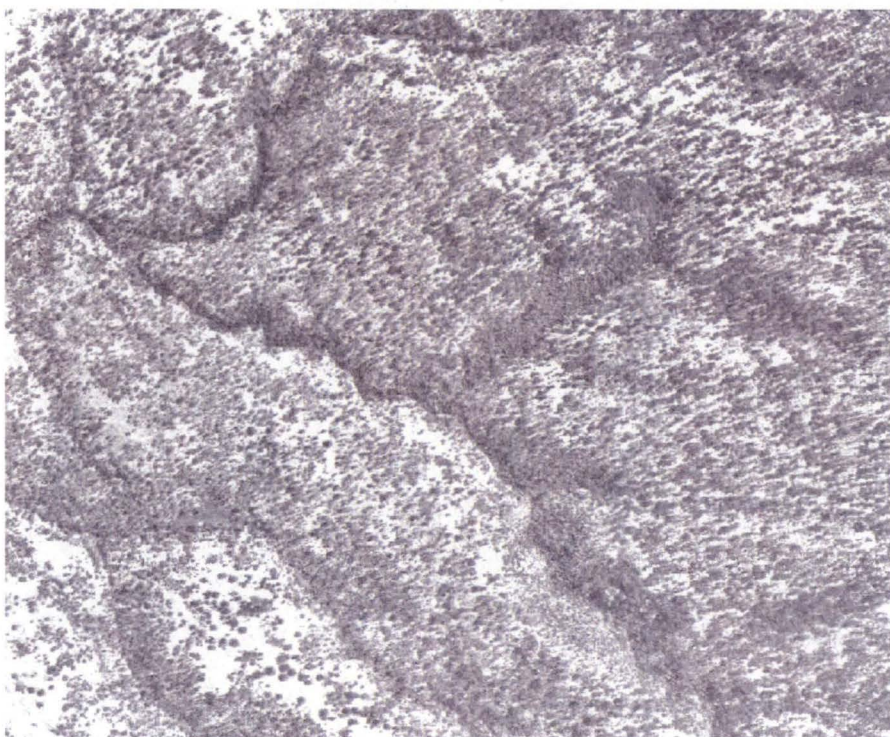
Plate 2.3 Riparian dry closed-forest along a watercourse (Triangle Flats, north east Tasmania).
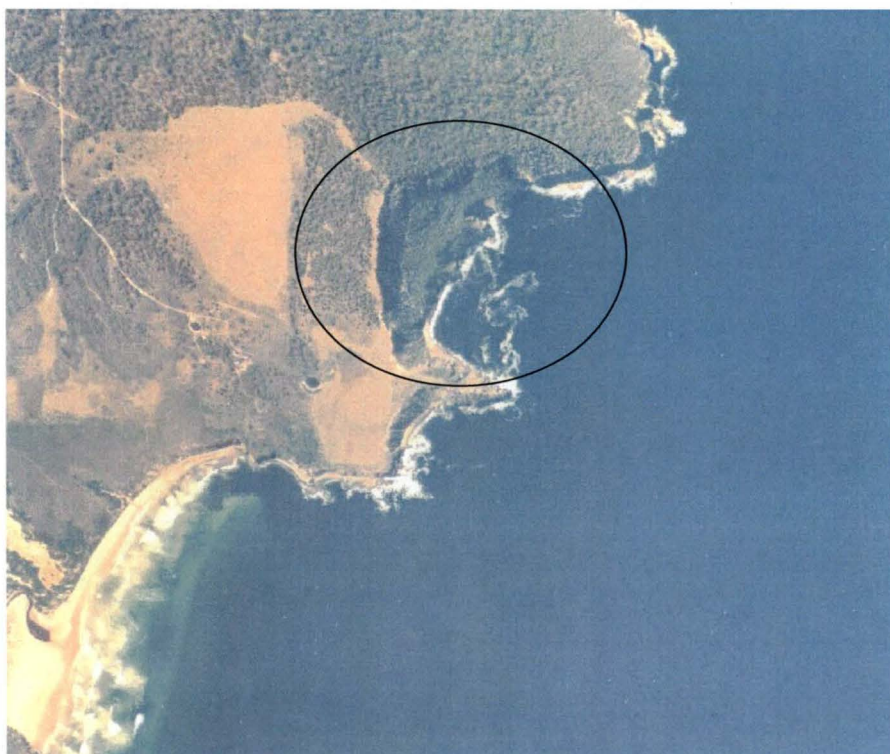
Plate 2.4 Dry closed-forest beneath coastal cliffs (Roaring Beach).
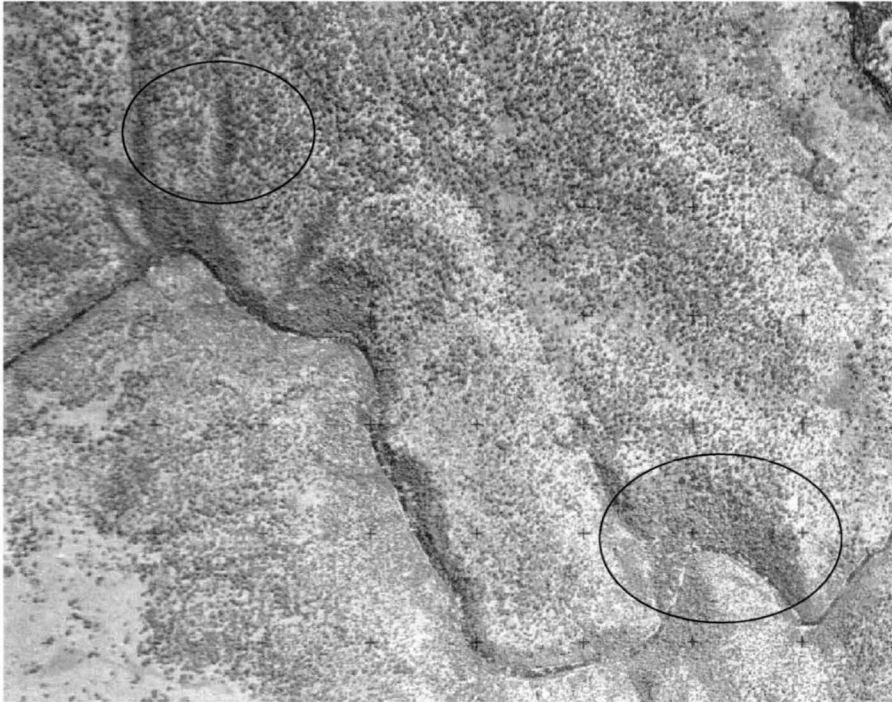
*Plate 2.5 Dry closed-forest in a gully with a steep southern aspect (upper left of image) &
miscellaneous non-gully dry closed-forest across a steep south/ southeast aspect (bottom
left of image) (North Esk River).*

Table 2.2 is a summary of the climates of Tasmanian dry closed-forest sites as
estimated by the program BIOCLIM. The average Tasmanian dry closed-forest site
has an annual precipitation of 827.8 mm, precipitation in the driest quarter of the
year of 157.5 mm, maximum temperature of the warmest quarter of 21.3 °C, and a
mean minimum temperature of the coldest quarter of 1.7 °C.

Table 2.2 The climate of Tasmanian dry closed-forest sites (N =183).

	Mean annual precipitation (mm)	Mean precipitation of the driest quarter (mm)	Maximum temperature of the warmest quarter (°C)	Minimum temperature of the coldest quarter (°C)
Mean value	827.8	157.5	21.3	1.7
Standard deviation	134.8	22.9	1.2	1.3
Minimum value	599.0	120.0	18.6	-0.4
Maximum value	1353.0	227.0	24.0	6.6

The vast majority of Tasmanian dry closed-forest stands occur on dolerite. There are an equal proportion of stands occurring on sedimentary and other substrates. This "other" group of substrates consists of granite, granodiorite, quartzwacke, rhyodacitic pyroclastics and Holocene deposits, and occurs mainly in the northeast of the state.
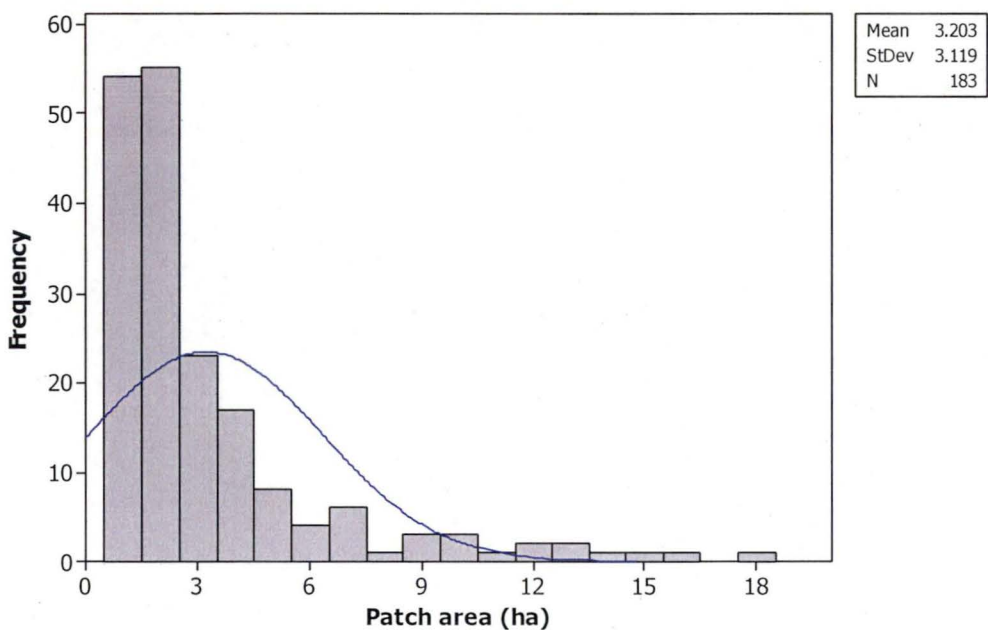
Figure 2.5 Distribution of dry closed-forest stand areas.

Most stands have an area of less than 3 hectares (Figure 2.5). The largest stand is at Triangle Flats near Blessington and is 17.9 hectares. The total mapped area of dry closed-forest in eastern Tasmania is 586.1 ha.
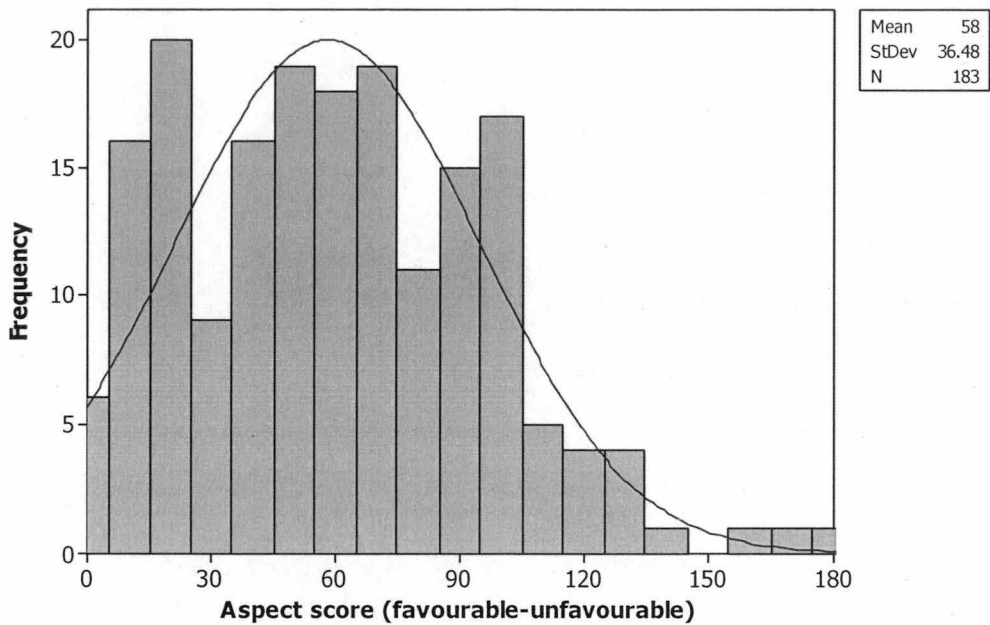
Figure 2.6 Distribution of stand aspect on a scale of 0 – 180, where 0 represents SE (favourable aspect) and 180 represents NW (unfavourable aspect).

The distibution of aspect scores (favourable – unfavourable) for 183 dry closed-forest stands is shown in Figure 2.6. The mean aspect is 58 degrees from SE. The distribution is skewed towards favourable aspects.

'Stands are protected from fire by NW topography' hypothesis

A comparison of the distribution of the heights of land surrounding the stands shows that the mean height to the NW is considerably greater than the other heights (Figure 2.7). For gully stands, heights to the left and right average around 75 m, whereas the height to the NW is some 50 m greater. A comparison of the distribution of the slopes shows that the mean slope to the NW is less than the slopes in other directions (Figure 2.8). For gully stands, slopes to the left and right average around 21 degrees, while the slope to the NW is approximately 3 degrees less.
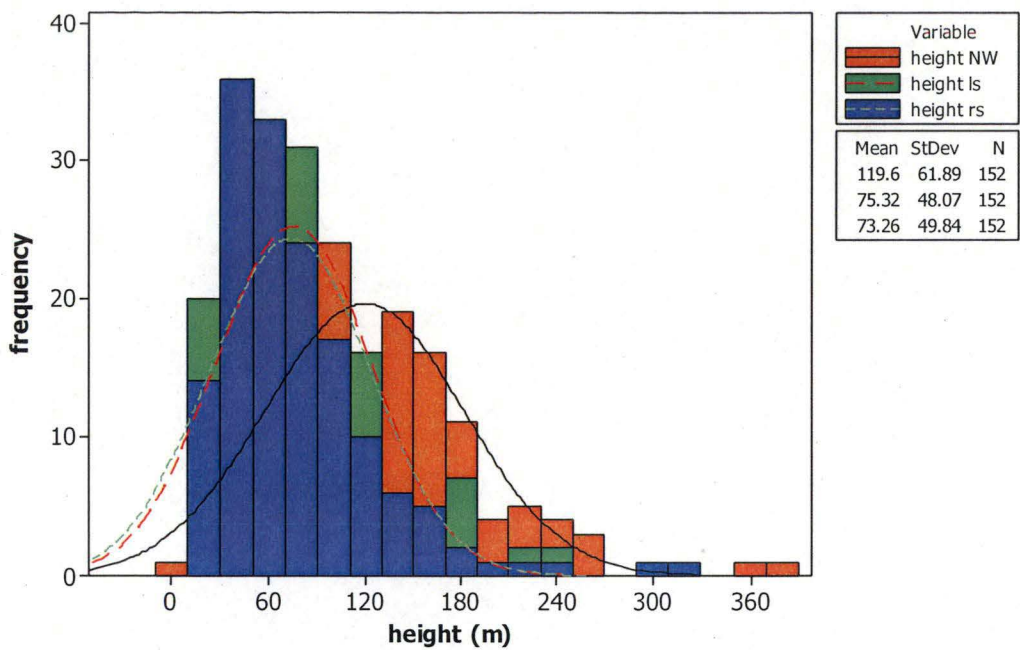
Figure 2.7 Distribution of heights of NW, left and right side topographies surrounding gully dry closed-forest stands.
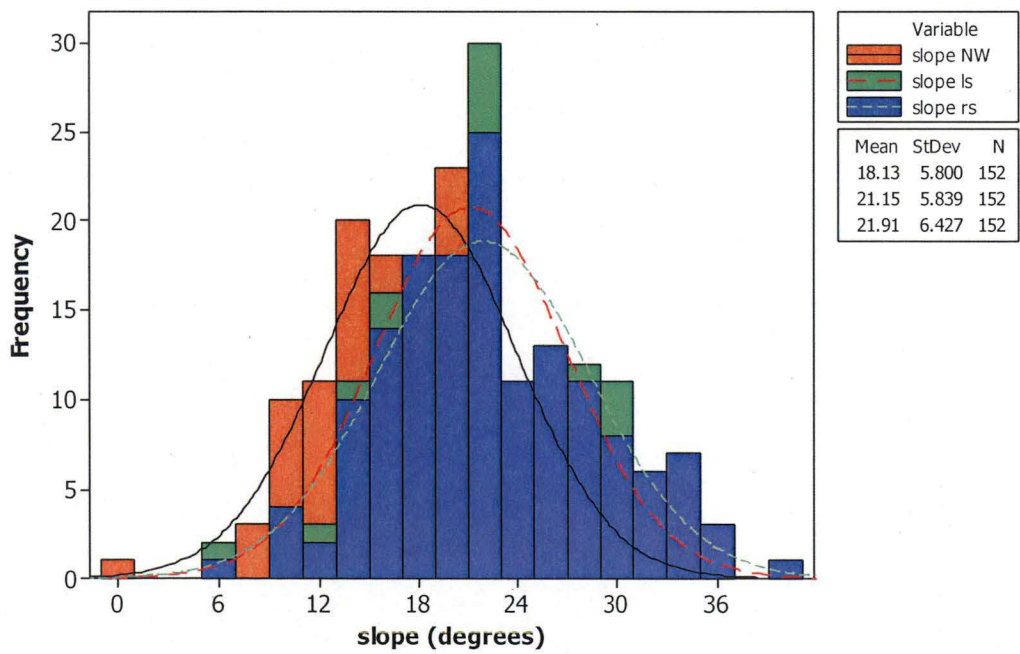
Figure 2.8 Distribution of slopes of NW, left and right side topographies surrounding gully dry closed-forest stands.

The height in the NW direction is significantly (p < 0.0001) greater than the heights on either the right or left side of the gully, while the heights on the left and right side are not significantly different (Table 2.3). Although the topography is higher

in a NW direction, the slopes are significantly (p < 0.001) less steep than those on the right and left side of the gully, while the difference between the slopes of the left and right side is insignificant (p = 0.052).

Table 2.3 Paired t-tests of mean differences between heights of right side, left side, and NW and associated slopes for gully dry closed-forest stands. See Table 2.1 for full variable names and explanations.

Variable pairs	N	Mean	SD	Test values
height ls	152	75.32	48.07	T-value = 0.50
height rs	152	73.26	49.84	P-value = 0.616
Difference	152	2.06	50.58	
height ls	152	75.32	48.07	T-Value = -9.47
height NW	152	119.57	61.89	P-Value < 0.001
Difference	152	-44.25	57.61	
height rs	152	73.26	49.84	T-Value –10.87
height NW	152	119.57	61.89	P-Value < 0.001
Difference	152	-46.31	52.50	
slope ls	152	21.15	5.84	T-Value = -1.96
slope rs	152	21.91	6.43	P-Value = 0.052
Difference	152	-0.76	4.77	
slope ls	152	21.15	5.84	T-Value = 7.58
slope NW	152	18.13	5.80	P-Value < 0.001
Difference	152	3.02	4.91	
slope rs	152	21.91	6.43	T-Value = 8.36
slope NW	152	18.13	5.80	P-Value < 0.001
Difference	152	3.78	5.57	

Influences on the physical nature of stands

Table 2.4 Results of multiple regression of gully dry closed-forest area and length versus stand environmental variables. See Table 2.1 for full variable names and explanations.

Stand physical variable	Effect	R^2_{adj}	T-value	P-value
Stand area (ha) (N=152)	height rs	0.34	4.37	<0.001
	nor		3.32	<0.001
	height ls		2.92	0.004
	asp		2.03	0.044
	drqpr		2.75	0.007
	slope NW		-1.67	0.098
	slope rs		2.87	0.005
	slope ls		-2.37	0.019
	dist pro top		-1.78	0.077
Stand length (m) (N=152)	height ls	0.28	3.15	0.002
	height rs		3.60	<0.001
	slope NW		-3.23	0.002
	asp		2.53 .	0.01
	slope rs		2.10	0.037
	nor		1.77	0.080

Table 2.5 Results of multiple regression of selected non-gully dry closed-forest stand area versus stand environmental variables. See Table 2.1 for full variable names and explanations.

Stand physical variable	Effect	R^2_{adj}	T-value	P-value
Stand area (ha) (N=32)	height NW	0.20	2.92	0.007
	maxtempwaqu		-1.50	0.144

Stepwise multiple regression of gully stand area versus environmental variables (Table 2.4) identified the variables of heights of the topography on the right and left side of the gully, slopes in all directions, northing, aspect, mean precipitation of the driest quarter, and distance between left and right side protective features for inclusion in a regression model. The strongest individual linear relationships between stand area and stand environmental variables are with height to the right side (R^2 = 0.135) and height to the left side (R^2 = 0.106). The regression equation is:

Stand area = - 16.4 + 0.401 height rs + 0.339 height ls + 0.0341 slope rs
- 0.0364 slope ls - 0.0124 slope NW + 0.00206 asp
+ 0.000003 nor - 0.284 dis pro top + 0.00534 drqpr

The regression has an R^2_{adj} value of 0.34 and the overall relationship is significant (F ratio = 9.62, p < 0.001). The relationships between stand area and all variables were positive except for slopes of the left side and NW topography, and distance between the left and right side protective features. All variable effects in the regression equation are significant at the p < 0.05 level except for slope of NW topography, aspect, and distance between the left and right side protective features.

Stepwise multiple regression of gully stand length versus environmental variables (Table 2.4) identified the variables of heights of the topography on the right and left side of the gully, slopes of the right side and NW topographies, northing, and aspect for inclusion in a regression model. The strongest linear relationships between stand length and stand environmental variables are also with height to the right side (R^2 = 0.131) and height to the left side (R^2 = 0.149). The regression equation is:

Stand length = - 4.16 + 0.271 height rs + 0.251 height ls - 0.0255 slope NW
+ 0.0193 slope rs + 0.00247 asp + 0.000001 nor

The regression has an R^2_{adj} value of 0.24 and the overall relationship is significant (F ratio = 10.45, p < 0.001). The relationships between stand length and all variables were positive except for slope to the NW. All variables effects in the regression equation are significant at the p < 0.05 level.

Stepwise multiple regression of non-gully stand area versus environmental variables (Table 2.5) identified height of the NW topography and the maximum temperature of the warmest quarter for inclusion in a regression model. For non-gully sites, the strongest individual linear relationship between patch area and stand environmental variables was with height to the NW (R^2 = 0.189). The regression equation is:

Stand area = 14.5 + 0.0288 height NW - 0.638 maxtempwaqu

The regression has a relatively poor fit (R^2_{adj} of 0.20) but the overall relationship is significant (F ratio = 3.56, p = 0.042). The relationship between stand area and height of NW topography is positive and the relationship between stand area and maximum temperature of the warmest quarter is negative. Only the relationship between stand area and height to the NW is significant at the p < 0.05 level.

Influences on the location of stands

Table 2.6 Results of paired t-tests between site environmental variables of gully dry closed-forest sites and matched non-dry closed-forest locations. See Table 2.1 for full variable names and explanations.

Variable pairs	N	Mean	SD	Test values
asp	66	50.348	34.000	T-value = -9.38
asp (matched site)	66	131.667	53.503	P-value < 0.001
Difference	66	-81.3182	70.3993	
height rs	66	71.3333	51.9062	T-Value = 3.69
height rs (matched site)	66	47.4242	34.4768	P-Value < 0.001
Difference	66	23.9091	52.6929	
height ls	66	61.8939	35.5156	T-Value = 1.94
height ls (matched site)	66	52.1212	43.6424	P-Value = 0.057
Difference	66	9.77273	40.96370	
height NW	66	101.818	55.916	T-Value = 5.57
height NW (matched site)	66	57.955	52.492	P-Value < 0.001
Difference	66	43.8636	63.9819	
slope rs	66	14.3939	5.5244	T-Value = 5.16
slope rs (matched site)	66	10.1667	5.7954	P-Value < 0.001
Difference	66	4.22727	6.65362	
slope ls	66	13.4242	5.6133	T-Value = 5.55
slope ls (matched site)	66	9.0909	4.7773	P-Value < 0.001
Difference	66	4.33333	6.34722	
slope NW	66	16.2424	5.3091	T-Value = 11.64
slope NW (matched site)	66	7.5303	4.9372	P-Value < 0.001
Difference	66	8.71212	6.08090	

Table 2.7 Results of paired t-tests of site environmental variables of non-gully dry closed-forest sites and matched non-dry closed-forest locations. See Table 2.1 for full variable names and explanations.

Variable pairs	N	Mean	SD	Test values
asp	11	27.727	19.540	T-value = -7.28
asp (matched site)	11	124.545	44.071	P-value < 0.001
Difference	11	-96.8182	44.1176	
height mr	11	97.7273	56.4962	T-Value = 2.31
height mr (matched site)	11	69.0909	33.8982	P-Value = 0.044
Difference	11	28.6364	41.1151	
height NW	11	90.9091	55.9383	T-Value = 1.96
height NW (matched site)	11	51.8182	40.3282	P-Value = 0.078
Difference	11	39.0909	65.9855	
slope mr	11	23.0909	8.5376	T-Value = 1.27
height mr (matched site)	11	20.4545	7.1185	P-Value = 0.233
Difference	11	2.63636	6.88873	
slope NW	11	20.9091	7.9430	T-Value = 6.10
slope NW (matched site)	11	6.2727	4.9415	P-Value < 0.001
Difference	11	14.6364	7.9533	

Paired t-tests of selected stand measurements for dry closed-forest sites and matched non-dry closed-forest sites are shown in Tables 2.6 & 2.7. Gully dry closed-forest stands have a significantly lower aspect score than the matched sites

(favourable aspect = aspect score of 0), significantly higher surrounding land than the matched sites except for the left side of the gully, and significantly steeper slopes in all three directions than the matched sites (Table 2.6). Non-gully dry closed forest stands also have a significantly lower aspect score than the matched sites, significantly greater main protective ridge heights than the matched sites, and significantly steeper NW slopes compared with the matched sites (Table 2.7). The NW height was not significantly different between non-gully stands and matched sites.

Discussion

Most Tasmanian dry closed-forest stands occur in gully situations and in that respect are examples of the 'small, often narrow edaphic isolates' refuge type of Webb & Tracey (1981). Many stands, especially those in the hinterland of Tasmania's east coast, display the features of "arrow-head" scrubs described by Webb & Tracey (1981). Gullies, which effectively occupy a local topographic low-point, are locations that afford stands protection from intense fires moving upslope (Ash 1988). Gullies are also a collecting point for soil, water and nutrients, which provide favourable conditions for dry closed-forest development and buffer the stands from the effects of drought. It has been suggested that a number of the rainforest trees of southern Australia have shallow root systems and thus have distributions limited to edaphically favourable sites (Barrett *et al.* 1996). This is unlikely to explain the predominance of Tasmanian dry closed-forest stands in gullies, as most dry closed-forest species also occur in the understorey of eucalypt forests occurring in drier situations. This would seem to indicate substantial drought tolerance among dry closed-forest species. Many examples of dry closed-forest occurring in non-gully situations, without favourable edaphic conditions, were identified in the present study. This indicates that edaphic limitations may not be the primary determinant of Tasmanian dry closed-forest development, which is in agreement with the findings of studies of dry closed-forest in the Northern Territory (Bowman & Fensham 1991; Bowman 1992).

The non-gully dry closed-forest sites of Tasmania are examples of the "small, relatively dry topographical isolates" refuge type of Webb & Tracey (1981). Such refuges are provided by rocky ground, resulting in an understorey that is free of grasses and therefore has a low potential to fuel a fire. There are no examples of "Topographic, edaphic, climatic isolates" refuges (*sensu* Webb & Tracey 1981) occupied by dry closed-forest in Tasmania. Such refuges commonly occur on fertile deep basalt soils in moderately low rainfall areas of sub-coastal eastern Australia.

Dry closed-forest stands can occur where the average annual rainfall is as low as 600 mm (Webb & Tracey 1981). Recurrent drought and associated fires in low rainfall areas supporting dry closed-forest have been identified as major limitations

on the distribution of this community (Fensham *et al.* 2003). Another significant

feature is the seasonal nature of rainfall in the tropics and subtropics. This

seasonality is less pronounced in the temperate zone. Table 2.8 shows the trend

from more extreme seasonality in the tropics to more evenly spread rainfall in the

temperate areas.

Table 2.8 Wettest and driest quarter rainfall figures for areas supporting dry closed-forest (data are sourced from Bureau of Meteorology records, with the nearest stations to areas supporting dry closed-forest being used).

Climate Zone	Location	Wettest quarter rainfall (% of annual rainfall total)	Driest quarter rainfall (% of annual rainfall total)
Tropics	Darwin Airport (Northern Territory, Lat:-12.4239 S, Long: 130.8925 E)	64	0.5
	Mt Surprise Township (Queensland, Lat:-18.1467 S, Long: 144.3183 E)	67	2
Subtropics	Taroom Post Office (Queensland, Lat:-25.6419 S Long: 149.7944 E)	41	14
	Mt Pikapene Forestry (New South Wales, Lat:-29.0375 S, Long: 152.6897 E)	42	11
Temperate	Bairnsdale (Victoria, Lat:-37.8333 S Long: 147.6500 E)	29	20
	Tasmanian dry closed-forest sites (N=183, approximate average Lat:-42 S, Long: 148 E)	31	19

Gillison (1987) defines dry rainforest (dry closed-forest) as a number of rainforest

formations "that normally reflect a marked response to seasonal variability".

Although Tasmanian dry closed-forest locations do not display significant

seasonality in rainfall compared with areas of northern Australia, there is

nonetheless a propensity for drought in the east of the state (Jackson 1988).

Drought produces an irregular rainfall deficit rather that seasonal rainfall deficit,

both having the same effect of causing substantial water stress for plants. Many of

the higher altitude Tasmanian dry closed-forest stands probably supplement a

marginal rainfall with moisture derived from fog stripping, as has been reported for

rainforest in other marginal rainfall areas, such as parts of New South Wales (Fisher

1985).

One major feature differentiating Tasmanian dry closed-forest and cool temperate

rainforest is the absence of dominant canopy trees from the genera *Nothofagus*

Atherosperma, Eucryphia, Athrotaxis, Lagarostrobos, Dacrydium, Phyllocladus

and *Diselma* (Jarman & Brown 1983). *Nothofagus cunninghamii* is a widespread

tree in cool temperate rainforest. The distributional limit of *N. cunninghamii*, a common dominant of cool temperate rainforest, in southeast Australia corresponds to an annual average rainfall of 930 mm and a driest quarter (January – March) average rainfall of 170-190 mm (Busby 1986). Busby's estimates are in agreement with the BIOCLIM analysis of the present study, in which the average dry closed-forest stand has a mean annual rainfall of 828 mm and a mean dry quarter rainfall of 157 mm, both below the minimum rainfall for the occurrence of *N. cunninghamii* given in Busby (1986). There are some examples of dry closed-forest occurring on rock scree in high rainfall areas such as on rocky ridges in the northwest of Tasmania and on the slopes of Mt Anne in the southwest (J.B. Kirkpatrick pers. comm.). But such examples are uncommon, arising due to deep rock scree limiting soil formation near the surface, and resulting in low water availability to plants.

The present study recorded the majority of stands growing on dolerite. This is most likely not in response to an edaphic preference, but rather to the dominance of this geology in eastern Tasmania. Dolerite covers about a third of Tasmania, most of this in eastern and central parts (Laffan & McIntosh 2005).

There are many references to rainforest preferentially growing on south and southeast-facing aspects (e.g. Fisher 1985; Neyland 1991; Barrett & Ash 1992), which are in agreement with the findings of the present study. These aspects are the most protected from drying northwesterly winds, and, in the case of southeast Australia, the direction of advancement of devastating fire-fronts. It is interesting and unusual for southern Australia that the dry closed-forests of Victoria preferentially face north and west (Peel 1999). For instance, at Billy Goat Bend in the east Gippsland district of Victoria, dry closed-forest survives on a drought-prone aspect that is suited to neither wetter rainforest species nor eucalypt species. This is also testament to the complete protection from fire that the rock scree provides for these stands. In seasonally dry parts of the east coast of Australia, such as the western Border Ranges of northeast New South Wales, dry closed-forest can also be found occupying unfavourable aspects, while the more favourable aspects are occupied by moist rainforest (Adam 1987). Very few Tasmanian dry closed-forest stands face north or west. The few stands that were mapped occupying these unfavourable aspects have extensive topographic protection in the northwest

direction, and although the aspect is susceptible to drying out, stands are still mostly protected from hot winds and fires.

The fact that the highest ground adjacent to stands was to their northwest supports the hypothesis that stands are a product of protection from fire. The results of the stepwise regression of gully stand size against these and other environmental variables did not include height to the northwest, while the left and right side heights were included. This apparent contradiction may be interpreted as meaning that high northwest topography provides protection from drying northwesterly summer winds and fire, and therefore allows a dry closed-forest stand to develop. However, the heights to either side of the gully determine the potential size of a stand. This is probably related to the influence that the left and right side topographies have on fire behaviour. The heights of the left and right side topographies determine the depth of a gully, and hence also determine the distance that a fire must progress downlsope to reach a stand. The paired t-test analysis also found a significantly lesser slope in the northwest direction compared with the right and left side. Fires are known to move with the least intensity down steep slopes (Unwin *et al.* 1985). The slope difference found between different directions in the present study may not be large enough to affect fire behaviour. Evidence for this is that slopes in all directions were identified in the regression equations of gully stand physical properties against environmental variables, suggesting that slope in general influences the physical nature of stands, probably through its effect on fire behaviour. Additionally, slope may influence the physical nature of stands by influencing the light regime, which in turn may influence the relative regeneration success of species of dry closed forest and eucalypt forest.

Northing was identified in the stepwise regression equation for gully area and length. The average stand size is smaller in southern Tasmania (south of a line through Swansea, average stand size 2.54 ha) compared with the north (average stand size 3.93 ha). There were no stands identified of more than 6 ha south of Maria Island (northing 5279000). Most large dry closed-forest stands in Tasmania occur around the latitude of Launceston (41° 25'). In addition to this, most large stands in the north of Tasmania occur in gully geomorphological situations that are suitable for the formation of riparian dry closed-forest stands (>750 m in length).

Riparian stands make a large contribution to the overall area of dry closed-forest in Tasmania, with twelve of the largest 20 stands being riparian. The distribution of riparian stands is skewed towards the north of Tasmania, where 10 out of 19 occur, compared with 5 in the east, and 4 in the south. Many of the northern Tasmanian riparian stands occur on the eastern side of the Tamar River, where numerous tributary creeks flowing towards the estuary have cut deeply into the surrounding low hills.

Aspect was also identified in the stepwise regression equation for gully area and length. The distribution of stand aspects relating to the moisture gradient was skewed towards a favourable southeast aspect. A group of stands from the east Tamar hills near Launceston have aspects within the range of 90 to 110 degrees from southeast. The local geography of the east Tamar hills consists of a low range running on a northwest-southeast axis parallel to the estuary. Streams finding the shortest route to the estuary have eroded gullies perpendicular to the range in a southwesterly direction. In this case it is the local topography that dictates the aspect that dry closed-forest stands occupy. The Tamar hills stands shift the average dry closed-forest stand aspect away from southeast. However aspects within 45 degrees of northwest do seem particularly unfavourable to dry closed-forest development in Tasmania.

A shortcoming of the present study was the inability to measure the small-scale aspect patterns of stands. Gully dry closed-forest stands are usually asymmetrical, with most of the stand occupying favourable southern and eastern aspects, and only a minor part of the stand occupying unfavourable north and west aspects on the adjacent side of the watercourse. The small-scale aspect preference of this vegetation type was not identified accurately by aerial photography examination, especially for stands occurring on very steep ground. Figures 2.11 and 2.12 show how gully orientation and small-scale aspect variation relate to each other. Figure 2.9 displays the location of a dry closed-forest stand at Symons Creek on the east Tamar. The aspect score of the gully is 100 degrees from southeast. However, this stand consists mainly of dry closed-forest vegetation growing across the slope adjacent to the gully that faces 0 – 20 degrees from southeast, and very little vegetation growing across the opposite slope facing 160 –180 degrees from

southeast. In contrast to this, Figure 2.10 shows a gully that does not support dry closed-forest that has an aspect score of 165 degrees from SE. The aspect scores of the adjacent sides of this gully are 90 and 135 degrees from SE. Neither aspect is favourable in terms of providing protection from northwesterly winds or a fire front approaching from this direction and therefore the situation does not support dry closed-forest vegetation.
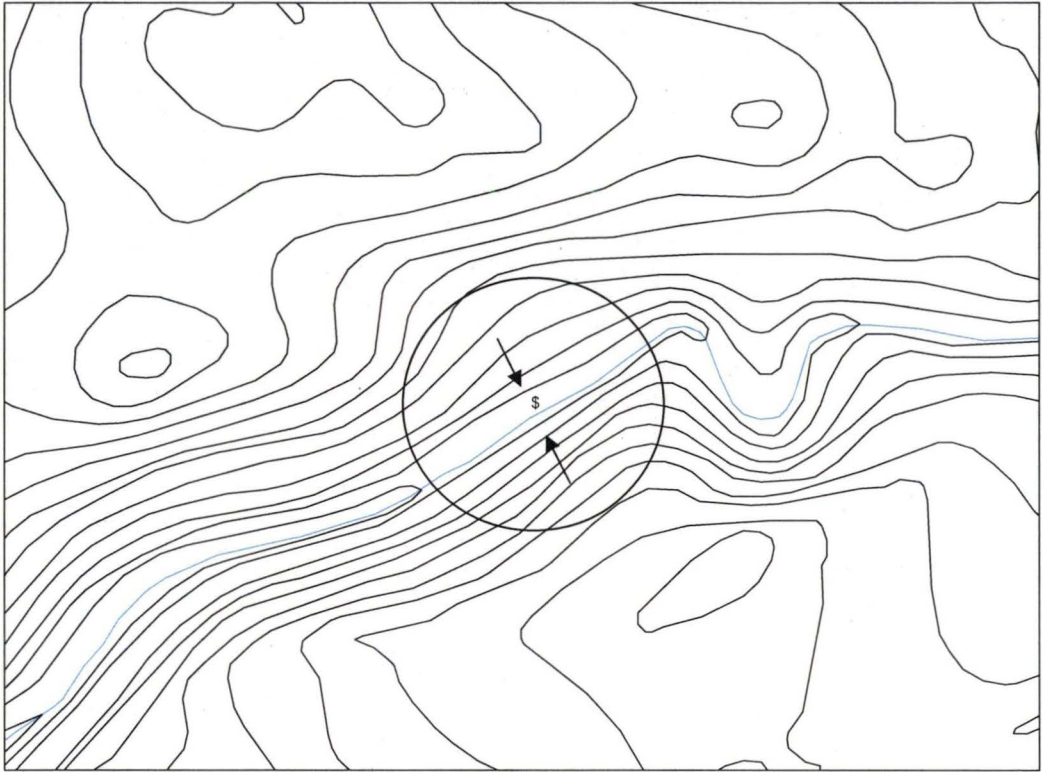
Figure 2.9 A gully dry closed-forest site at Symons Creek, east Tamar, showing aspects of adjacent slopes (arrows indicate direction of aspect).

Figure 2.10 A gully site that does not support dry closed-forest with an unfavourable aspect of 100 degrees from SE showing aspects of adjacent slopes (arrows indicate direction of aspect).

Large stands in gullies between 0-110 degrees from southeast have considerable asymmetry and the majority of the dry closed-forest vegetation grows on slopes with a favourable aspect. Dry closed-forest does not thrive in gullies with aspects 135-180 from southeast because there are few or no available slopes with an aspect that is favourable.

No real differentiation was found in factors that may help to explain stand area and stand length (large lengths generally being riparian stands). Similar factors were identified in both stand area and stand length regression equations.

Height to the NW was a factor in the regression of non-gully dry closed-forest stand area against stand environmental variables. As mentioned previously the heights to the left and right side measure the depth of gullies and hence may indicate the level of fire protection afforded to a stand. These measures are not applicable to non-gully dry rainforest stands. The height of the topography in a northwest direction is strongly correlated with the height of the main ridge (correlation coefficient =

0.827). However, unlike northwest topography, main ridge topography was not identified for inclusion in the stepwise regression equation.

The results of paired t-tests of localities that support dry closed-forest and adjacent localities that do not, found significant differences between locations in terms of the heights and slopes in the three directions, and aspect, which were the same factors that influenced the size of dry closed-forest stands. This suggests that, along with determining the nature of dry closed-forest stands, these same variables are also important factors determining whether a site is capable of supporting dry closed-forest in the first place. Sites suitable for dry closed-forest establishment are orientated more to the southeast and have considerably steeper and higher surrounding hills compared to adjacent locations that are unsuitable for the establishment of this community.

In the present study, results of the regression of patch dimensions versus environmental variables produced a relatively poor fit at best (max R^2_{adj} of 0.34). Field observations in the present study indicated a close association between dry closed-forest stands and rocks, either as a "rock-mulch" covering the ground or in a protective uphill cliff-line. This could be a missing factor that explains a substantial portion of the variation in the size of stands. In the context of Australian dry closed-forest, the link has been made in the literature between rocky ground and fire protection (e.g. Webb & Tracey 1981; Clayton-Greene & Beard 1985; Kirkpatrick *et al.* 1987; Kirkpatrick *et al.* 1988; Ash 1988; Williams 1993; Peel 1999). Rock in the form of both "rock mulch" and cliff-lines can provide a very effective barrier to fire infiltration (Plates 2.6 & 2.7). Some stands have light internal rock cover but are protected from fire by a cliff-line at the upslope boundary. Therefore, effective measures of fire protection as provided by rock should take into account both ground cover and rock barriers in assessing the protection afforded to a stand.
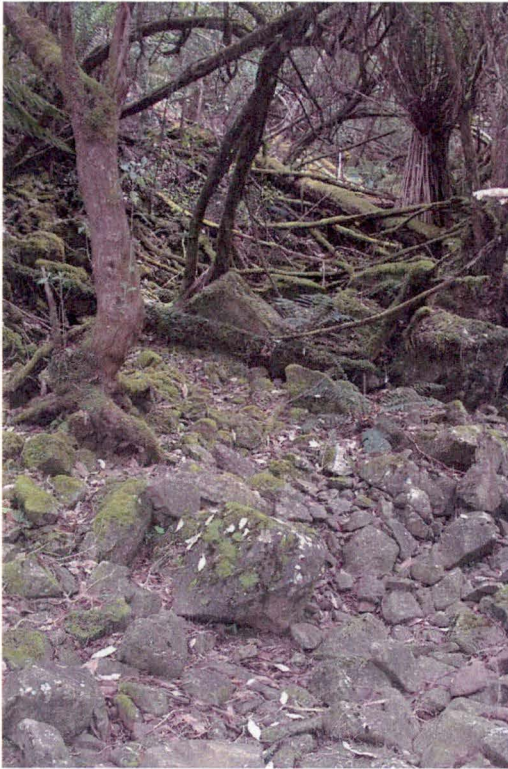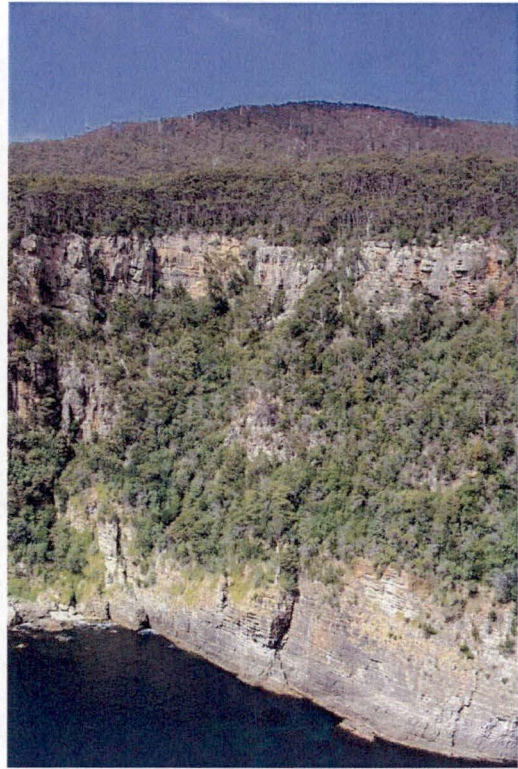
a)   b)

Plate 2.6 Dry closed-forest is commonly associated with rocky sites. For example, a) the ground within stands is often covered in 'rock mulch', and b) stands regularly occur beneath upslope cliff-lines.

In conclusion, the relationship between dry closed-forest stands, in terms of distribution and physical properties, and factors such as aspect, topography and rock, seems to be determined by their influence on fire frequency.

Chapter 3 - Floristic variation of Tasmanian dry closed-forest

Abstract

Floristic variation in and between Tasmanian dry closed-forest stands was documented. Six floristic sub-communities were distinguished by cluster analysis, and a number of common and characteristic species were identified in each sub-community. These sub-communities were differentiated by many environmental variables, especially by mean annual precipitation, northing, soil pH, and precipitation of the driest quarter. The small-scale distribution pattern of some of the major canopy species within stands was related to moisture supply and rock cover, both important determinants of fire-frequency. This community has floristic affinities with the remnant cool temperate rainforests of eastern Tasmania, and other dry closed-forests of southeast Australia, in particular dry rainforests of the East Gippsland district of Victoria.

Introduction

This study investigates the floristic composition of an eastern Tasmanian closed-forest community with affinities to Australian dry closed-forest (*sensu* Specht 1970), otherwise known as dry rainforest. Rainforest has a patchy distribution in Australia, occupying a narrow band relatively close to the coast from Tasmania and Victoria in the south, through the eastern states, and across the monsoonal Northern Territory and northwest of Western Australia (Webb & Tracey 1981). In the less humid and more seasonal environments in this range, dry closed-forest persists in fire-protected refuges. Dry closed-forests are known regionally as monsoon rainforest in the tropical north of Australia, softwood scrub and vine thicket in sub-coastal Queensland and New South Wales, and dry rainforest or vine forest generally east of the Great Dividing Range in Queensland, New South Wales and Victoria.

The floristic composition of dry-closed forest varies substantially within its extensive distribution. Monsoon rainforests of northern Australia are dominated by plants closely allied to those in the moist tropical forests of this region. This has led to the suggestion that monsoon rainforest has originated relatively recently from the moist rainforests of the Palaeotropics (Barlow & Hyland 1988). Australian monsoon rainforests are similar to those found elsewhere in Australasia (Whitmore 1984). Many of the constituent plants of monsoon rainforest are thought to have evolved in response to past extreme climates (Gillison 1987). Dry closed-forests are known to colonise newly disturbed environments. For instance, monsoon rainforest patches are commonly recorded growing on Holocene landforms (Russell-Smith & Dunlop 1987).

Further south, common plants occurring in North Queensland dry closed-forest are *Brachychiton australis, Drypetes deplanchei, Gyrocarpus americanus, Diospyros humilis, Geijera salicifolia, Planchonella cotinifolia* and *Strychnos psilosperma* (Fensham 1995). This community in New South Wales has a strong representation from the plant families Sapindaceae (22 spp.), Euphorbiaceae (19 spp.) Rutaceae (21 spp.), Celastraceae (6 spp.), Myrtaceae (14 spp.) and Moraceae (7 spp.) (Floyd 1990). In the Sydney region of New South Wales, dry closed-forests contain the

species *Toona australis, Brachychiton populneus, Ehretia acuminata, Ficus rubiginosa, Dendrocnide excelsa, Claoxylon australe, Backhousia myrtifolia, Hymenanthera dentata, Notelaea longifolia, Trema aspera, Derringia amaranthoides, Pomaderris aspera* and *Serringia arborescens (*Keith & Benson 1988*)*. Along the south coast of New South Wales common species are *Brachychiton populneus, Ficus rubiginosa, Pittosporum undulatum, Alectryon subcinereus, Notelaea venosa,* and *Hymenanthera dentatum* (Keith & Bedward 1999). In the southernmost mainland dry closed-forests of the east Gippsland district of Victoria *Brachychiton populneus, Pittosporum undulatum, Rapanea howittiana, Acronychia oblongifolia, Acmena smithii, Acacia* spp., *Coprosma quadrifida, Solanum pungetium,* and *Hymenanthera dentata* are dominant species (Cameron 1992*)*. *Rapanea howittiana* is an important species in Victoria, here being at the southernmost point of its distribution. East Gippsland dry-closed-forests are ecologically related to other dry rainforest communities previously described for the southern parts of New South Wales (Keith & Benson 1988, Keith & Bedward 1999). Cameron (1992) notes that the dry rainforest flora of Victoria shows some similarities with the dry country flora of Northwest Victoria, where genera that occur in rainforest, such as *Beyeria, Pittosporum, Marsdenia,* and *Alectryon,* are also found. Additionally, Cameron (1992) lists a number of New South Wales dry rainforest genera that also occur in arid/semi-arid eastern South Australia and western New South Wales. Along with fossil evidence (Kershaw *et al.* 1991), these remnant taxa occurring in arid regions may point to a more widespread dry rainforest distribution during the Tertiary (Cameron 1992). Alternatively, these species could represent survivors of wetter rainforests that have contracted in more recent dry climates.

Despite having a broad distribution from the tropics to the temperate zone, northern and southern dry closed-forest display some floristic convergence, with genera such as *Brachychiton, Acacia, Alectryon, Pittosporum* and *Ficus* occurring in both regions.

Dry-closed forests are no different from other Australian rainforests in that they occupy refuges in the landscape that avoid most fires (Webb & Tracey 1981). However, few sites are entirely impervious to fire and many rainforest plants are

occasionally subject to burning. Many rainforest plants have the capacity to regenerate vegetatively following infrequent low to moderate intensity fires (Stocker 1981; Unwin et al. 1985; Floyd 1990; Williams 2000). Vegetative regeneration following fire and other disturbances has also been reported for a number of species occurring in the community investigated in the present study (Woolward 1983). In addition to fire, drought stress can also affect the potential for colonisation of a site by rainforest species. Dry rainforest at Billy Goat Bend in eastern Victoria has an inhospitable aspect that faces north and is on a massive scree slope beneath cliffs (Cameron 1992). The aspect in combination with reflected sunlight from the boulders result in high ambient temperatures in summer, and the paucity of soil available between the rocks limits plant water uptake. The site is effectively a fireproof niche and hence meets one requirement for rainforest development. However, because of the dry nature of the site the only successful colonisers are dry rainforest trees with extreme drought tolerance such as *Pittosporum undulatum* and *Eleaocarpus reticulatus* (Cameron 1992).

Despite structurally qualifying as rainforest vegetation (*sensu* Specht 1970), the dry closed-forests of eastern Tasmania do not meet the requirements of the floristic based Tasmanian rainforest definition which states that: cool temperate rainforest is a forest dominated by one or more of *Nothofagus*, *Atherosperma*, *Eucryphia*, *Athrotaxis*, *Lagarostrobos*, *Dacrydium*, *Phyllocladus* and *Diselma* (Jarman & Brown 1983).

This study investigates the floristic composition of Tasmanian dry closed-forest, and aims to explain regional variation in this composition in terms of site environment. The floristic composition of dry closed-forest is compared with some other southern Australian closed-forest communities.

Methods

Data collection

Stands were located on aerial photographs of the eastern half of Tasmania. The community occurs in the drier parts of Tasmania, which are predominantly on the eastern side of the island. Therefore areas with an annual average rainfall exceeding approximately 1000 mm, and, hence, with sufficient moisture to support temperate rainforest dominated by *Nothofagus cunninghamii* (Busby 1986), rather than dry closed-forest, were not included in the study area. Stands were relatively easy to distinguish from temperate rainforest in that dry closed-forest generally has a smooth canopy when compared with temperate rainforest and lacks the distinctive conical crowns of *Atherosperma moschatum* emerging above the main canopy. Distinguishing between other gully communities such as *Acacia melanoxylon* scrub or *Melaleuca* stands proved more difficult, with ground truthing showing that a number of aerial-photograph-interpreted dry closed-forest stands belonged to one of these communities. Fieldwork was undertaken between May 2002 and May 2004. Data were collected from 61 dry closed-forest stands, the locations of which are shown in Figure 3.1.

Vascular plant species lists were compiled from each stand. In the field the following were also recorded: major stand dominant tree/shrub, major stand sub-dominant tree/shrub, rock cover, fern cover, and canopy cover. The dominant and subdominant species covers were estimated using a cover scale of 1 = <1%, 2 = 1-5%, 3 = 5-25%, 4 = 25-50%, 5 = 50-75%, 6 = >75%. The dominant species was the species that scored 4 or greater on this scale. If more than one species dominated this was recorded as 'mixed dominance'. The subdominant species was the species that scored next highest on the cover scale. If there was mixed dominance no subdominant was recorded. For analysis, dominant and sub-dominant species were categorised as 1 = *Beyeria viscosa*, 2 = *Olearia argophylla*, 3 = *Pomaderris apetala*, 4 = other species, 5 = mixed dominance, and 6 = no obvious dominant. For rock cover, fern cover, and canopy cover, a visual estimation of percentage cover was made using the same scale as above. For each stand, a sample of the surface 5 cm of soil was collected, after removal of surface litter, from at least 5 random

locations. These 5 samples were combined for later analysis. A number of off-site topographic and climatic variables were also measured. Stand geocoordinates, altitude, main stand aspect, and geomorphic situation were determined from 1:25000 scale topographic maps from the TASMAP series. Geology was determined from 1:50000 scale geology maps, and categorised as 1 = Jurassic dolerite, 2 = sandstone, mudstone, or siltstone, and 3 = other. Geomorphic situation was grouped into the following categories: 1 = gully, 2 = steep gully with southern aspect, 3 = riparian, 4 = beneath cliffs, and 5 = miscellaneous. Stand area and average stand slope were also calculated on topographic maps using the stand outlines translated from aerial photographs.
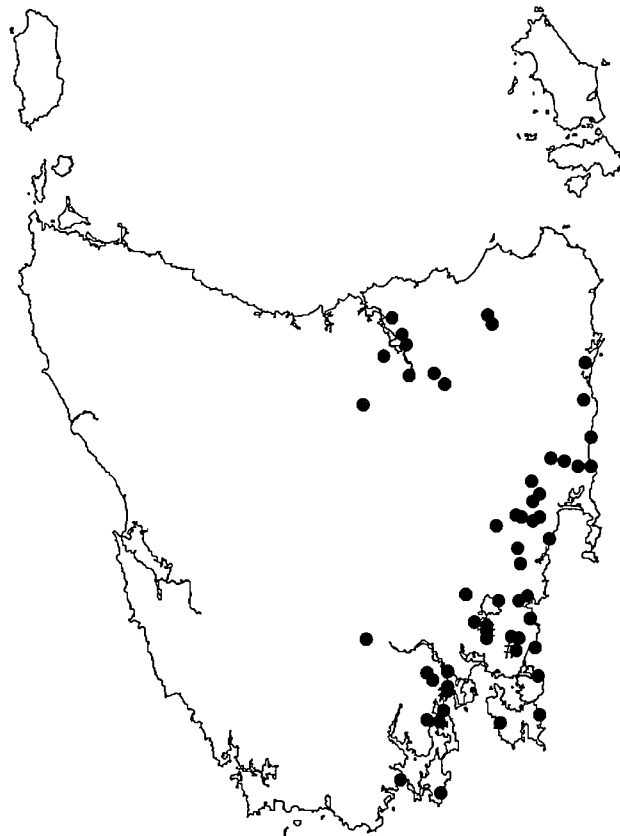
Figure 3.1 Location of 61 dry closed-forest stands sampled in the present floristic study.

A more detailed examination of the vegetation was undertaken at 27 out of the 61 stands. A transect of contiguous quadrats was laid out at each stand. The dimension of the quadrats was 4 x 5 m, with the total length of the transect being between 20 and 50 m in most cases and 90 m at the Truganini Reserve stand. The long

transect at Truganini reserve was completed in a trial phase of the study where the vegetation surveying methods were tested. As this transect took 2 days to complete, the length of the surveying transect at subsequent stands was scaled down to a maximum of 50 m to reduce survey completion time. The final length of each transect was constrained by such factors as the density of the vegetation and the shape of the stand. The narrowness of some stands necessitated measuring out two transects to make up 50 m in total. Transects were located within the stand in an area which was deemed to be representative of the overall dominant stand vegetation and was orientated at right angles to the slope of the land to pick up as much topographic variation as possible. All transects were within the boundary of the dry closed-forest vegetation. However, in some cases, because of a diffuse boundary it was impossible to avoid sampling some ecotonal vegetation along with the dry closed-forest vegetation. The cover abundance of all vascular plant species occurring within each quadrat was estimated using a scale of $1 = <1\%$, $2 = 1$-5%, $3 = 5$-25%, $4 = 25$-50%, $5 = 50$-75%, $6 = >75\%$. Cover of rock, ferns, bryophytes, leaf litter, fallen dead wood, bare ground, grasses, herbs, and lilies/sedges was measured using the following procedure. A central tape was extended at a height of 0.5 -1 m above the ground through the centre of the quadrat parallel to its long edge (5 m length). Distances occupied by the different cover types were recorded and a total calculated for each quadrat. When two cover types overlapped each other, each was measured as if the obscuring cover was absent (for example bryophytes covering rock, both are covering the same area of ground but are measured as distinct ground cover). For analysis the distance measures for each cover type were converted into percentages and assigned to categories. The relatively small number of quadrats with cover data for ferns, leaf litter, and bryophytes necessitated broad categories of $1 = 0$-39, and $2 = >40$ to satisfy the requirements of χ^2 analyses, while for the remaining cover types the categories were $1 = 0$-39, $2 = 40$-79, and $3 = >79$.

Canopy cover was approximated by matching the degree of crown openness, looking skyward from the centre of a quadrat, with photographs of crown openness in Walker & Hopkins (1990). The scale used was $1 = < 40\%$, $2 = 40$-50%, $3 = 50$-60%, $4 = 60$-65%, $5 = 65$-70%, and $6 = >70\%$. For analysis canopy cover values were assigned to categories of $1 = < 50\%$, $2 = 50$-59%, $3 = 60$-69%, and $4 = >$

70%. Canopy height and height of emergent individuals, if present, was visually estimated from the centre of each quadrat. For analysis canopy heights were assigned to categories of 1 = 0-4 m, 2 = 5-9 m, 3 = 10-14 m, 4 = 15-19 m, and 5 = 20-24 m, while the height of emergent individuals were assigned to categories of 1 = none, 2 = 10-14, 3 = 15-19, 4 = >19. Aspect was measured with a compass at the top of each quadrat. For analysis the aspect values were assigned to two categories of 1 = 45-225, and 2 = 226- 44. These categories were chosen because they are representative of a soil moisture gradient in Tasmania that is at a maximum at southeast aspects (hence category 1 is centred around 135 degrees), and at a minimum at northwest aspects (hence category 2 is centred around 335 degrees). The slope of the ground was measured with a clinometer. Some analyses required slopes to be assigned to categories. These categories were: 1 = 0-16 degrees, 2 = 17-33 degrees, and 3 = >33 degrees.

BIOCLIM analysis

To determine features of the climate of individual sites the program BIOCLIM was used from the software package ANUCLIM 5.1 (Houlder *et al.* 2000). BIOCLIM interpolates climatic parameters for sites without long-term weather records from surrounding weather stations with long-term records. Of the many variables that BIOCLIM produces, variables applied to the present study were annual precipitation, precipitation of the driest quarter, maximum temperature of the warmest quarter, and minimum temperature of the coldest quarter. These data provide a useful guide to probable climate when study sites are scattered in areas of with few weather stations, such as in State forests and National Parks. This was the situation with this particular study. However, there is the problem that the more sparsely the weather stations are scattered the less certain one can be about the validity of the interpolated data.

One of the major issues in interpolating the climatic variables for a location from surrounding climate records is the variation that can occur over small distances, especially in hilly terrain. Neyland (1991) suggests that extrapolation from climate stations in Tasmania is generally not possible as local topographic effects produce steep climatic gradients. One such sharp gradient exists in eastern Tasmania from

the east coast to the crest of the eastern ranges in the hinterland. For example the annual average rainfall at Chain of Lagoons, 7 km east of Gray on the coast, is less than 800 mm, while the annual average rainfall at Gray on the crest of the range is more than 1200 mm. Neyland (1991) may be cautious about extrapolating climatic data in Tasmanian terrain, but some assumptions from knowledge of the prevailing weather patterns can be the basis of informed estimation of such climates. For example, significant rainfall in coastal eastern Tasmania is commonly related to the presence of low-pressure systems off the east coast directing a flow of moist air up onto the coastal ranges. In such a situation it is reasonable to assume that the highest rainfall will be experienced at the crest of the escarpment, where the cloud is forced up against the range. The data outputs of BIOCLIM for rainfall at some dry closed-forest locations in the eastern tiers near the escarpment edge were substantially underestimated. Two rainfall transects were drawn between climate stations that represented the Midlands, the Eastern Tiers plateau, and the east coast. One transect ran through Campbell Town, Lake Leake, and Bicheno, and the other transect ran through Oatlands, Lake Tooms, Swansea. These transects are approximate straight lines, and by combining the distance, elevation and 3 climate points it is possible to draw an approximated rainfall curve that has a maximum at the crest of the escarpment (Figure 3.2). Dry closed-forest locations that had potentially erroneous rainfall outputs from BIOCLIM were corrected using these rainfall curves. A suspected erroneous site was assigned to one of these two curves; whichever fell closest to the site. The position of a site can be approximately expressed as a combination of a) distance from Tiers escarpment and b) elevation. These two figures can then be read of the rainfall curves and a corrected rainfall estimated.

Campbell Town to Bicheno rainfall curve
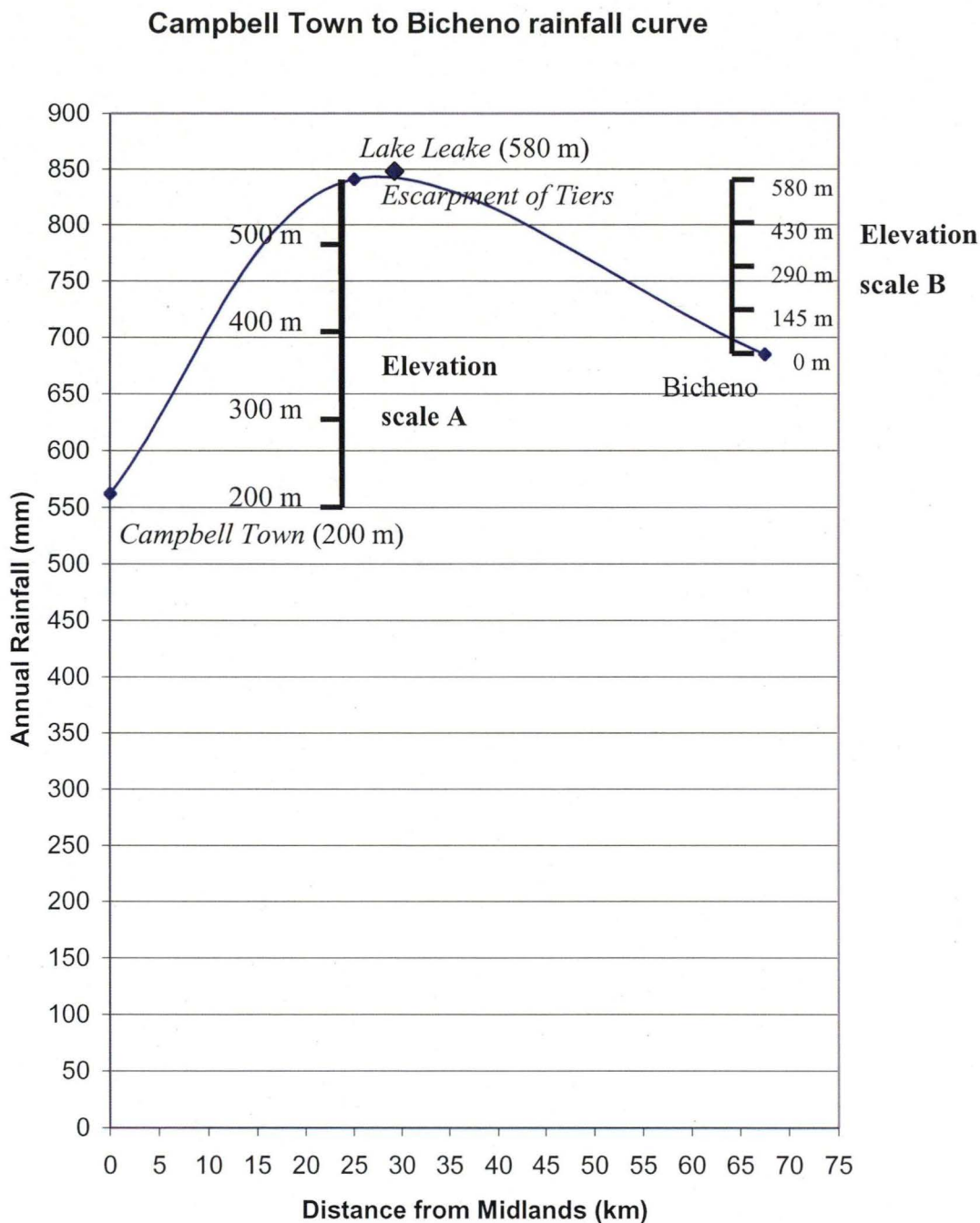
Figure 3.2 Estimated rainfall curve for Campbell Town to Bicheno. To use the graph: firstly, locate the site in km either side of the crest of the Eastern Tiers (28 km on the bottom distance scale) – find the corresponding point on the curve for that distance from the escarpment – record this as rainfall 1. Secondly, locate the elevation of the site from either the elevation scale A (west of the escarpment) or elevation scale B (east of the escarpment) – find the corresponding point on the curve for that elevation – record this as rainfall 2. Corrected rainfall figure is the average of rainfall 1 (distance correction) and rainfall 2 (elevation correction).

Data analysis

In the laboratory, soil pH and electrical conductivity (EC) of a 1:5 soil/water suspension were determined (Rayment & Higginson 1992). Extractable phosphorus and total nitrogen levels were measured using methods from Jackson (1967) and total organic carbon was determined using the Walkley & Black method (1934).

The species presence/absence data was examined using cluster analysis in PC-ORD (McCune & Mefford 1999). Exotic species and ephemeral species such as orchids were not included in the analysis. The settings used for the cluster analysis were Euclidean distance measure and Ward's group linkage method. Ward's method aims to obtain the minimum variance within groups. This method avoids distortion by minimising the error sum of squares, and is less prone than other methods to chaining (McCune and Grace 2002). The 25% information remaining level was chosen to cease aggregation, which produced six groups. A nonmetric multidimensional scaling (NMS) ordination of the species and environmental data was performed using the default settings in PC-ORD. NMS is a commonly used method for the graphical representation of data because of its distance-preserving properties, which retain the rank order of among-sample dissimilarities in the rank order of distances (Clarke 1993). Environmental vectors were fitted to the ordination space using a joint plot cut-off value of $R^2 = 0.15$.

TWINSPAN (Two-way Indicator Species Analysis) (Hill 1979) was performed in PC-ORD on the species presence-absence data and an ordered-table produced of the species by the 61 dry closed-forest stands. Exotic species, ephemeral species such as orchids, and singletons were not included in this analysis. This table was re-ordered into the sub-community groups derived from the cluster analysis. Following visual scrutiny changes were made to the ordering of the species where appropriate to provide coherent clumps of species presence and absence that could usefully distinguish floristic assemblages between the sub-communities (Appendix 1). Significant differences between dry closed-forest sub-communities were tested using one-way ANOVA for continuous variables with Tukey's pair-wise comparison, and χ^2 analysis for categorical variables. Some variables were stand-based and others were quadrat-based. A summary of the variables measured, their

abbreviations and any categories used in data analysis is presented in Table 3.1. All vascular plant nomenclature follows Buchanan (1999).

At the quadrat level, the original species cover values collected in the field were lumped into two large groups of "light cover" (cover values 1-3) and "dominant cover" (cover values 4-6) for analysis. For a particular closed-forest tree species, light cover quadrats represent a small area that is not particularly suited to the growth of that species while quadrats with a dominant cover represent a favourable locality. The strength and significance of the relationships between these cover classes for particular species and environmental variables were determined using χ^2.

Table 3.1 Environmental, edaphic and climatic variables, including abbreviations and class definition.

Variable	easting	northing	altitude (m a s l)	fern cover (%)	rock cover (%)	litter cover (%)	bryophyte cover (%)	fallen dead wood cover (%)	bare ground cover (%)	grass cover (%)	herb cover (%)	lily/sedge cover (%)	canopy cover (%)
Abbreviation	eas	nor	alt	fer	roc	lit	bry	fdw	bgd	gra	her	lil	can
categories	-	-	-	1 = 0-39 2 = >40	1 = 0-39 2 = 40-79 3 = >79	1 = 0-39 2 = >40	1 = 0-39 2 = >40	1 = 0-39 2 = 40-79 3 = >79	1 = 0-39 2 = 40-79 3 = >79	1 = 0-39 2 = 40-79 3 = >79	1 = 0-39 2 = 40-79 3 = >79	1 = 0-39 2 = 40-79 3 = >79	1 = <50 2 = 50-59 3 = 60-69 4 = >70

Variable	main canopy height (m)	height of emergent trees (m)	geology	geomorphology situation	dominant tree/shrub species	sub-dominant tree/shrub species	slope (degrees)	aspect (degrees)	mean annual precipitation (mm)	precipitation of the driest quarter of the year (mm)	temperature of the warmest quarter of the year (°C)	temperature of the coldest quarter of the year (°C)	soil pH
Abbreviation categories	mch 1 = 0-4 2 = 5-9 3 = 10-14 4 = 15-19 5 = 20-24	hem 1 = none 2 = 10-14 3 = 15-19 4 = >19	geol 1 = Jurassic dolerite 2 = sandstone, mudstone, siltstone 3 = other	geom 1 = gully 2 = steep gully with southern aspect 3 = riparian 4 = beneath cliffs 5 = miscellaneous	dom 1 = *Beyeria viscosa* 2 = *Olearia argophylla* 3 = *Pomaderris apetala* 4 = other species 5 = mixed dominance 6 = no obvious dominant	sub 1 = *Beyeria viscosa* 2 = *Olearia argophylla* 3 = *Pomaderris apetala* 4 = other species 5 = mixed dominance 6 = no obvious dominant	slo 1 = 0-16 2 = 17-33 3 = >33	asp 1 = 45-225 2 = 226-44	anpr -	drqpr -	tempwaqu -	tempcoqu -	pH -

Variable	soil electrical conductivity (µS/cm)	total nitrogen (%)	extractable phosphorus (ppm)	total organic carbon (%)	Area of patch (ha)	Maximum patch width (m)	Total patch length (m)	Length from top to middle of patch (m)	Length from bottom to middle of patch (m)	Stand altitude range (m)	Height of main protective ridge (m) (non-gully stands only)	Height of ridge at head of gully (m)	Height of ridge on right side of gully (m) (facing downstream)
Abbreviation categories	EC -	total N -	extr P -	total C -	area -	maxpawi -	topale -	letm -	lebm -	altr -	hemr -	hehog -	hers -

Variable	Height of ridge NW direction from gully (m)	Height of ridge on left side of gully (m) (facing downstream)	Slope of main protective ridge (degrees) (non-gully stands only)	Slope of head of gully (degrees)	Slope of right side of gully (degrees) (facing downstream)	Slope of left side of gully (degrees) (facing downstream)	Slope of NW side of gully (degrees)	Distance between left and right ridges above gully (m)	Distance of stand from coast (km)
Abbreviation categories	heNW -	hels -	slmr -	slhog -	slrs -	slls -	slNW -	dislr -	disco -

Results

Vascular plant species survey

Determination of floristic sub-communities

A total of 173 vascular plant taxa were recorded. There are relatively even numbers of taxa of tree, shrub, herb, and ferns (Table 3.2). Sixteen species were exotic.

Lifeform	no. of taxa	no. of identified exotic taxa
tree	34	3
shrub	30	3
herb	42	7
fern	30	0
grass	13	2
scrambler/climber	8	2
orchid	5	0
lily/sedge	11	0
total	173	17

Table 3.2 Breakdown of vascular species recorded from Tasmanian dry closed-forest into lifeform and origin groups.

The most commonly recorded vascular plant species were the trees *Pittosporum bicolor, Acacia dealbata, Pomaderris apetala, Notelaea ligustrina, Beyeria viscosa, Olearia argophylla* and *Bedfordia salcina*, the shrub *Coprosma quadrifida*, the ferns *Polystichum proliferum, Pteridium esculentum, Microsorum pustulatum, Asplenium flabellifolium*, and the herbs *Hydrocotyle hirta* and *Oxalis perennans* (see Appendix 2 for a table of mean frequencies of taxa by sub-community). A full list of the vascular plant species of Tasmanian dry closed-forest and their lifeforms is shown in Appendix 3.

A cluster analysis of the species composition of 61 dry closed-forest stands is displayed in Figure 3.3. Six dry closed-forest sub-communities were accepted.
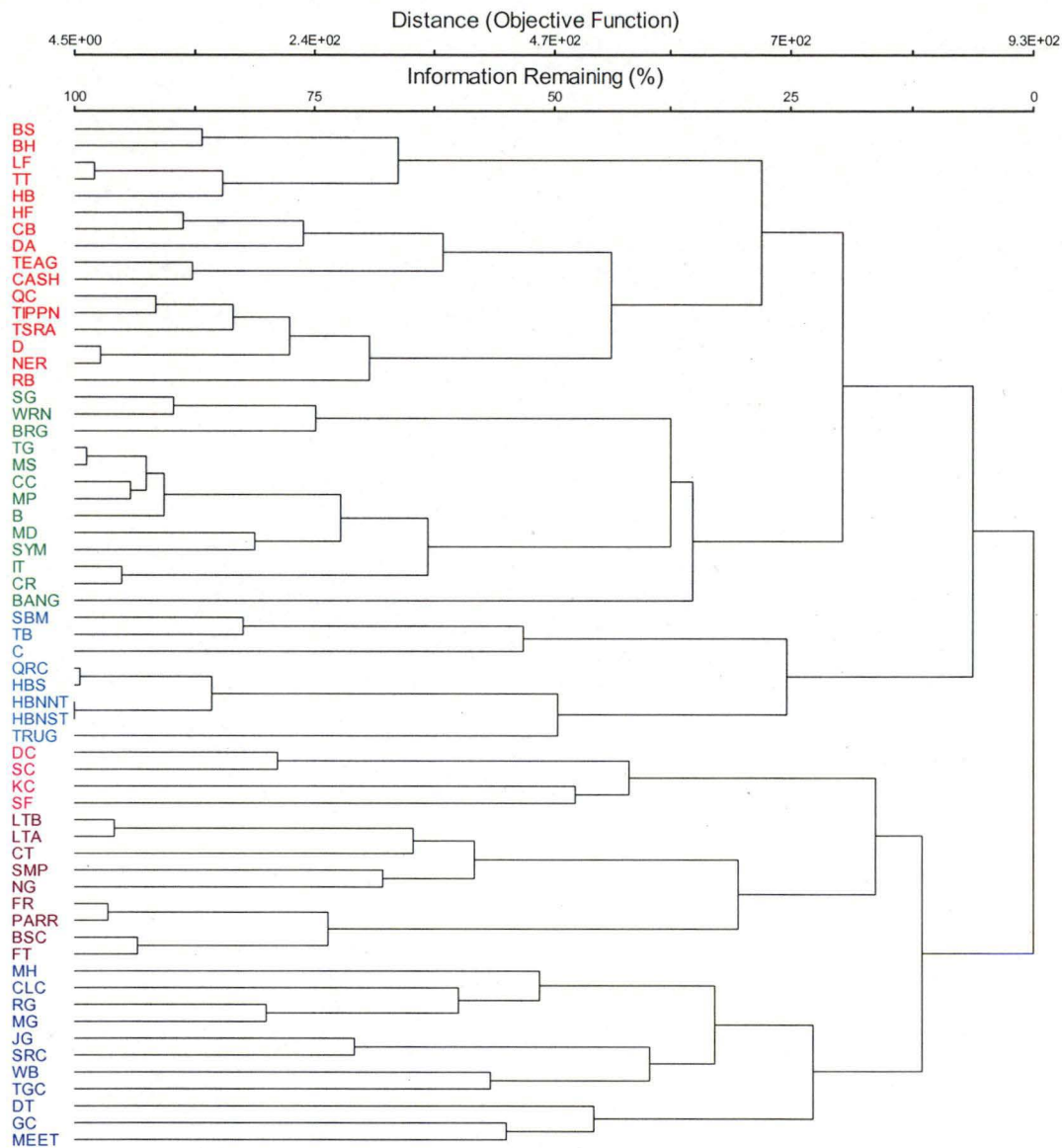
Figure 3.3 Dry closed-forest species composition groupings at 61 stands (Cluster analysis using Ward's Method and Euclidean distance measure). Different colours distinguish groups.

Description of floristic sub-communities

Common vascular plant species are identified as those species that occur at more than 1/3 of stands of a sub-community. Characteristic species are those species that occur at 1/3 or more of the stands in a sub-community with the limitation that no more than 2 of the sub-communities record this species in that frequency. In each sub-community description, stands are listed alphabetically and species are listed alphabetically by lifeform. For reference to the floristic sub-community descriptions, Figure 3.4 is a map of the bioregions of Tasmania.
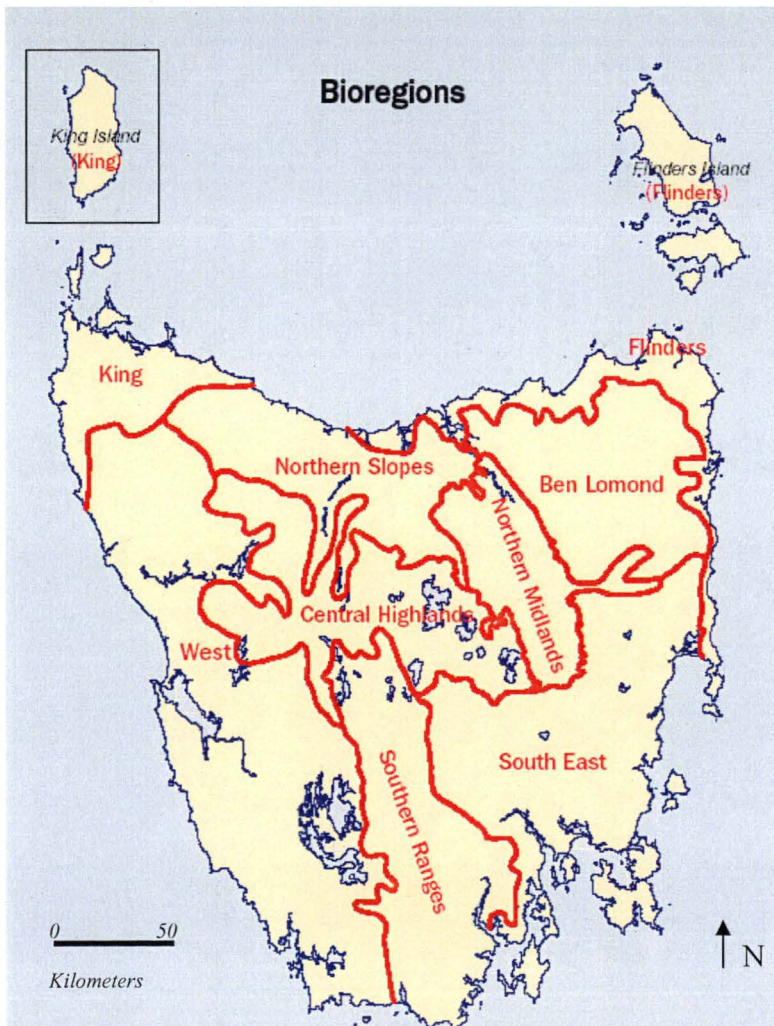
Figure 3.4 Bioregions of Tasmania (source: Department of Primary Industries, Water & Environment. Produced by Australian Bureau of Statistics, Hobart.

Sub-community A

(n = 16 stands) - Bedggood Hill, Block & Stable Ck, Casuarina Highway, Cloudy Bay, Daley's, Douglas Apsley, Harding's Falls, Hellfire Bluff, Lost Falls, North Esk River, Quoin Cliffs, Roaring Beach, Teagardens, Three Thumbs, Tippogoree Hills, Trevallyn SRA.
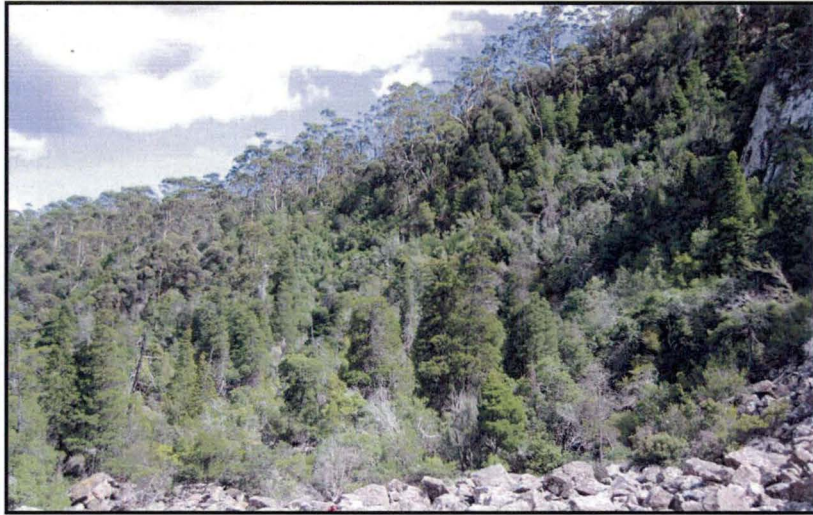
Plate 3.1 Sub-community A beneath coastal cliffs. Hellfire Bluff, southeast Tasmania.
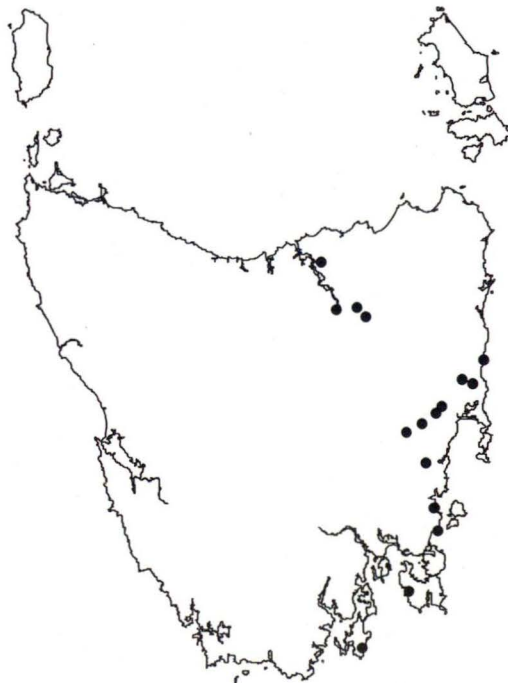
Figure 3.5 The distribution of sub-community A.

Common vascular plant species

Acaena novae-zelandiae	herb	*Lepidosperma gunnii*	lily/sedge
Hydocotyle hirta	herb	*Clematis aristata*	climber
Oxalis perennans	herb	*Coprosma quadrifida*	shrub
Urtica incisa	herb	*Pimelea drupacea*	shrub
Viola hederacea	herb	*Bedfordia salicina*	shrub/tree
Asplenium flabellifolium	fern	*Beyeria viscosa*	shrub/tree
Ctenopteris heterophylla	fern	*Pomaderris apetala*	shrub/tree
Dicksonia antarctica	fern	*Zieria arborescens*	shrub/tree
Hymenophyllum cupressiforme	fern	*Acacia dealbata*	tree
Microsorum pustulatum	fern	*Acacia melanoxylon*	tree
Pellaea falcata	fern	*Exocarpos cupressiformis*	tree
Polystichum proliferum	fern	*Notelaea ligustrina*	tree
Pteridium esculentum	fern	*Olearia argophylla*	tree
Rumohra adiantiformis	fern	*Pittosporum bicolor*	tree

The most characteristic plant species of this sub-community are the sedge *Lepidosperma gunnii* and the fern *Hymenophyllum cupressiforme*.

Recorded mainly in the South East bioregion of Tasmania, this sub-community is also found to a lesser extent in the Ben Lomond, Northern Midlands and Flinders bioregions (Figure 3.5). This sub-community contains most of the common dry closed-forest plant species and for that reason can be viewed as being a generic form of dry closed-forest. This formation has a widespread distribution and a broad environmental range. For example the altitudinal range is between 100 and 510 m a.s.l. Stand areas were estimated at between 1 and 8.2 hectares. Precipitation ranged from 627 - 1083 mm p.a., with rainfall in the driest quarter of 136 - 211 mm. Except for a site at Teagardens Ck, which occurred on granite, all examples of this community were on dolerite. The geomorphic situation of this community is varied and includes gullies, beneath coastal cliffs and waterfalls and on flat benches at gully heads. With few characteristic species, this community is best distinguished by absence of the species that define the other sub-communities.

Sub-community B

(n = 13 stands) - Bangor, Bicheno, Bluff River Gorge, Carlton River, Cunny Creek, Iles Tier, Morrison Sugarloaf, Mount Direction, Mount Phipps, Spinning Gum CA, Symons Creek, Tiger Gully, Wilson's Ridge nth.

Plate 3.2 Sub-community B at Symons creek east of the Tamar River in northern Tasmania.
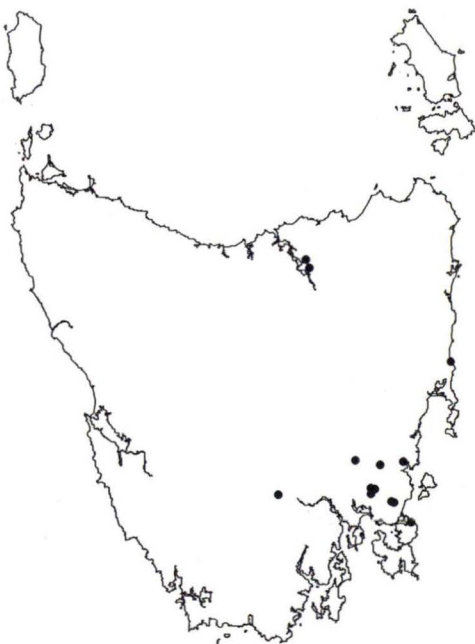
Figure 3.6 The distribution of sub-community B.

Common vascular plant species

Hydrocotyle hirta	herb	*Acacia verticillata*	shrub/tree
Oxalis perennans	herb	*Asterotrichion discolor*	shrub/tree
Urtica incisa	herb	*Bedfordia salicina*	shrub/tree
Viola hederacea	herb	*Beyeria viscosa*	shrub/tree
Asplenium flabellifolium	fern	*Pomaderris apetala*	shrub/tree
Dicksonia antarctica	fern	*Zieria arborescens*	shrub/tree
Polystichum proliferum	fern	*Acacia dealbata*	tree
Pteridium esculentum	fern	*Exocarpos cupressiformis*	tree
Lepidosperma laterale	lily/sedge	*Notelaea ligustrina*	tree
Lomandra longifolia	lily/sedge	*Olearia argophylla*	tree
Clematis aristata	climber	*Pittosporum bicolor*	tree
Coprosma quadrifida	shrub	*Acacia melanoxylon*	tree
Lomatia tinctoria	shrub	*Prostanthera lasianthos*	tree
Olearia lirata	shrub		

Characteristic species of this sub-community are the lily/sedge *Lomandra longifolia* and the shrub/tree *Asterotrichion discolor*. The important defining species of this sub-community is *A. discolor,* a Tasmanian endemic tall-shrub species from the southeast of the state. *A. discolor* may be one of very few plant species that is virtually an obligate component of dry closed-forest. Emerging after disturbance, most often resulting from bushfire, *A. discolor* forms dense stands on the boundary of dry closed-forest stands. When mature this species is present as distinctive tall, bare emergent single stems with a tuft of foliage at the very top.

This sub-community occurs mainly in the South East bioregion of Tasmania with one site just outside within the border of the Southern Ranges bioregion at Cunny Creek near Westerway (Figure 3.6). There are also a few isolated occurrences in the Northern Midlands bioregion in the hills on the east side of the Tamar River. Patch size varied substantially, from 0.8 hectares to 13.3 hectares of riparian forest at Symons Creek on the east Tamar. Site altitude also varied considerably from 2 m a.s.l at the Bangor stand near Dunalley in the lee of sand dunes to 420 m a.s.l at Spinning Gum CA in the southern Midlands. The driest location was Spinning Gum CA with an average annual rainfall of 664 mm while the wettest site was Mount

Direction on the East Tamar where the average annual rainfall is 1053 mm. Spinning Gum CA also experiences a low driest quarter rainfall of 142 mm, while the highest rainfall for the driest quarter of the year was 183 mm, shared between Bicheno on the east coast and Iles Tier in the Carlton River watershed. Most stands occurred on dolerite geology. The stand at Spinning Gum CA was beneath a sandstone cliff-line but the soil was enriched considerably by erosion of the dolerite upslope of the sandstone. Bluff River Gorge was on soil derived from sandstone and the stand at Bangor was on Quaternary deposits of sand behind sand dunes.

Sub-community C

(n = 8 stands) - Coningham CA, Hinsby Beach sth, Hinsby Beach nth (nth tributary), Hinsby Beach nth (sth tributary), Quarry Reserve Creek, South Brown Mtn, Tinderbox, Truganini Reserve.

Plate 3.3 Sub-community C at Tinderbox, in southeast Tasmania.
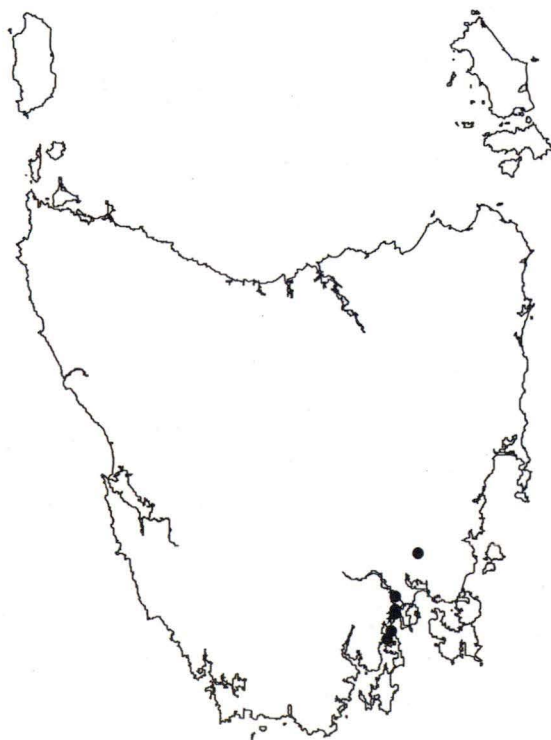
Figure 3.7 The distribution of sub-community C.

Common vascular plant species

Cardamine lilacina	herb	*Clematis aristata*	climber
Galium australe	herb	*Coprosma quadrifida*	shrub
Goodenia ovata	herb	*Correa reflexa*	shrub
Hydocotyle hirta	herb	*Olearia viscosa*	shrub
Oxalis perennans	herb	*Zieria arborescens*	shrub
Senecio linearifolius	herb	*Acacia verticillata*	shrub/tree
Senecio minimus	herb	*Asterotrichion discolor*	shrub/tree
Urtica incisa	herb	*Bedfordia salicina*	shrub/tree
Viola hederacea	herb	*Bursaria spinosa*	shrub/tree
Asplenium flabellifolium	fern	*Pomaderris apetala*	shrub/tree
Asplenium flabellifolium	fern	*Acacia melanoxylon*	tree
Microsorum pustulatum	fern	*Exocarpos cupressiformis*	tree
Polystichum proliferum	fern	*Notelaea ligustrina*	tree
Dianella revoluta	lily/sedge	*Olearia argophylla*	tree
Dianella tasmanica	lily/sedge	*Pittosporum bicolor*	tree
Lomandra longifolia	lily/sedge	*Prostanthera lasianthos*	tree
Billardiera longiflora	climber	*Poa labillardierei*	grass

Characteristic plant species of this sub-community are the herbs *Cardamine lilacina, Galium australe, Goodenia ovata, Senecio linearifolius,* and *Senecio minimus,* the fern *Asplenium bulbiferum,* the lily/sedges *Dianella tasmanica, Dianella revoluta,* and *Lomandra longifolia,* the climber *Billardiera longiflora,* the shrub *Correa reflexa,* the shrub/trees *Asterotrichion discolor* and *Bursaria spinosa,* the tree *Prostanthera lasianthos,* and the grass *Poa labillardierei.*

This sub-community is found within 50 km of Hobart in the South East bioregion of Tasmania (Figure 3.7). Stand size varies considerably depending on the geomorphic situation of the stand. For example the smallest stand surveyed was 0.8 hectares in size in a gully in the hills behind Taroona south of Hobart. In contrast there is an extensive riparian example of 7 hectares on the southern slopes of Brown Mountain near Runnymede. The altitudinal range of stands was 110 – 340 m a.s.l. The community occurred within a narrow precipitation band with rainfall estimated to be 733 - 837 mm p.a., with rainfall in the driest quarter of 158- 174 mm. Note that the stand at South Brown Mountain contained *Atherosperma*

moschatum in the upper reaches of the creek, which could indicate the climate at this stand is a little wetter than the prediction for the location derived by the BIOCLIM program. All of the representative stands of this sub-community occur on dolerite geology and the geomorphic situation is in gullies, ranging from small shallow gullies to deep extensive gullies able to support long riparian stands. The characteristic plant species of this sub-community are generally light-loving and hardy, such as *Bursaria spinosa* and *Correa reflexa*. Also, there are a number of tussock-forming monocots such as *Dianella* spp. and *Lomandra longifolia*.

Sub-community D

(n = 4 stands) - Dalco Creek, Knight's Creek, Snug Falls, Spring Creek.

Plate 3.4 Sub-community D at Dalco Creek, northeast of Southport in southern Tasmania.
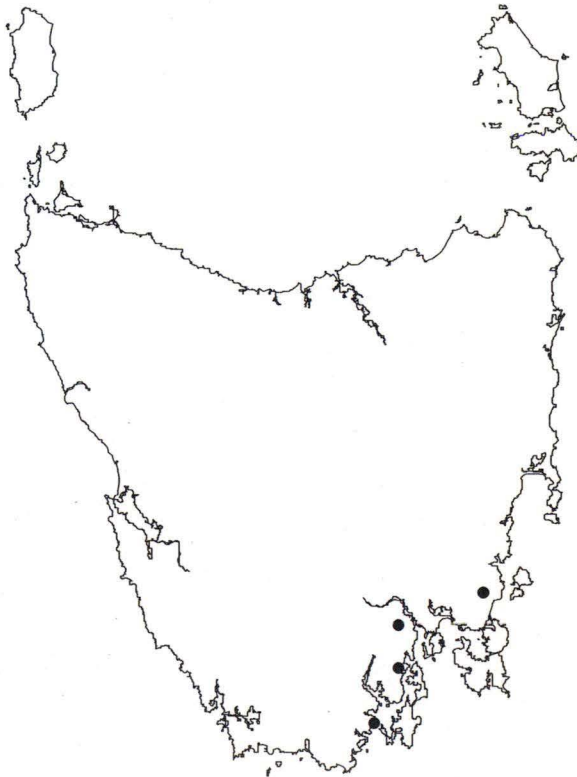
Figure 3.8 The distribution of sub-community D.

Common vascular plant species

Hydrocotyle hirta	herb	*Aristotelia peduncularis*	shrub
Oxalis perennans	herb	*Coprosma quadrifida*	shrub
Urtica incisa	herb	*Cyathodes divaricata*	shrub
Blechnum chambersii	fern	*Cyathodes glauca*	shrub
Blechnum wattsii	fern	*Gaultheria hispida*	shrub
Ctenopteris heterophylla	fern	*Olearia viscosa*	shrub
Dicksonia antarctica	fern	*Pimelea drupacea*	shrub
Grammitis billardierei	fern	*Bedfordia salicina*	shrub/tree
Histiopteris incisa	fern	*Pomaderris apetala*	shrub/tree
Huperzia varia	fern	*Acacia dealbata*	tree
Hymenophyllum australe	fern	*Acacia melanoxylon*	tree
Microsorum pustulatum	fern	*Atherosperma moschatum*	tree
Polystichum proliferum	fern	*Notelaea ligustrina*	tree
Pteridium esculentum	fern	*Nothofagus cunninghamii*	tree
Gahnia grandis	lily/sedge	*Olearia argophylla*	tree
Lepidosperma laterale	lily/sedge	*Pittosporum bicolor*	tree
Clematis aristata	climber	*Prostanthera lasianthos*	tree
Acacia riceana	shrub		

Characteristic plant species of this sub-community are the ferns *Blechnum chambersii, Grammitis billardierei, Histiopteris incisa, Hymenophyllum australe,* and *Huperzia varia,* the lily/sedge *Gahnia grandis,* the shrubs *Acacia riceana, Aristotelia peduncularis, Cyathodes divaricata, Cyathodes glauca,* and *Gaultheria hispida,* and the trees *Atherosperma moschatum, Prostanthera lasianthos,* and *Nothofagus cunninghamii.*

Except for one site at Dalco Creek in the Southern Ranges bioregion all examples of this community were found in the South East bioregion of Tasmania (Figure 3.8) at altitudes between 150 - 660 m a.s.l. Examples of this community had estimated areas of between 1.5 and 3.9 hectares. This sub-community represents the wet end of the spectrum of dry closed-forest, and shows affinities to both dry closed-forest and temperate rainforest. Annual average precipitation ranged from 847 mm at Spring Creek near Nugent to 1208 mm at Dalco Creek near Southport, with rainfall in the driest quarter of 180 mm at Spring Creek and 239 mm at Knight's Creek on

the slopes of Mt Wellington. Except for the site at Snug Falls, which occurs on sedimentary geology, this community was found on dolerite-derived soils. The geomorphic situation of this community is in protected locations within deep gullies or beneath waterfalls, as at Snug Falls. Eleven out of thirty-four of the common plant species recorded were ferns, a testament to the moist microclimate this sub-community occupies.

Sub-community E

(n = 9 stands) - Big Sassy Creek, Cluan Tiers, Fern Tree, Forester River, Loila Tier A, Loila Tier B, Notley Gorge, Parr's Rivulet, St Mary's Pass.

Plate 3.5 Sub-community E at Big Sassy Creek in the Eastern Tiers.
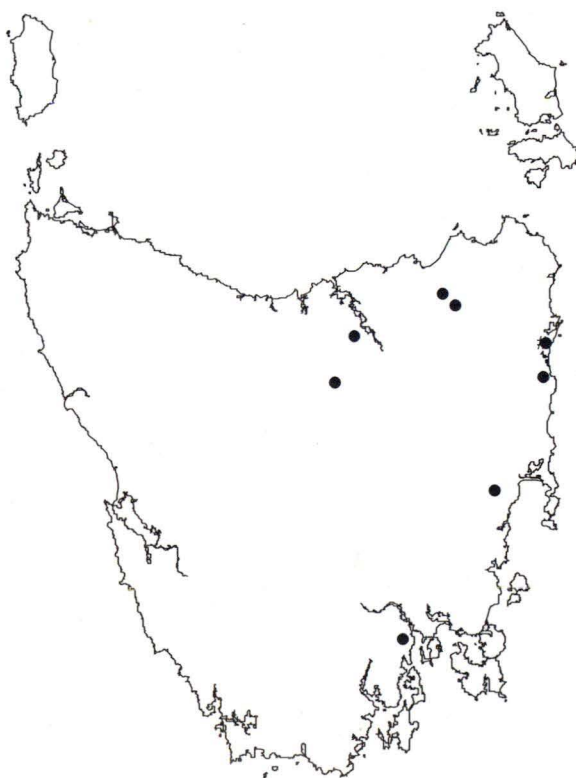
Figure 3.9 The distribution of sub-community E.

Common vascular plant species

Urtica incisa	herb	*Asplenium flabellifolium*	fern
Oxalis perennans	herb	*Clematis aristata*	climber
Hydrocotyle hirta	herb	*Parsonsia brownii*	climber
Blechnum wattsii	fern	*Lepidosperma laterale*	lily/sedge
Ctenopteris heterophylla	fern	*Coprosma quadrifida*	shrub
Grammitis billardierei	fern	*Olearia lirata*	shrub
Pteris tremula	fern	*Pimelea drupacea*	shrub
Blechnum nudum	fern	*Bedfordia salicina*	shrub/tree
Histiopteris incisa	fern	*Zieria arborescens*	shrub/tree
Rumohra adiantiformis	fern	*Beyeria viscosa*	shrub/tree
Asplenium bulbiferum	fern	*Bursaria spinosa*	shrub/tree
Polyphlebium venosum	fern	*Pomaderris apetala*	shrub/tree
Hymenophyllum cupressiforme	fern	*Atherosperma moschatum*	tree
Pellaea falcata	fern	*Olearia argophylla*	tree
Hymenophyllum rarum	fern	*Acacia dealbata*	tree
Dicksonia antarctica	fern	*Pittosporum bicolor*	tree
Polystichum proliferum	fern	*Acacia melanoxylon*	tree
Microsorum pustulatum	fern	*Notelaea ligustrina*	tree
Pteridium esculentum	fern		

Characteristic plant species of this sub-community are the ferns *Asplenium bulbiferum, Grammitis billardierei, Histiopteris incisa, Hymenophyllum cupressiforme, Hymenophyllum rarum, Pellaea falcata, Polyphlebium venosum, Pteris tremula, Rumohra adiantiformis* and *Blechnum nudum,* the climber *Parsonsia brownii,* the shrub/tree *Bursaria spinosa,* and the tree *Atherosperma moschatum.* The common plant species of this sub-community include a large proportion of ferns (17 out of 37 species), which makes this sub-community the most fern rich of all the dry closed-forest formations.

The stands in this sub-community are widely spread across the state and occur in the South East, Flinders, Ben Lomond and Northern Slopes bioregions (Figure 3.9). Stand sizes range from 1.1 hectares to a large 13.5 hectares riparian example at St Marys Pass. Site altitudes are between 150 and 530 m a.s.l. These stands occur in

a relatively moist climate with an average annual rainfall of between 825 and 1083 mm. The rainfall in the driest quarter is 157- 213 mm. A large proportion (7 out of 9) of these stands grow on non-dolerite geology, specifically, granite in the north east, and quartzwacke, and rhyodacitic pyroclastics in the east. The stand at Cluan Tiers was in a gully beneath sedimentary cliffs with some dolerite enrichment from upslope erosion. Most sites were recorded from gully situations, but stands were also observed in gorges below waterfalls, on flat benches at gully heads and across steep south and east facing slopes.

Sub-community F

(n = 11 stands) - Clements Creek, Diamond Tier, Goatrock Creek, Jonathans Gully, Meetus Falls, Mount Henry, Mountain Gully, Razorback Gully, Saddle Rock Creek, Tater Garden Creek, Waterfall Bay.
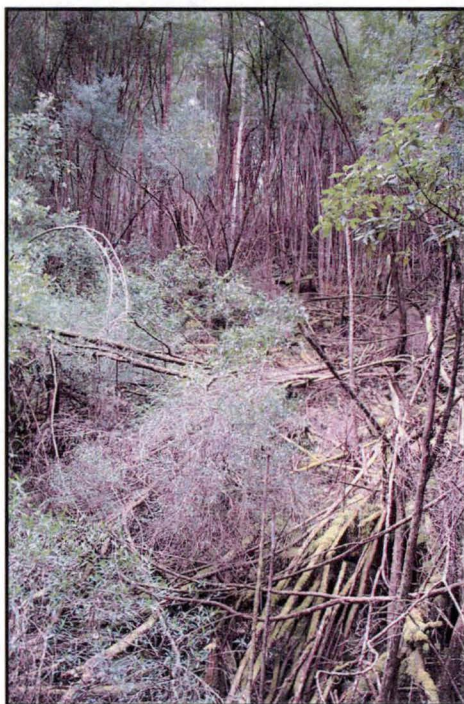
Plate 3.6 Sub-community F at Razorback gully, near the boundary of Buckland Military Training Area in southeast Tasmania.

Figure 3.10 the distribution of sub-community F.

Common vascular plant species

Acaena novae-zealandiae	herb	*Olearia lirata*	shrub
Galium australe	herb	*Olearia viscosa*	shrub
Geranium potentilloides	herb	*Pimelea drupacea*	shrub
Hydrocotyle hirta	herb	*Zieria arborescens*	shrub
Oxalis perennans	herb	*Acacia verticillata*	shrub/tree
Urtica incisa	herb	*Bedfordia salicina*	shrub/tree
Viola hederacea	herb	*Beyeria viscosa*	shrub/tree
Asplenium flabellifolium	fern	*Pomaderris apetala*	shrub/tree
Blechnum wattsii	fern	*Notelaea ligustrina*	tree
Ctenopteris heterophylla	fern	*Olearia argophylla*	tree
Dicksonia antarctica	fern	*Poa labillardierei*	grass
Microsorum pustulatum	fern	*Lepidosperma laterale*	lily/sedge
Polystichum proliferum	fern	*Luzula* spp.	lily/sedge
Pteridium esculentum	fern	*Clematis aristata*	climber
Carex spp.	lily/sedge		
Coprosma quadrifida	shrub		
Cyathodes glauca	shrub		

Characteristic plant species of this sub-community are the herbs *Galium australe*, *Geranium potentilloides*, the lily/sedges *Luzula* spp, and *Carex* spp., the shrub *Cyathodes glauca*, and the grass *Poa labillardierei*.

This sub-community occurs in the South East bioregion of Tasmania (Figure 3.10). Stands are found in the hilly country of the east coast hinterland. It typically occurs in gullies, but this sub-community was also recorded growing on steep-south facing slopes at Clements Creek, beneath a waterfall at Meetus Falls and on sea cliffs at Waterfall Bay. Stand areas range between 1.3 and 5.5 hectares. Altitude is in the range of 120- 590 m. Waterfall Bay seems to be an outlier, with a wetter climate and different geology to the other sites. The specifics of Waterfall Bay's site environment are bracketed in the following summary because of its outlier nature. Average annual precipitation is 628 - 830 (1031) mm with a minimum quarterly rainfall ranging between 127.5 -162.8 (203) mm. Except for the site at Waterfall Bay (sedimentary) all of the stands are on dolerite geology.

Floristic variability relating to the environment

a) Between stands

The NMS ordination of the species and environmental data for the 61 stands was labelled by the 6 dry closed-forest sub-communities derived from the cluster analysis, and shows approximate agreement with these groupings (Figure 3.11). Environmental vectors that showed some linear trend with respect to the location of stands in ordination space were mean annual precipitation, soil pH and northing (Figure 3.11).
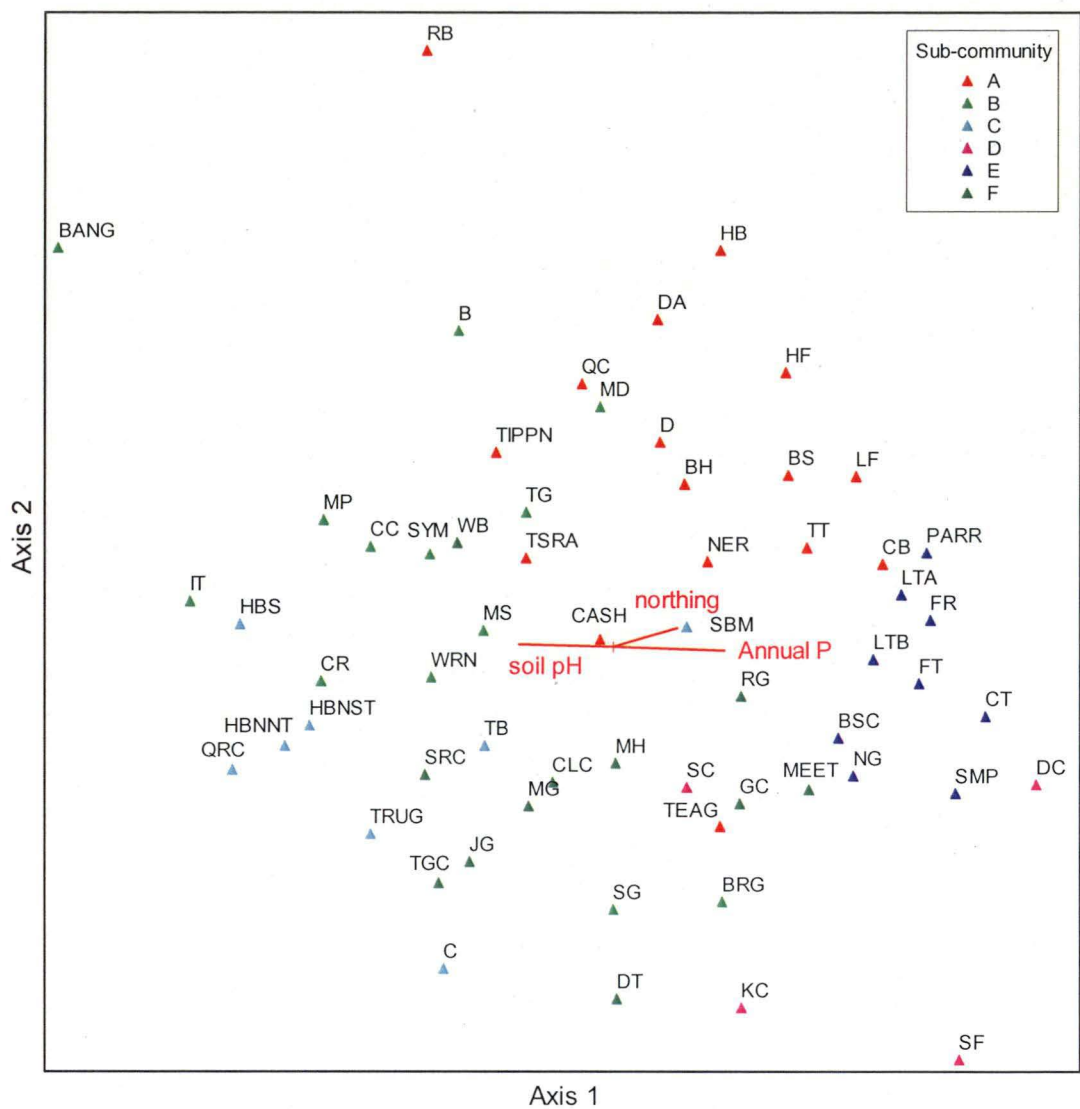
Figure 3.11 NMS ordination of the species composition of 61 dry closed-forest stands showing environmental vectors. Cut-off value for vectors is $R^2 = 0.15$. Annual P = mean annual precipitation. Sub-community groups were derived from cluster analysis.

In agreement with the ordination, further analysis revealed that the variables identified in the ordination and also the variable precipitation of the driest quarter showed significant differences ($p < 0.05$) between sub-communities (Figure 3.12).

Pair-wise comparison of sub-communities in terms of continuous environmental variables is shown in Table 3.3. This table also contains the outcome of pair-wise analysis of significant differences between sub-communities with respect to

categorical environmental variables. These categorical variables are geology, geomorphology, rock cover, fern cover, canopy cover, and aspect.

Not all sub-communities pairs had variables that significantly differentiated them at the level of P < 0.05 (Table 3.3). Mean annual precipitation significantly differed between the most sub-community pairs. Northing had the next most numerous total of significant pairings, then soil pH and precipitation of the driest quarter.

The significance levels of these differences for the continuous variables are displayed in Table 3.4 along with the mean values of each variable for each sub-community. The majority of the variables for which data were collected did not significantly vary between sub-communities. The mean values of categorical variables are displayed in Table 3.5. Refer to the mean values in Tables 3.4 and 3.5 for verification of the trends described in the following descriptions of differences in environmental variables between sub-communities.

Northing varies significantly between sub-communities, indicating some geographic separation of sub-communities. Sub-communities A, B and E show no clear distinct regionalism. The other sub-communties have stands that are concentrated in one particular region of the state. Specifically, sub-community C is found in the Hobart region, sub-community D is found in the south of the state, and sub-community F occurs in the Eastern Tiers.

The most obvious difference in soil pH between sub-communities is between sub-community C, and all other sub-communities except sub-community F. Sub-community C has a considerably higher soil pH than the soil from other sub-communities.

Mean annual precipitation was significantly higher for sub-community D compared with all other communities apart from sub-community E. Mean annual precipitation was also significantly higher for sub-community E compared with all other sub-communities apart from sub-community D. Sub-community D has significantly higher dry quarter precipitation than sub-communities A, B, C, and F.

The maximum temperature of the warmest quarter significantly differed between sub-communities A and D. Stands from sub-community A have the highest

average maximum temperature of the warmest quarter of all the sub-communities, while sub-community D has the lowest average temperature.

The χ^2 comparisons for geology showed a significant difference between sub-communities A and E, and C and E. Both A and C are found mainly on dolerite, while a large proportion (7 out of 9) of the stands from the latter sub-community occuring on granite, quartzwacke, or rhyodacitic pyroclastics.

Geomorphology significantly varies between sub-communities A and C. C consists of stands that occur mostly in deep gullies (63% of the stands of this sub-community), while A has only 1 stand that occurs in a deep gully (6% of the stands of this sub-community).

The χ^2 comparisons for rock cover were significant between sub-communities A and E. The same sub-communities also had a significance difference in fern cover. Sub-community A has significantly higher rock cover than sub-community E. In contrast sub-community A has significantly less fern cover than sub-community E.

Canopy cover varies significantly between sub-communities A and C, and A and F. Sub-communities C and F both have significantly less dense canopy cover than sub-community A.

Aspect varies significantly between sub-communities C and E. Sub-community E has significantly more stands than sub-community C with an aspect in the range of centred around northwest (226 to 44 degrees).

Dry Rainforest Sub-Community versus Northing

Dry rainforest Sub-community versus soil pH
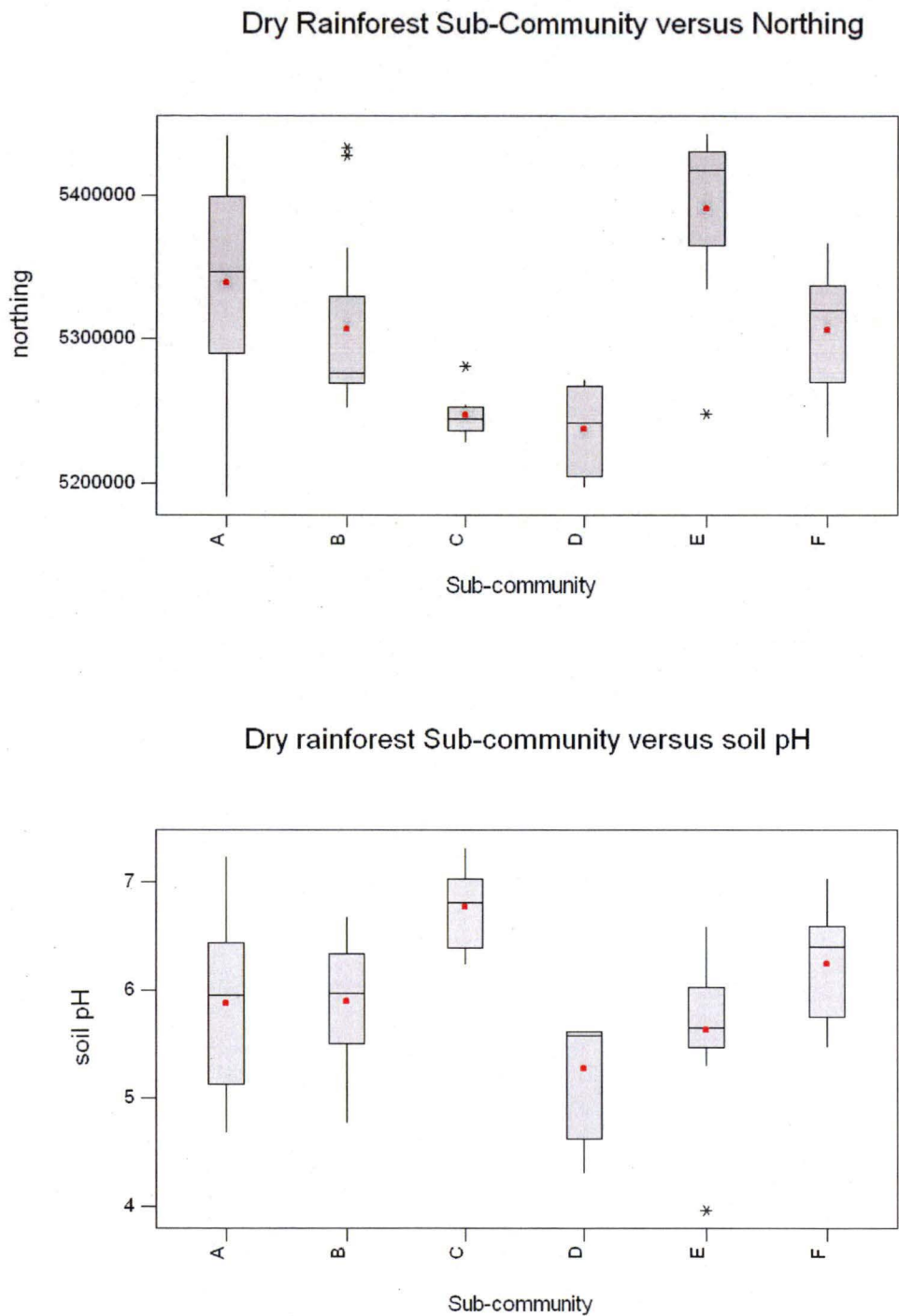
Figure 3.12 Boxplot diagrams of continuous environmental variables that showed significant differences (p ≤ 0.05) between sub-communities. (On interpreting the boxplots - Solid circles are mean values, horizontal lines within the boxes are the median values, asterisks are outlier values, the box bottom is at the 25th percentile and the box top is at the 75th percentile. Whiskers extending from the boxes designate the highest and lowest values, asterisks are outliers).

Dry Rainforest Sub-community versus Mean Annual Precipitation (mm)
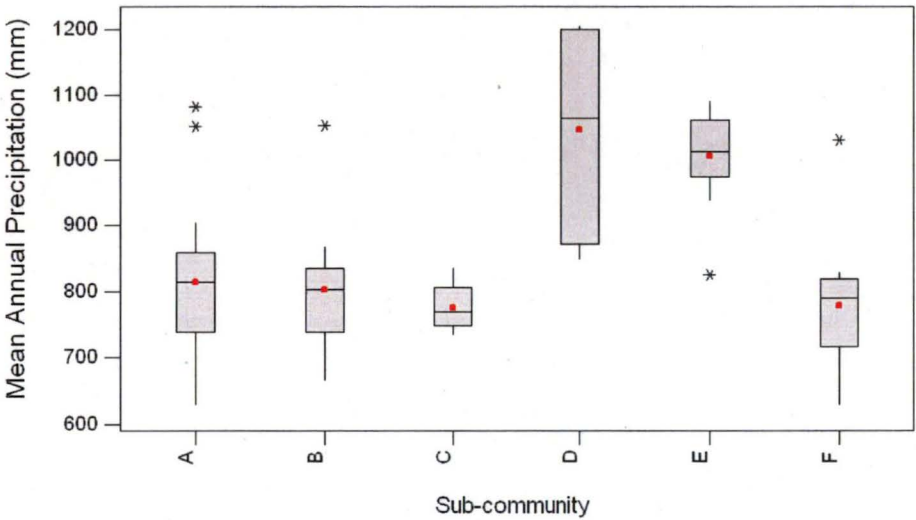
Dry Rainforest sub-community versus Mean Precipitation of the Driest Quarter (mm)
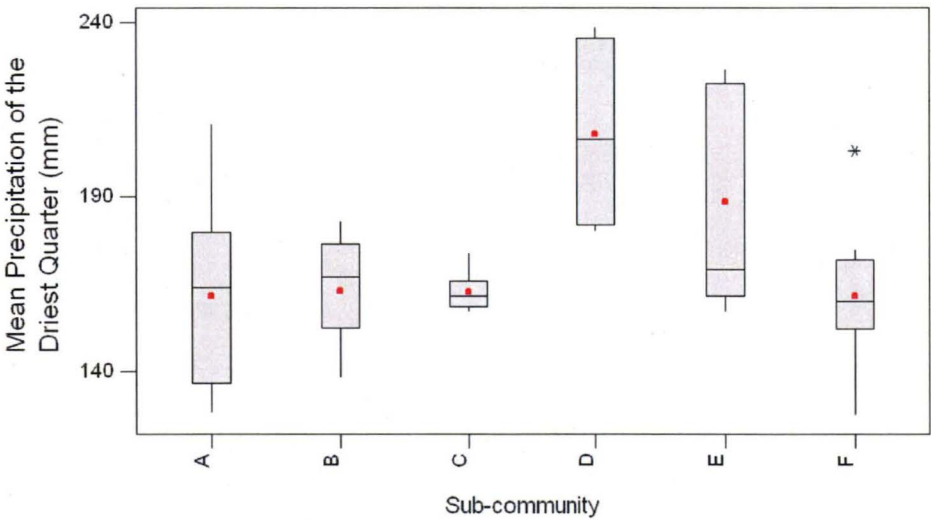
Figure 3.12 coninued. (Boxplot diagrams of continuous environmental variables that showed significant differences (p ≤ 0.05) between sub-communities).

Table 3.3 Significant differences (P < 0.05) between dry closed-forest sub-communities for environmental variables. Analysis undertaken was one-way Anova with Tukey's comparison for continuous variables and χ^2 analysis for categorical variables. See Table 3.1 for variable abbreviations and category specifics.

	A	B	C	D	E	F
A	–		nor, pH, geom, can	nor, anpr, drqpr, tempwaqu	anpr, geol, roc, fer	can
B		–	pH	anpr, drqpr, litt	nor, anpr	
C	nor, pH, geom, can	pH	–	pH, anpr, drqpr	nor, pH, anpr, geol, asp	
D	nor, anpr, drqpr, tempwaqu	anpr, drqpr, litt	pH, anpr, drqpr	–	nor	anpr, drqpr
E	anpr, geol, roc, fer	nor, anpr	nor, pH, anpr, geol, asp	nor	–	nor, anpr
F	can			anpr, drqpr	nor, anpr	–

Table 3.4 Mean values for significant variables by sub-community. See Table 3.1 for category explanations. Data were analysed using one-way Anova with Tukey's comparison for continuous variables and χ^2 analysis for categorical variables.

	A	B	C	D	E	F
Northing (p <0.001)	5339266.1	5306915.4	5247480.6	5238298.3	5391158.7	5306745.5
soil pH (p = 0.002)	5.9	5.9	6.8	5.3	5.6	6.2
mean annual precipitation (mm) (p <0.001)	814.1	803.1	775.1	1045.8	1005.9	778.6
precipitation of the driest quarter (mm) (p = 0.002)	161.6	163.0	162.9	208.0	188.4	161.6
temperature of the warmest quarter (p = 0.050)	21.1	20.8	20.5	19.2	20.9	20.2
rock cover (category) (p = 0.040)	2.2	1.6	1.4	1.8	1.3	1.8
aspect (category) (p = 0.030)	1.1	1.2	1.0	1.3	1.4	1.1
fern cover (category) (p = 0.010)	1.0	1.2	1.1	1.0	1.3	1.1
canopy cover (category) (p = 0.020)	2.8	1.9	1.6	2.5	2.6	1.6
geology (category) (p = 0.004)	1.1	1.2	1.0	1.3	2.3	1.1
geomorphology situation (category) (p = 0.020)	4.1	2.4	2.0	2.8	3.1	2.4

Table 3.5 Percentages for significant categorical environmental variables by sub-community. All variables are significant at P <0.05 using χ^2 analysis. See Table 3.1 for category explanations. Greyed out areas represent categories that do not apply to a variable.

Sub-community quadrats and data categories		rock cover	fern cover	llitter cover	bryophyte cover	canopy cover	dominant tree/shrub species	main canopy height	height of emergent trees
A (n=102)	1	20	96	70	49	6	25	0	15
	2	16	4	30	51	14	18	45	30
	3	65			0	36	8	55	55
	4					44	34	0	0
	5						15		
B (n=36)	1	78	83	33	94	6	0	0	0
	2	19	17	67	6	14	19	0	0
	3	3			0	42	42	100	17
	4					39	31	0	83
	5						8		
C (n=28)	1	61	71	75	79	14	11	0	0
	2	14	29	25	21	11	21	93	71
	3	25			0	50	11	7	18
	4					25	32	0	11
	5						25		
D (n=10)	1	0	100	100	30	20	0	0	50
	2	60	0	0	70	10	0	50	0
	3	40				50	20	50	50
	4					20	40	0	0
	5						40		
E (n=40)	1	78	73	33	77	25	8	0	0
	2	15	28	68	23	15	15	50	0
	3	8				23	42	50	100
	4					37	27	0	0
	5						8		
F (n=10)	1	70	100	70	60	10	10	0	100
	2	30	0	30	40	20	0	0	0
	3	0				60	50	100	0
	4					10	30	0	0
	5						10		

b) Within stands

There are a number of environmental variables that show significant differences (P ≤ 0.05) differences between sparse (species cover <25%) and dominant (species cover >25%) species cover (Table 3.6).

In areas of heavy rock cover (>79 %), significantly more quadrats were recorded with a dominant cover of *A. melanoxylon* than a sparse cover. A similar association was recorded for *Olearia argophylla*, while the opposite is apparent for *P. apetala*.

For areas of light bryophyte cover, significantly more quadrats have a dominant cover of *P. apetala* than a sparse cover.

In areas with tall emergent trees (>19 m), significantly more quadrats have a dominant cover of *P. apetala* than a sparse cover. In areas with moderately tall emergent trees (15-19 m), significantly more quadrats have a dominant cover of *Olearia argophylla* than a sparse cover. Contrasting this, in areas without emergent trees or with short emergent trees (10-14 m), significantly more quadrats have a dominant cover of *Beyeria viscosa* than a sparse cover.

In areas with a low main canopy height of between 5-9 m, significantly more quadrats have a dominant cover of *A. melanoxylon* (commonly an emergent species) than a sparse cover.

In areas of moderate canopy cover (50-59 %), significantly more quadrats have a dominant cover of *Pittosporum bicolor* than a sparse cover.

Table 3.6 P-values from χ^2 analyses for environmental variables that significantly differ between sparse and dominant quadrat species cover for common dry closed-forest tree/shrub species.

	Rock cover	Bryophyte cover	Height of emergents	Canopy height	Canopy Cover
Pomaderris apetala	0.001	0.019	0.0199		
Acacia melanoxylon	0.0094			0.0084	
Beyeria viscosa			0.01		
Olearia argophylla	0.0282		0.0094		
Pittosporum bicolor					0 0207

Figures 3.13 and 3.14 show examples of the variation in species cover of the dominant vascular plant species along transects at two Tasmanian dry closed-forest stands. Figure 3.13 is from Bedggood Hill near Bicheno and is an example of dry closed-forest occurring on a steep southeast-facing slope. This transect extended from near the gully bottom to a point 50 metres upslope. It is apparent that *Olearia argophylla, Notelaea ligustrina, Pittosporum bicolor* and *Coprosma quadrifida* are concentrated towards the gully, while *Olearia lirata, Zieria arborescens* and *Pomaderris apetala* are concentrated further upslope and away from the gully bottom.

Figure 3.14 is a transect from the slopes of Mount Henry in the eastern Tiers. This transect crossed the gully with the majority of the quadrats facing ENE and the opposite side of the gully facing south. Some similarities are apparent between this example and the transect at Bedggood Hill in that *N. ligustrina* and *O. argophylla* are most common near the bottom of the gully. Unlike Bedggood Hill, at this stand *C. quadrifida* is not common and its distribution does not coincide with the gully bottom. *P. apetala* and *B. viscosa* occur predominantly on opposite sides of the gully, with *B. viscosa* on the south-facing side and *P. apetala* on the steeper ENE aspect. *Bedfordia salicina* is most common only on the fringe of the stand on the ENE aspect.

Topographic profile of transect
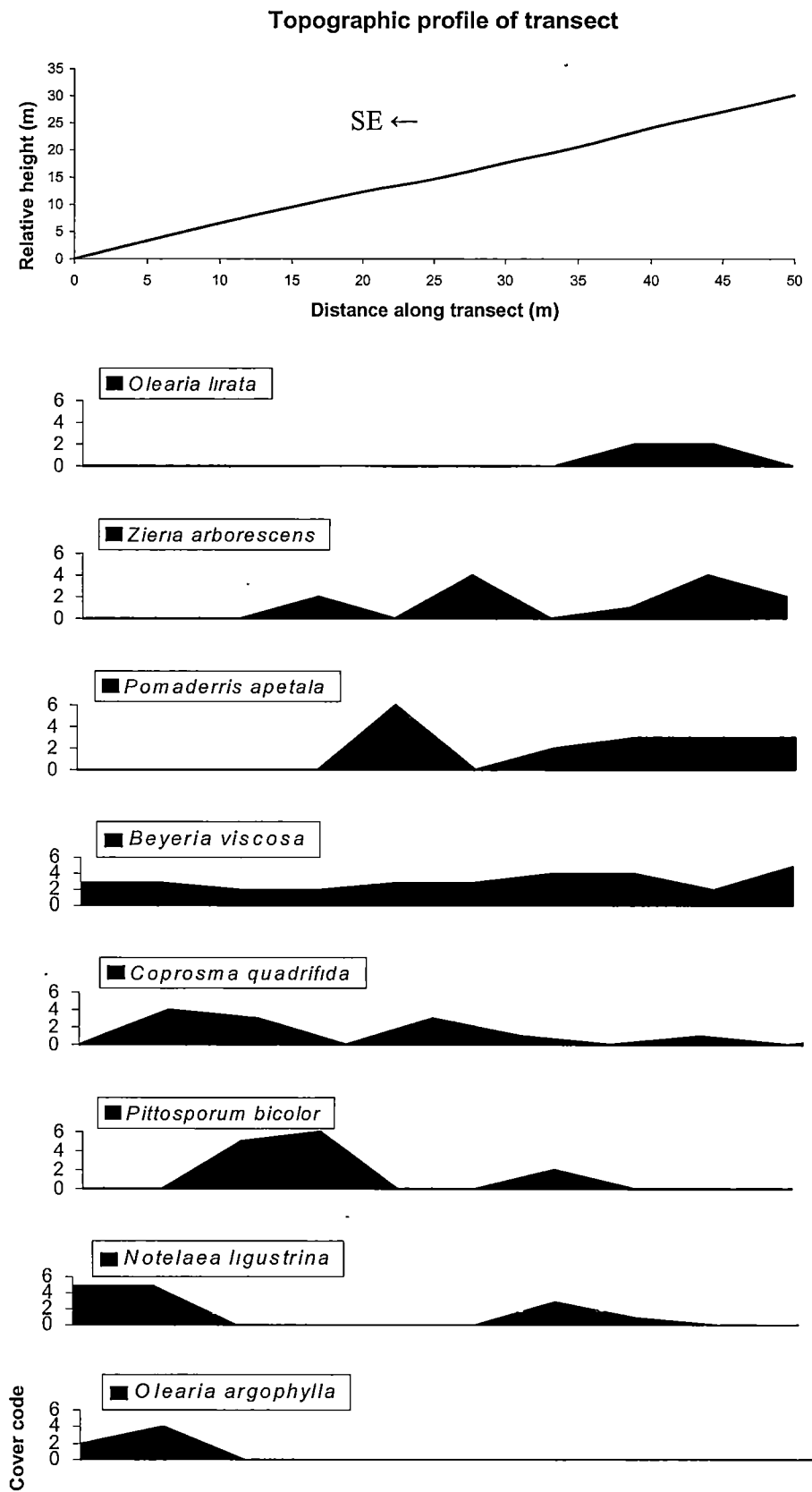
Figure 3.13 Species cover along Bedggood Hill transect, east coast of Tasmania (cover code is 1 = <1%, 2 = 1-5%, 3 = 5-25%, 4 = 25-50%, 5 = 50-75%, 6 = >75%).

Topographic profile of transect
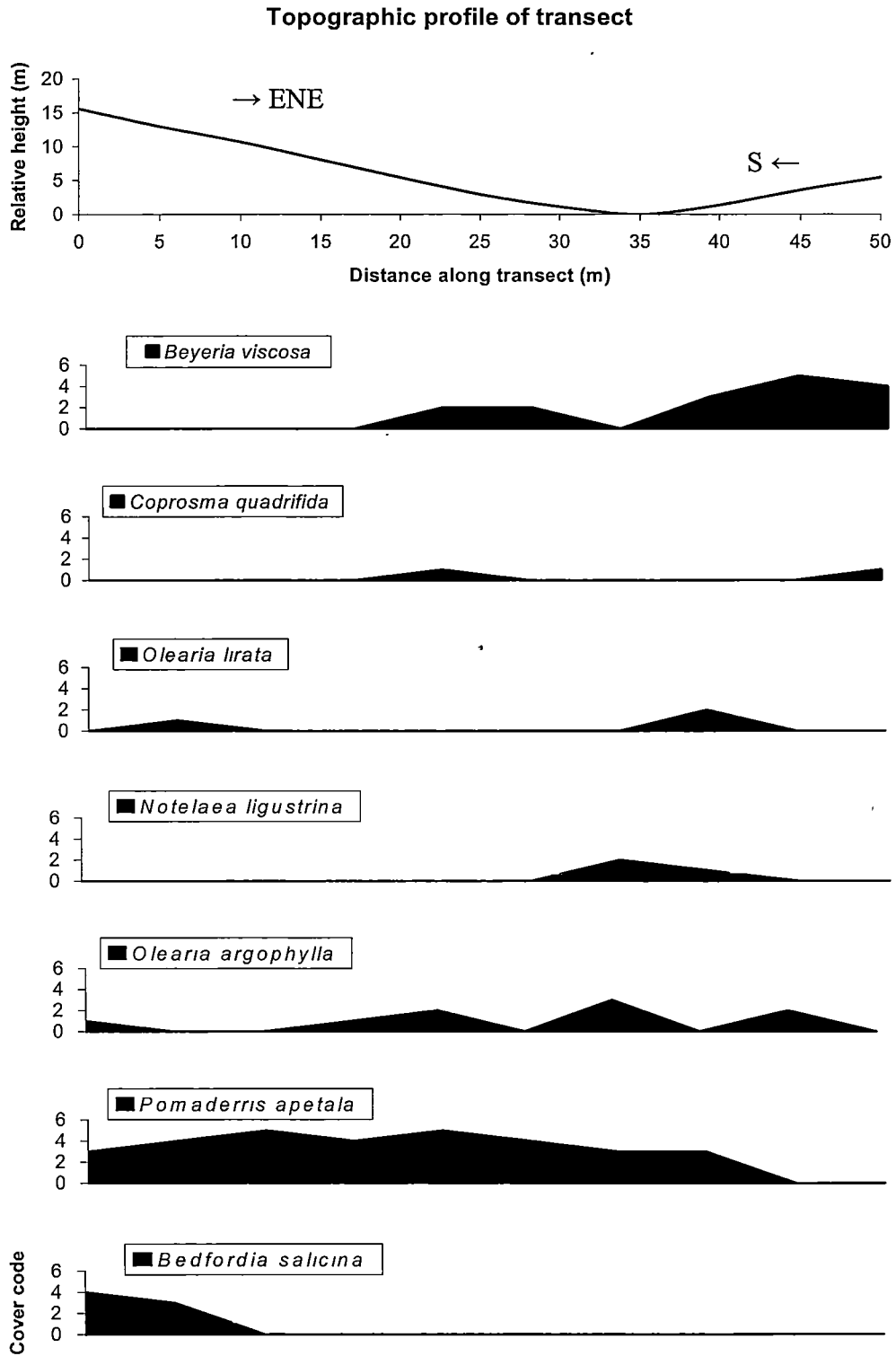
Figure 3.14 Species cover along Mount Henry transect, Eastern Tiers (cover code is 1 = <1%, 2 = 1-5%, 3 = 5-25%, 4 = 25-50%, 5 = 50-75%, 6 = >75%).

Discussion

Description of floristic sub-communities

The sub-communities show substantial similarity in species composition. However, a number of characteristic species were identified in other sub-communities that are useful in differentiation. Presence of *Asterotrichion discolor* in a stand suggests the sub-community is either B or C. If the stand contains cool temperate rainforest elements such as *Nothofagus cunninghamii* or *Aristotelia peduncularis* the sub-community is D. The presence of a diverse fern flora, including the species *Pellaea falcata*, *Polyphlebium venosum*, *Pteris tremula*, *Histiopteris incisa*, *Blechnum nudum* and *Hymenophyllum rarum*, indicates sub-community E.

Sub-community C was made up of stands containing a substantial number of plant species that favour disturbed zones abutting the adjacent eucalypt forest. Such disturbed boundaries are a common feature of the stands surrounding suburban Hobart. A combination of factors may be contributing to this dominance of boundary species, most notably a recent fire that burned through the area in 1998 and a lower population of herbivorous animals than in more remote areas. Native herbivorous animals are not prominent on the urban periphery of Hobart and introduced livestock was removed from these hills in the 1940's. More recently, without these controlling influences on the plants of the dry closed-forest-eucalypt forest ecotone, the boundary may have become less distinct, and there may be more fuel available and, hence, more intense fires than in the past. Many of the Hobart stands are also not particularly rocky when compared with other dry closed-forest stands in the state. Dry closed-forest is present around Hobart due to topographic fire protection afforded by the moist, dark gullies. Rockiness provides more effective fire protection than topography alone, leaving these stands vulnerable to attrition caused by bushfire.

Sub-community D shows some similarities to temperate rainforest, as is evidenced by the presence of a number of temperate rainforest indicator species (Jarman & Brown 1983) including *Atherosperma moschatum*, *Nothofagus cunninghami*, *Gaultheria hispida*, and *Gahnia grandis*. The combined effects of summer drought and fire effectively limit *N. cunninghamii* to relatively wet areas (Howard 1973).

N. cunninghamii was always in low numbers in sub-community D, usually occurring in the riparian zone due to limitations imposed by the dry summers and chance fire events experienced at these sites.

Floristic affinities

Along the streams of the Eastern Tiers there is a gradient from dry closed-forest at low altitudes to forests that are floristically similar but contain *Atherosperma moschatum* at higher altitudes where the moisture supply is presumably not as limited. Dry closed-forest with *A. moschatum* (predominantly stands of sub-communities D and E) is largely equivalent to the 'callidendrous sassafras-musk' formation described by Neyland (1991) in his study of the relict cool temperate rainforests of eastern Tasmania.

There have been some early references in Tasmania to vegetation that would be included within the dry closed-forest of this study. Curtis (1969) makes reference to a specialised gully flora that occurs on the lower slopes of Mount Wellington near Hobart in gullies that are protected from the dry north-westerly winds. Dry closed-forest has been described by Harris & Brown (1980) on dolerite scree beneath the coastal cliffs of Hellfire Bluff in southeast Tasmania. Woolward (1983) undertook a study of the ecology of this community occurring in gullies around Hobart. Plant communities floristically equivalent to dry closed-forest are described in Kirkpatrick *et al.* (1995). These communities are *Callitris rhomboidea- Bedfordia salicina* closed-forest, *Bedfordia salicina- Olearia argophylla* closed-scrub, *Notelaea ligustrina* closed-forest, *Pomaderris apetala- Beyeria viscosa- Asterotrichion discolor* closed-forest, and *Acacia dealbata- Beyeria viscosa- Geranium potentilloides* low-closed riparian forest. Dry closed-forest sub-communities B and C from the present study are differentiated from the other sub-communities by the presence of *Asterotrichion discolor*, and are floristically equivalent to the community *Pomaderris apetala- Beyeria viscosa- Asterotrichion discolor* closed-forest listed in Kirkpatrick *et al.* (1995). A number of these communities are mapped within the mapping units *Notelaea- Pomaderris- Beyeria* forest (NNP), and Broad-leaf Scrub (SRB) in the TASVEG mapping program of the Tasmanian Department of Primary Industries, Water & Environment.

Descriptions of these mapping units can be found in Harris & Kitchener (2005). These two units include a facies of this community that occurs in the northwest and west of Tasmania. This facies has similar species composition but is an early successional stage in the regeneration of wet eucalypt forest (Harris & Kitchener 2005). Recently, Kirkpatrick *et al.* (2004) have made mention of a developing dry closed-forest community growing behind an active dune system on the Tasman Peninsula in southeast Tasmania.

Tasmanian dry closed-forest has some floristic affinity to other closed-forest communities in Tasmania, Victoria and New South Wales. The vascular plant species composition of this community displays close affinities with cool temperate rainforest in eastern Tasmania. The species lists from this study and that compiled by Neyland (1991) in his study of the relict cool temperate rainforests of eastern Tasmania were compared. Seventy-three percent of the species and 81% of the genera recorded in eastern Tasmanian cool temperate rainforest also occur in Tasmanian dry closed-forest. In particular, dry closed-forest sub-community E has a similar species composition to the formation 'callidendrous sassafras-musk' described by Neyland (1991). Tasmanian dry closed-forest as a whole is floristically related to other dry closed-forests in southern Australia. A comparison of the species list from Tasmanian dry closed-forest and that for Gorges dry closed-forest from East Gippsland, Victoria (Peel 1999) showed that 23% of the species and 51% of the genera recorded from Victoria dry closed-forest are also found in Tasmanian dry closed-forest. These figures decrease further north in Australia to 11% of species and 31% of genera recorded from Western Sydney dry closed-forest (Benson & Bedward 1999). Tasmanian dry closed-forest and Victorian and southern New South Wales dry closed-forest share a number of genera that characterise the communities (*Notelaea, Pittosporum, Coprosma, Pomaderris*) (Cameron 1992; Keith & Benson 1988). *Beyeria viscosa* is also acknowledged as a rare and important species occurring in Victorian dry closed-forest (Peel 1999), and is a dominant species in Tasmanian dry closed-forest. The 'fern-gully' flora of Victoria is very similar to Tasmanian dry closed-forest. A comparison between the dry closed-forest species list of the present study and a list of species from fern gully vegetation (Patton 1933) reveals that 51% of species and 79% of genera from

the fern gully vegetation were also recorded on the species list compiled in the present study. Patton (1933) mentions a high number of fern species among the fern-gully flora, and along with the presence of *Atherosperma moschatum* this seems to suggest an affinity with sub-community E of the present study.

In summary, these comparisons show that Tasmanian dry closed-forest has close affinities to cool temperate rainforest. However, there are also considerable similarities in the species composition of this community and that of other Australian closed-forest communities.

The dry-closed forest occurring behind coastal sand dunes at Bangor in southeast Tasmania was the only stand of this type identified in the present study, and is mentioned in the sand dune vegetation study of Kirkpatrick *et al.* (2004). If there are other unidentified stands in the study area, they are likely to be uncommon. Littoral rainforest in the lee of coastal headlands or sand dunes is also not common on the Australian mainland. For example it is estimated that littoral rainforest accounts for just 0.6% of the remaining rainforest in New South Wales (Floyd 1990). However, a sand-sheet form of dry closed-forest (mapped as Broad-leaf Scrub (SBR) by the Tasmanian Department of Primary Industries, Water & Environment vegetation TASVEG mapping program) consisting of a species composition similar to that of dry closed-forest is relatively common around the south and southwest coasts of Tasmania (Harris & Kitchener 2005). *Pomaderris apetala* usually dominates coastal broad-leaf scrub, and other common species are *Cenarrhenes nitida, Monotoca elliptica* and some emergent *Eucalyptus nitida* (Harris & Kitchener 2005). The most common coastal Tasmanian dry closed-forest formation occurs on scree slopes beneath the ubiquitous dolerite cliffs of the southeast of Tasmania, such as those on the Tasman Peninsula and Bruny Island. Harris & Brown (1980) describe one such dry closed-forest community at Hellfire Bluff, just to the north of the Tasman Peninsula. They term the community *Callitris rhomboidea - Notelaea ligustrina* low closed-forest. One of these dry closed-forest patches was sampled again in the current study, and, along with Roaring Beach and Waterfall Bay, represented coastal dry closed-forest stands on coastal cliff scree. Roaring Beach and Waterfall Bay are separated from the other stands, along with Bangor (Figure 3.2), indicating a substantially different species composition

compared to the non-coastal dry closed-forest stands. The two coastal dry closed-forest stands surveyed at Waterfall Bay and Roaring Beach have substantially different species composition when compared with non-coastal dry closed-forest stands as a group. Hellfire Bluff was more similar to non-coastal dry closed-forest, and was not isolated in the ordination space (Figure 3.2).

Floristic variability relating to the environment

Between-stands

There is an obvious moisture factor determining the species composition of Tasmanian dry closed-forest sub-communities. The few limited examples of sub-communities D and E documented in this study occur on moister sites than the other sub-communities and also have a less pronounced dry spell, meaning that there is an environment favouring moisture-dependent species such as *Atherosperma moschatum* and *Nothofagus cunninghamii*. Stands of sub-community D and E represent part of a closed-forest continuum that exists from dry-closed forest in the low rainfall midlands of Tasmania to disjunct cool temperate rainforest patches in the wetter coastal escarpment of eastern Tasmania. Where to draw the line between vegetation that is dry closed-forest and vegetation that is cool-temperate rainforest is difficult in this transitional part of the spectrum. This is exemplified by stands that contain one or two *N. cunninghamii* among a complete dry rainforest flora.

Small-scale (quadrat-based) relationships

Areas of sparse rock cover were shown to support a dominant cover of *Pomaderris apetala* and *Olearia argophylla*. The association of *P. apetala* with areas of sparse bryophyte cover represents a secondary effect of this association with rock cover. Rock is a favourable bryophyte substrate, and areas of sparse rock cover do not therefore favour a heavy cover of bryophytes. The association of *P. apetala* with less rocky ground may be linked to its capability for long-term soil seed storage. Ground that has a heavy rock cover naturally also has shallow surface soil, and therefore is unfavourable for long-term storage of seed. Additionally, the small seed size of *P. apetala* may contain insufficient resources for *P. apetala* seedlings to

reach light through heavy rock cover. Also having small seeds, *O. argophylla*
probably has similar difficulties as *P. apetala* in emerging through heavy rock
cover. A dominant cover of *Acacia melanoxylon* was associated with heavy rock
cover, although this species also was observed growing on areas of little or no rock
cover. It could be that marsupials prefer to browse young *A. melanoxylon*
individuals that are growing on more open areas of ground, the result of which
would allow more *A. melanoxylon* growing on rockier areas to survive.

The relationship between a dominant cover of *Beyeria viscosa* and areas without
emergent trees or with short emergent trees is probably indicative of areas of recent
fire disturbance that have allowed dense *B. viscosa* regeneration, but have not had
time to develop an emergent tree layer. *Olearia argophylla* and *Pomaderris apetala*
both had dominant cover in areas that supported relatively tall emergent trees. A
dominant cover of *Olearia argophylla* is a feature of the later stages of wet eucalypt
forest recovery following fire (Ashton 2000). Therefore, it may be that the
association between areas with a dominant cover of *O. argophylla* and moderately
tall emergent trees may indicate the area is well recovered from fire disturbance,
and hence enough time has passed for the development of a significant emergent
tree layer. Also, *O. argophylla* and *P. apetala* dominance is commonly associated
with less rocky areas, where deeper soil and lack of rock impediment to root growth
may allow the development of taller vegetation, including a taller emergent
component.

The association between a dominant cover of *A. melanoxylon* and areas with a low
main canopy height of between 5-9 m may be representative of the effects of
growing on rocky ground. As discussed above, a dominant cover of *A. melanoxylon*
commonly occurs on rocky areas. Rocky ground may limit the potential height of
the main canopy to a low stature because of shallow soil formation and rocky soil
impeding root growth. *A. melanoxylon* also emerges following fire disturbance, and
stands with a dominant cover of *A. melanoxylon* and a relatively low canopy height
may indicate an early successional stage in stand development after fire.

The association between a dominant cover of *P. bicolor* and a moderate canopy
cover probably arises because of the nature of the distribution of this species in dry

closed-forest. *P. bicolor* predominantly occurs as large widely scattered individuals. In the present study a dominant cover of *Pittosporum bicolor* was generally found where a single large *P. bicolor* covered a quadrat. These areas had a substantial canopy cover but not as heavy as areas where dense growth of smaller species, such as *B. viscosa* occurred.

In summary, the present study of Tasmanian dry closed-forest vegetation differentiated 6 floristic sub-communities. There are a number of characteristic species that differentiate these sub-communities. There are also significant differences between these sub-communities relating to many environmental variables, the most obvious of these being moisture. The small-scale distribution of some of the major canopy species within stands is related to a number of environmental variables. Two of the most important of these variables appear to be moisture supply and rock cover, both important determinants of fire-frequency. Tasmanian dry closed-forest has floristic affinities with cool temperate rainforest in eastern Tasmania, and other closed-forests of southeast Australia, especially the dry closed-forests and fern-gully vegetation of Victoria.

Chapter 4 - The structure and regeneration of Tasmanian dry closed-forest

Abstract

The structure and regeneration dynamics of 27 Tasmanian dry closed-forest stands were examined. The location of major dry closed-forest species was mapped along transects, and nearest neighbour relationships identified between individuals. Size-class analysis and spatial analysis of nearest neighbour relationships was undertaken. A major aim was to determine whether or not the community is self-replacing, a distinguishing characteristic of rainforest vegetation. The results of the size-class analysis of individuals of dry closed-forest species indicated that *Beyeria viscosa*, *Pomaderris apetala*, *Asterotrichion discolor*, *Bedfordia salicina*, and *Zieria arborescens* regenerate primarily following exogenous disturbance. In contrast, *Notelaea ligustrina*, *Pittosporum bicolor*, *Acacia melanoxylon*, and *Coprosma quadrifida* appear to be able to continuously regenerate in the absence of exogenous disturbance, and therefore are self-replacing. *Olearia argophylla* initially requires disturbance for establishment, but maintains dominance of a stand by extensive coppicing. Dry-closed forest that has not experienced fire for a relatively long period has a high proportion of these self-replacing species, and as such shows some similarity to rainforest vegetation. A nearest neighbour analysis showed that, in general, clumping between species or within species was not significant. Although this was the case for established individuals, seedlings were commonly clumped around large trees. This pattern reflects seed dispersal from birds perching in these large trees.

Introduction

Tasmanian dry closed-forest (*sensu* Specht 1970) occurs as small disjunct stands, primarily in drier eastern parts of the island, where local topography provides protection from fire (see Chapter 2). This community has ecological affinities with dry closed-forest (dry rainforest) on the Australian mainland (Gillison 1987). There is also considerable floristic similarity between Tasmanian dry closed-forest and other closed-forests of southeast Australia (see Chapter 3). This chapter investigates the structure and regeneration dynamics of Tasmanian dry closed-forest.

Small trees/ tall shrubs that are more commonly found in the understorey of eucalypt forest (Cunningham and Cremer 1965) dominate the dry closed-forests of Tasmania. This vegetation community commonly grows deep within gullies and often on ground that is covered with a thick layer of rock scree. This suggests a close relationship between the community and fire (see Chapter 2). Thus, dry closed-forest follows the rule of Australian rainforest communities in that topographic situations are favoured that naturally exclude all but the fiercest of fires (Bowman 2000).

Previous to the present study, there have been few studies that have investigated aspects of the regeneration dynamics of the study community (Woolward 1983; Kirkpatrick *et al.* 2004). Some knowledge of the ecology and regeneration patterns of a number of the most common dry closed-forest species can be gleaned from studies of plants in the understorey of wet eucalypt forest (Cunningham & Cremer 1965; Ashton 2000). Cunningham & Cremer (1965) discussed the establishment of some common Tasmanian and Victorian wet eucalypt understorey species after logging and/or burning. They observed *Zieria arborescens, Pomaderris apetala, Olearia argophylla*, and *Acacia dealbata* regenerating very densely following disturbance, even if these species were not a significant component of the understorey before the disturbance. They also noted that *O. argophylla* is wind-dispersed and invades a burnt area from adjacent sources, while the seed of some *Acacia* species can be stored in the soil for long periods of up to 100 years, germinating when stimulated to do so by a bushfire (Cunningham and Cremer 1965). Ashton (2000) suggested that an *Olearia argophylla* and *Atherosperma*

moschatum dominated understorey might be a late stage in the succession pathway following fire in the Wallaby Creek area of Victoria.

Knowledge of the regeneration dynamics of a plant community can be deduced from the size-class structure of its component species. Self-replacing rainforest species regenerate primarily in gaps created by small-scale endogenous disturbances such as tree-fall. Pioneer and climax species are different guilds of species that regenerate in large and small gaps respectively (Swaine & Whitmore 1988). The size-class distribution of self-replacing species is inherently different to that of species that require large-scale exogenous disturbance for regeneration. In self-replacing species most individuals are from the small size-classes and there is a steady decline in numbers of individuals as their size increases. An inverse J-shaped curve is expected for a self-replacing tree species. For species requiring large-scale exogenous disturbance, such as that provided by a bushfire, the size-class distribution shows distinct pulses of regeneration following disturbance events. This results in a size-class distribution graph with one or more peaks in numbers of individuals with breaks in-between. This shape indicates that the species does not have sufficient individuals in the smaller size-classes to contribute to the next generation, and, in the absence of a flush of small individuals after another disturbance, the species will disappear.

Knowledge of the regeneration dynamics of a plant community can also be deduced from a study of the spatial arrangement of two distinct groups of individuals or species. For instance, spatial segregation of two species may indicate a preference for different environments at a small-scale or perhaps differences in regeneration strategies following disturbance. In the Northern Territory, Fensham & Butler (2004) documented the spatial arrangement of dry closed-forest individuals that were in the process of invading the surrounding *Eucalyptus* savanna. They found significant clumping of dry closed-forest regeneration around mature savanna trees, possibly the result of seeds being dispersed by the birds that roost in these large trees. A similar process seems to be occurring in abandoned farmland adjacent to subtropical rainforest in southern Queensland (Toh *et al.* 1999) and in late successional *Banksia marginata* woodland converting to dry closed-forest behind

sand dunes in southeast Tasmania (Kirkpatrick *et al.* 2004).

Numerous studies have been conducted into the regeneration processes operating in tropical rainforests, which may be similar to those operating in dry closed-forest. Such studies include investigations of factors influencing the survival of young emerging plants, such as herbivory (Núñez-Farfán & Dirzo 1988; Nadolny 1999), drought (Lieberman & Mingguang 1992) and darkness (Delissio *et al.* 2002). In addition, size-class distribution patterns have been commonly used to deduce regeneration strategies and site disturbance histories in rainforests. For instance, Debski *et al.* (2000) used size-class distribution analysis in a Queensland subtropical rainforest to deduce that the regeneration of the dominant tree *Sloanea woolsii* requires large-scale disturbance, most likely to be cyclones in this region. Many rainforest trees are incapable of growing past sapling stage beneath a closed canopy, and only reach maturity after a small-scale disturbance such as tree-fall allows an increase in light-levels, which stimulates growth. Reliance on gap formation for establishment, and an inability to regenerate beneath a closed-canopy is displayed in a number of Tasmanian rainforest trees, such as *Phyllocladus aspleniifolius* (Read & Hill 1988), *Athrotaxis selaginoides* (Cullen 1987, Cullen 1991), and *Athrotaxis cupressoides* (Cullen & Kirkpatrick 1988).

This chapter reports an investigation of the dynamics of dry closed-forest species from 27 dry closed-forest stands in eastern Tasmania. One of the major objectives is to determine whether or not the community is self-replacing. A number of questions were posed relating to the spatial distribution of the major dry closed-forest species: Is there evidence that species are growing in clumps? How are seedlings and saplings distributed in relation to large individuals? These results are used to answer several more general questions: is Tasmanian dry closed-forest "rainforest" according to the current Australian and Tasmanian rainforest definitions? How does the community regenerate? Are there any threats to the long-term viability of the community in Tasmania?

Methods

In order to select stands for investigation of the vegetation structure, an initial ordination classification of the data collected in the preliminary floristic survey was performed. Stands were selected to cover the floristic range shown by these analyses. Details of this analysis can be found in Chapter 2.

Vegetation mapping

A transect of contiguous quadrats was laid out at each stand. The dimensions of the quadrats were 4 metres wide and 5 m long with the total length of the transect being between 20 and 50 m in most cases and 90 m at the Truganini Reserve stand. The final length of each transect was constrained by such factors as the density of the vegetation and the shape of the stand. The narrow gully nature of some stands necessitated measuring out two transects to make up 50 m in total. Transects were located within the stand in an area which was deemed to be representative of the overall dominant stand vegetation and was orientated at right angles to the slope of the land where possible to pick up as much topographic variation as possible. All transects were within the boundary of the dry closed-forest vegetation. However, in some cases, because of the diffuse boundary between communities some ecotonal vegetation was sampled along with the dry dry closed-forest vegetation. The location of each tree, shrub, sapling and seedling was recorded using x, y coordinates. Its species was noted and girth at breast height (gbh) measured for all individuals with a gbh ≥ 5 cm. For individuals that were coppiced or that had numerous low-branching stems, the gbh of each stem was measured and recorded as belonging to the one individual. The total basal area of such an individual is the sum of the basal area of these stems.

Analysis

Vegetation structure

For each stand the basal area of individuals was calculated. These data were used to calculate basal area (m²/ha) and relative dominance of species (basal area of a given species/ basal area of the stand). Size-class frequency analysis of the dominant

species was also performed. Not all stands had adequate numbers of individuals of every species for a size-class distribution analysis. Therefore some species are only represented by a small number of analyses. It should be noted that the gbh size-class distribution graphs are produced so that the first size-class of 0-2 cm gbh represents seedlings and that the second size class of 2-4 cm gbh represents saplings (recorded in the field as any individual with a gbh ≤ 5 cm).

Spatial patterns

One common approach to testing for spatial segregation of two species is to create a nearest neighbour contingency table and to use a χ^2-test of independence (Pielou 1961, Dixon 1994). There are inaccuracies in Pielou's test in that some spatial patterns of segregation are not identified. Also, the approach is inappropriate for completely mapped data (Dixon 1994). There are a number of other tests for spatial segregation between two species, including methods based on distances to nearest neighbours (Diggle 1983), Ripley's K-function (Ripley 1981), and four-term local quadrat covariance (Dale 1999). An extension of the spatial pattern analysis technique developed by Dixon (1994) for testing for segregation between two species is to test for segregation between more than two species (Dixon 2002).

Only individuals with a gbh ≥5 cm were included in the spatial analysis of the present study. However, observations of the spatial relationships between seedlings and mature individuals were noted. The reasoning behind excluding small individuals from the spatial analysis was that their occurrence is likely to be ephemeral. Therefore only established individuals representative of established dry closed-forest vegetation were included in the analysis. A Microsoft Excel macro was used to identify an individual's nearest neighbour, the species of the nearest neighbour, the distance between the nearest neighbour pair, and the counts and properties of reflexive neighbours (see Dixon 1994). Reflexive nearest neighbours are pairs of points that are nearest neighbours of each other (Dixon 1994). A nearest neighbour contingency table was then produced (e.g. Peilou 1961). This was the basic input data used to test for spatial segregation of species. The methods used in this chapter closely follow the approach of Dixon (2002). The following is a summary of the calculations used in this method. Refer to Dixon's paper for further

details.

The expected cell counts under the hypothesis of random labelling are derived from

$$\mathrm{E}\,N_{ij} = N_i(N_i - 1)/(N-1) \qquad \text{if } i = j \text{ and}$$

$$\mathrm{E}\,N_{ij} = N_i\,N_j/(N-1) \qquad \text{if } i \neq j$$

where $\mathrm{E}\,N_{ij}$ is the expected number of species i whose nearest neighbour is species j, N_i is the number of species i and N is the total number of locations.

The next step is to obtain a measure of the segregation of species i firstly for self-segregation, where self-segregation refers to the segregation of individuals of the same species for individuals of other species:

$$S_i = \log \frac{N_{ii}/(N_i - N_{ii})}{(N_i - 1)/(N - N_i)}$$

and secondly a pairwise segregation test for an association between two species:

$$S_{ij} = \log \frac{N_{ij}/(N_i - N_{ij})}{EN_{ij}/(N_i - EN_{ij})}$$

note that the simplified equation (14) for S_{ij} in Dixon (2002) was not used in the present study as it provides results inconsistent with the examples in Dixon's paper. In preference use the equation for S_{ij} given above.

Values of the segregation index S_i larger than 0 indicate that species i is segregated. The larger the value of S_i the greater the degree of segregation. Values of S_i less than 0 indicate that species i is found as a nearest neighbour of itself less frequently than expected from random labelling. Values of S_i close to 0 are consistent with random labelling of the neighbours of species i. Similar to the interpretation of S_i, values of the segregation index S_{ij} larger than 0 indicate that species j is found more often as a nearest neighbour of species i than is expected under random labelling. Values of S_{ij} less than 0 indicate that species j is found less frequently as a nearest neighbour of species i than is expected under random labelling. Values of S_{ij} close

to 0 approximate random labelling of the neighbours of species i.

Next the hypothesis is tested that $v_{ij} = v_{ij}*$ where j may equal i

v_{ij} is defined as the number of times species i has a neighbour j

$v_{ij}*$ is the corresponding expected number if the N points were randomly labelled

This can be tested by simulation or by relying on asymptotic normality.

$$Z_{ij} = \frac{N_{ij} - EN_{ij}}{\sqrt{VarN_{ij}}} \qquad \text{where } j \text{ may equal } i$$

This statistic has an asymptotic normal distribution with mean 0 and variance 1. The asymptotic p-value can be obtained from tables of the standard normal distribution (z tables). A p-value cut-off of 0.05 was used as a measure of significance.

$$VarN_{ii} = (N + R)P_{ii} + (2N - 2R + Q)P_{iii} + (N^2 - 3N - Q + R)P_{iiii} - N^2 P^2{}_{ii}$$

where j may equal i

$VarN_{ii}$ is a product of the association between individuals of a species ($Pii, Piii, Piiii$), quantities that depend on the spatial arrangement of points (R, Q), and the total number of points (N). $P_{ii}, P_{iii}, P_{iiii}$ are the probabilities that a randomly chosen pair, triplet, or quartet of points, respectively are the indicated species.

$$P_{ii} = \frac{N_i(N_i - 1)}{N(N - 1)}$$

$$P_{iii} = \frac{N_i(N_i - 1)(N_i - 2)}{N(N - 1)(N - 2)}$$

$$P_{iiii} = \frac{N_i(N_i - 1)(N_i - 2)(N_i - 3)}{N(N - 1)(N - 2)(N - 3)}$$

$$P_{ij} = \frac{N_i(N_j - 1)}{N(N - 1)}$$

$$P_{iij} = \frac{N_i(N_i-1)(N_j-2)}{N(N-1)(N-2)}$$

$$P_{iijj} = \frac{N_i(N_i-1)N_j(N_j-1)}{N(N-1)(N-2)(N-3)}$$

The quantities of R and Q are derived from the spatial arrangement of points, and are not dependent on the absolute frequencies of individuals of a particular species (Dixon 1994). A simple illustration of how these values relate to the spatial arrangement of points is provided in Dixon (1994).

$R = 2$(number of reflexive pairs)

$Q = 2(N_2 + 3N_3 + 6N_4 + 10N_5 + 15N_6)$ where N_2 = a point with a single reflexive nearest neighbour, N_3 = a point with 2 reflexive nearest neighbours and so on. As a geometric rule no point can have more than 6 reflexive nearest neighbours.

The combined 'overall and species specific test of random labelling' of Dixon (2002) was not included in this study as the same information was extractable from the tests on each pair of species.

Results

Vegetation structure

Basal area for 27 dry closed-forest stands ranged considerably with a low value of 18.27 m^2/ha and a high value of 108.56 m^2/ha. The mean basal area for all stands was 49.06 m^2/ha. Plant species that make a major contribution to the basal area of the dry closed-forest stands are grouped in terms of relative dominance in Table 4.1. Fourteen major groupings of species dominance are apparent. Broadly these groups are 1a-1c; *Pomaderris apetala* dominated, groups 2a-2c; *Olearia argophylla* dominated, group 3; *Notelaea ligustrina* dominated, group 4; *Acacia melanoxylon* dominated, group 5; *Bedfordia salicina* dominated, group 6; *Beyeria viscosa* dominated, group 7; *Acacia dealbata* dominated, group 8; *Pittosporum bicolor* dominated, and group 9; mixed stands showing no obvious dominants. The majority of stands with an above average basal area were dominated by species that have large maximum girths when mature, such as *Acacia melanoxylon*, *Acacia dealbata*, and *Notelaea ligustrina*. Small stand basal areas were recorded at stands that display one of two very different structures. The first structure consists of widely scattered large mature individuals and little else (for instance Spinning Gum CA - Plate 4.1). The other structure consists of dense stands of relatively small species, such as *Beyeria viscosa, Pomaderris apetala,* and *Bedfordia salicina* and very few large individuals. This was particularly apparent at Truganini Reserve (stand basal area of 20.39 m^2/ha), Coningham CA (stand basal area of 18.27 m^2/ha), and Dalco Creek (stand basal area of 31.85m^2/ha), at which densities of 17470, 11600, and 21800 stems/ha in the 0-19 cm gbh size-class were measured. This is considerably higher than the average of 3062 individuals/ha in this size-class for the other 24 stands. Plate 4.2 shows the dense nature of the Dalco Creek stand.

Table 4.1 Dominant and sub-dominant canopy tree species at 27 Tasmanian dry closed-forest stands (31 transects in total) based on relative dominance data (dominant species groups are numbered according to the most dominant species at the stand e.g. groups 1a-1c consist of Pomaderris apetala dominated stands). Species that contribute most to the stand basal area are listed first.

Dominant species (≥33% of stand basal area)	Stand name and basal area m^2/ha	Sub-dominant species (≥25% of total stand basal area)
1a) *Pomaderris apetala*	St Mary's Pass (51.35)	*Olearia argophylla*
	Mount Henry (23.53), Cunny Creek (27.83)	-
	Coningham CA (18.27)	-
1b) *Pomaderris apetala* with *Acacia melanoxylon*	Mount Direction HS Transect 1 (108.55)	-
1c) *Pomaderris apetala* with *Bedfordia salicina*	Dalco Creek (31.85)	-
2a) *Olearia argophylla*	Tiger Gully (26.27)	*Bedfordia salicina*
	Three Thumbs T1 (62.48), Daley's (44.42), Tinderbox (55.33), Quoin Cliffs Transect 1 (38.68)	- - - -
2b) *Olearia argophylla* with *Acacia melanoxylon*	Quoin Cliffs T2 (84.74)	-
2c) *Olearia argophylla* with *Acacia dealbata*	Spinning Gum CA (38.77)	-
3) *Notelaea ligustrina*	Roaring Beach (28.91)	*Pomaderris apetala*
	Hellfire Bluff Transect 1 (99.30)	*Olearia argophylla*
	Hellfire Bluff Transect 2 (81.62)	-
	Block & Stable Creek (46.31)	-
4) *Acacia melanoxylon*	Mt Direction Transect 2 (61.10)	*Olearia argophylla*
	Hardings Falls (86.20)	
	Trevallyn SRA (54.30)	*Notelaea ligustrina*
5) *Bedfordia salicina*	Knights Creek (26.61)	
	Cloudy Bay (31.50)	*Acacia verticillata*
6a) *Beyeria viscosa* with *Pomaderris apetala*	Truganini Reserve (20.39)	-
6b) *Beyeria viscosa* with *Olearia argophylla*	Lost Falls T1 (78.84)	-
7) *Acacia dealbata* with *Olearia argophylla*	Loila Tier B (54.71)	-
8) *Pittosporum bicolor*	Bangor (23.24)	*Olearia argophylla*
9) Mixed stands with no clear dominance	Lost Falls T2 (34.35)	*Bedfordia salicina, Beyeria viscosa*
	Sth Brown Mtn (27.80)	-
	Three Thumbs T2 (74.60)	*Notelaea ligustrina*
	Forester River (44.44)	*Pomaderris apetala, Acacia melanoxylon*
	Notley Gorge (47.62)	*Acacia melanoxylon*
	Bedggood Hill (36.02)	*Beyeria viscosa, Notelaea ligustrina*

Plate 4.1 Open understorey beneath large Olearia argophylla at Spinning Gum CA stand.

Plate 4.2 Dense stand of Pomaderris apetala at Dalco Creek stand.

Figures 4.1 to 4.10 display the size class distributions of the major tree and shrub

species at the 27 dry closed-forest stands. Note that for each species the graphs are approximately ordered with respect to the developmental stage of the community of individuals from that species. For example in Figure 4.1 the first handful of *Beyeria viscosa* size-class distribution graphs are examples of stands with relatively young *B. viscosa* of small diameter, while the graphs of *B. viscosa* towards the end of Figure 4.1 are examples of somewhat more mature dry closed-forest stands with individuals from larger size-classes.

The first group of stands (Hellfire Bluff to Trevallyn SRA) have a large proportion of *B. viscosa* seedlings and few individuals in larger size-classes (Figure 4.1). Along with seedlings, there is a sapling component in the next five stands (South Brown Mountain to Lost Falls), but still there are few large *B. viscosa* individuals. An approximate inverse J-shape is detected in the curves of the distribution of individuals from the final four stands (Hardings Falls to Truganini). These stands have more large individuals between sapling size and 40 cm gbh than in the previous stands. An inverse J-shape to the size-class distribution can indicate continuous regeneration of species. For the *B. viscosa* distributions there is a common dip in each graph in the frequency of individuals in the size-class just bigger than sapling (4-6 cm), which probably indicates self-thinning of dense stands of saplings.

A similar pattern to that just described for *B. viscosa* is observed in *Pomaderris apetala* (Figure 4.2). The first group of stands (Roaring Beach to Lost Falls) contain *P. apetala* seedlings and few larger individuals. The next group of stands (Harding's Falls to Bedggood Hill) have the largest cohort of *P. apetala* individuals as saplings. At the next group of stands (Coningham CA to Mount Henry) the size-class distribution approximates an inverse J-shaped shape. As with *B. viscosa*, *P. apetala* at these stands is not necessarily continuously regenerating as one may conclude from the size-class distribution shape. This becomes apparent when looking at more mature examples of *P. apetala* from the last five stands (Mount Direction HS to Cunny Creek), which all show obvious pulses of regeneration from previous disturbance events. In the absence of another large disturbance event these stands have no small individuals of *P. apetala* present to replace the larger

individuals when they die.

Coprosma quadrifida is a shrub that is commonly found in the understorey of Tasmanian dry closed-forest. It is normally found as individuals of small diameter and any larger individuals occur at low density. The size-class distribution of *C. quadrifida* (Figure 4.3) is moderately consistent across stands, with most individuals in the seedling or sapling cohort. The only stands that contained a significant proportion of *C. quadrifida* in medium size-classes were Coningham CA, Truganini and Forester River.

Figure 4.4 displays the size-class distribution of *Olearia argophylla*. The stands at Dalco Creek, Truganini, and St Mary's Pass consist of individuals of *O. argophylla* less than 50 cm gbh. The St Mary's Pass stand has a distinct peak of *O. argophylla* individuals centred on 25 cm gbh. At all of the remaining stands *O. argophylla is* sparsely spread across size-classes. In mature stands such as these *O. argophylla* is widely spaced, of large girth (e.g. 242 cm gbh at Tinderbox), and has extensive spreading crowns. Accordingly the density of *O. argophylla* is low in these stands but the contribution to the overall stand basal area can be substantial.

The *Asterotrichion discolor* size-class distribution (Figure 4.5) consists of mainly seedlings at the Tinderbox and Daley's stands, with Daley's also having a low frequency of *A. discolor* individuals spread across larger size-classes. The Truganini stand contains individuals mainly less than 20 cm gbh, while the Spinning Gum stand has no individuals less than 20 cm gbh.

The size-class distribution of *Bedfordia salicina* is displayed in Figure 4.6. There is a gradual shift from individuals in small size-classes at Coningham to a dominance of larger individuals and no small individuals at Tiger Gully.

Figure 4.7 is of the size-class distribution of *Zieria arborescens*. This species occurred within stands infrequently and individuals are usually of relatively small gbh.

Acacia melanoxylon was a common component of dry closed-forest stands, but never occurred in high densities. The size-class distribution of *A. melanoxylon* is displayed in Figure 4.8. At the Cunny Creek and Truganini stands *A.*

melanoxylon is predominantly found as seedlings (0-2 cm size-class). This is in contrast to Quoin Cliffs, where *A. melanoxylon* individuals fall into relatively large size-classes and there are no small individuals present.

Like *A. melanoxylon*, *Notelaea ligustrina* was commonly recorded from most stands but usually consisted of few individuals. For this reason there are only two stands which had enough individuals to show a meaningful size-class distribution analysis (Figure 4.9). Both the Lost Falls and Block & Stable Creek stands had size-class distributions of *N. ligustrina* individuals that were similar. This consisted of a large number of individuals as seedlings and a low frequency of individuals spread over increasingly larger gbh size-classes. The maximum size of an individual *N. ligustrina* was 136 cm gbh at Block & Stable Creek.

Figure 4.10 shows the size-class distributions for *Pittosporum bicolor* individuals at two dry closed-forest stands. *P. bicolor* was an infrequent component of dry closed-forest, and was most common at higher rainfall sites. Truganini and Dalco Creek each had enough individuals of *P. bicolor* for analysis. Both consisted of young individuals less than 20 cm gbh. This gives the erroneous impression that *P. bicolor* only occurs as small individuals in dry closed-forest, but this is not the case. Most commonly there are a few large mature *P. bicolor* individuals, similar in many respects to the pattern for *N. ligustrina*.

Information was collected on the dispersal mode of major dry closed-forest tree species and the various regeneration strategies that these species adopt (Table 4.2). Four out of ten species are bird-dispersed (*Pittosporum bicolor, Notelaea ligustrina, Coprosma quadrifida & Beyeria viscosa*). Another two are sometimes bird-dispersed (*Pomaderris apetala & Zieria arborescens*), but more often are gravity-dispersed (Cunningham & Cremer 1965). The remaining four species have seeds that are either gravity-dispersed or wind-borne. *Bedfordia salicina, Beyeria viscosa, Pomaderris apetala, Zieria arborescens, Coprosma quadrifida, Olearia argophylla, Asterotrichion discolor,* and *ligustrina* are capable of vegetative regeneration. Large individuals of *O. argophylla* often have an extensive canopy formed coppice growth. Some species were also observed sprouting along their trunk after falling down on rocky unstable slopes (Table 3.2).
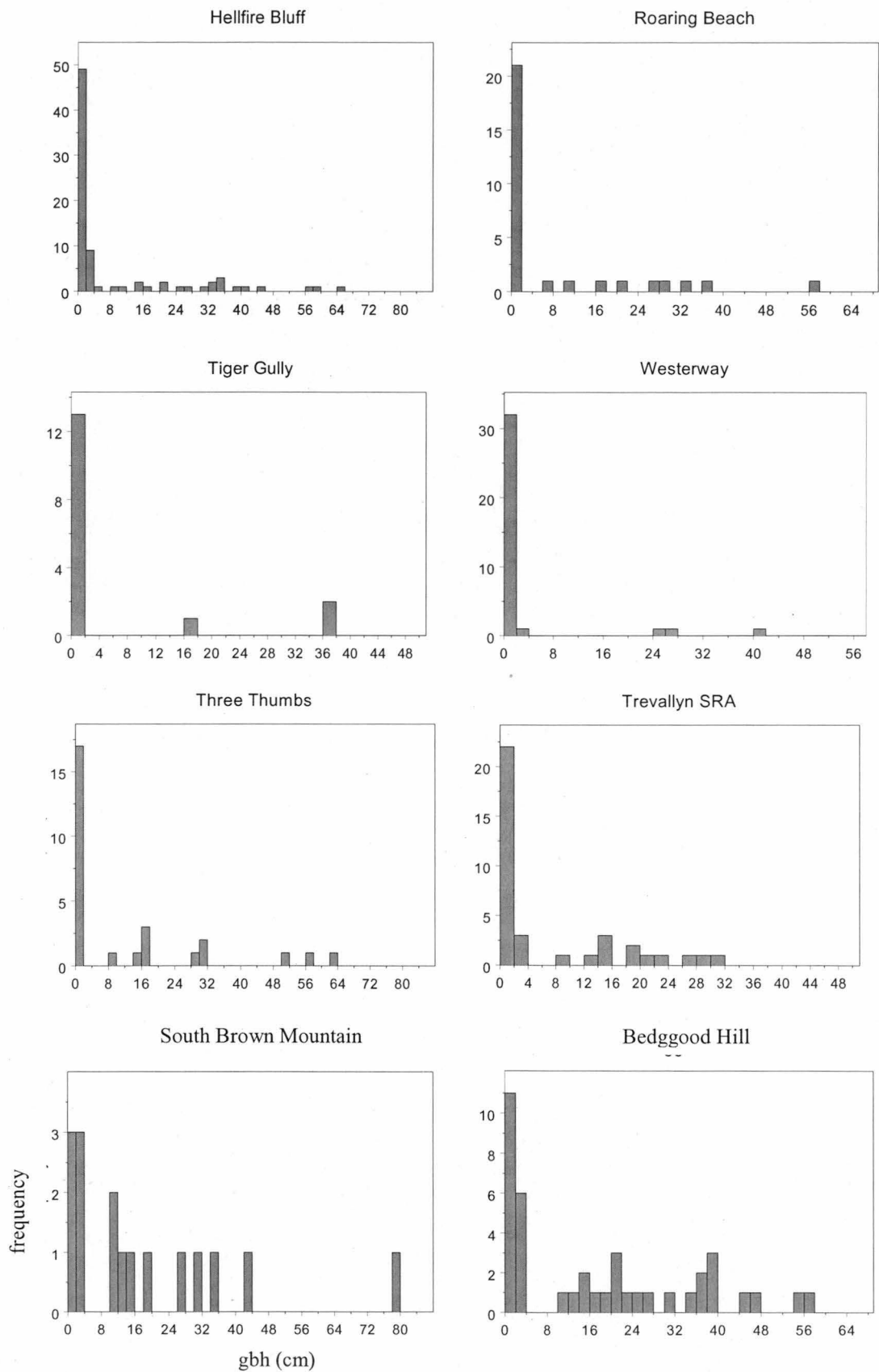
Figure 4.1 *Beyeria viscosa* size-class distribution (continued on next page).
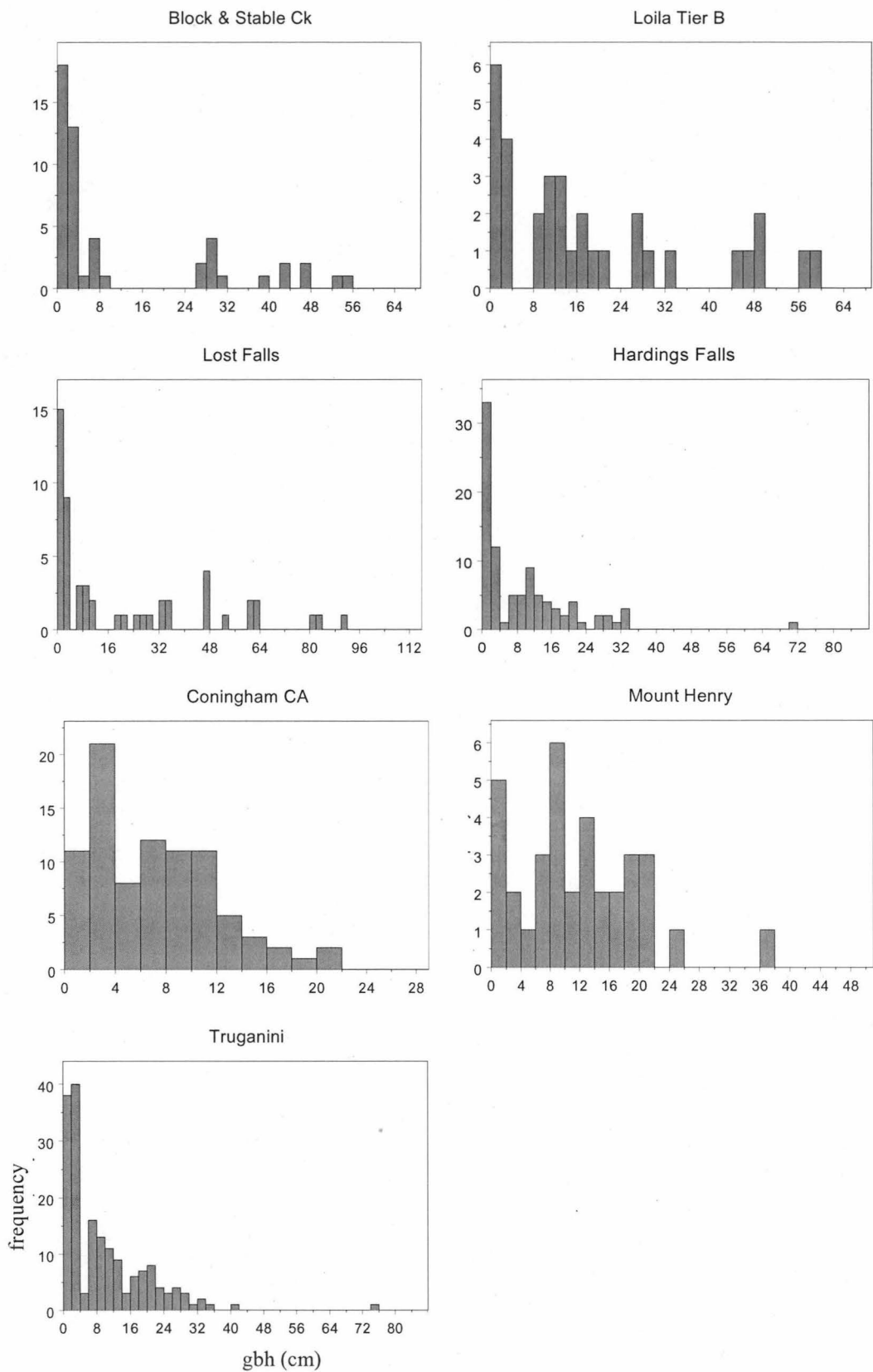
Figure 4.1 *Beyeria viscosa* size-class distribution (continued from previous page).
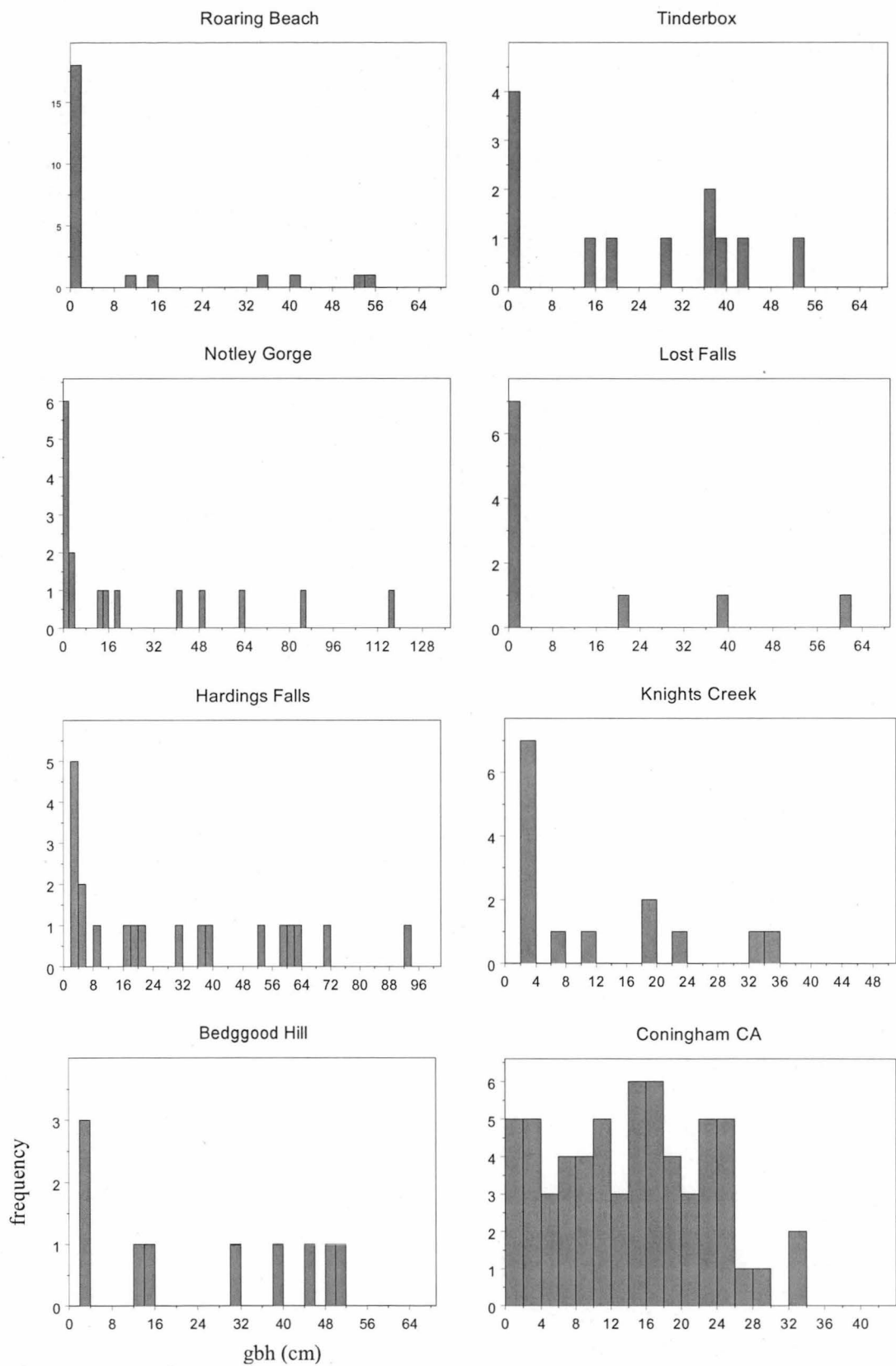
Figure 4.2 *Pomaderris apetala* size-class distribution (continued on next page).
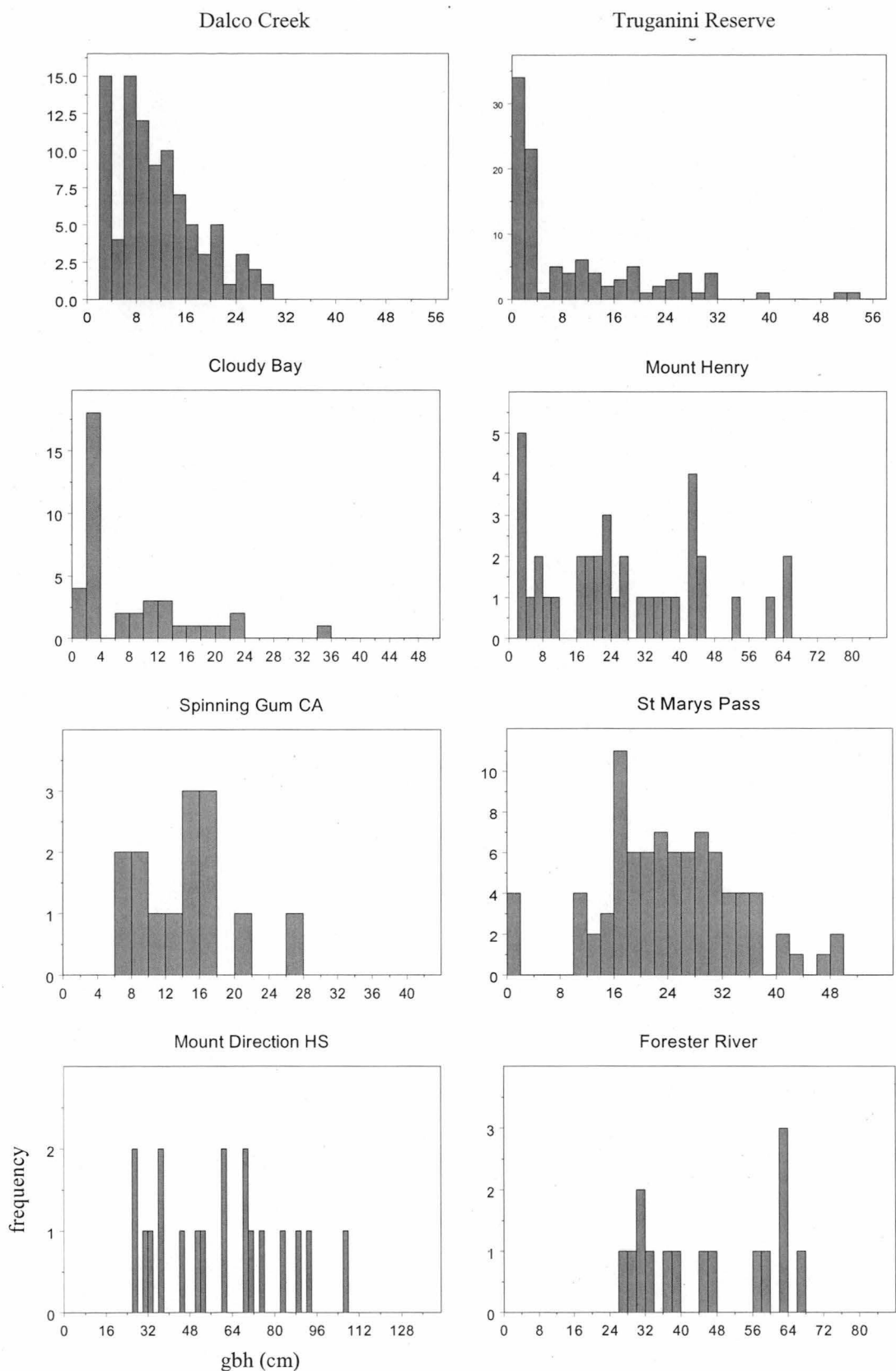
Figure 4.2 *Pomaderris apetala* size-class distribution (continued on next page).
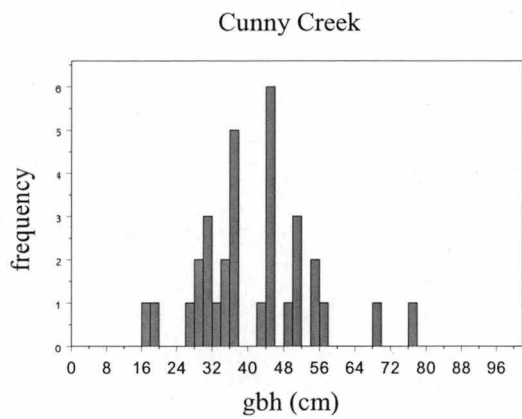
Cunny Creek

Figure 4.2 *Pomaderris apetala* size-class distribution (continued from previous page).
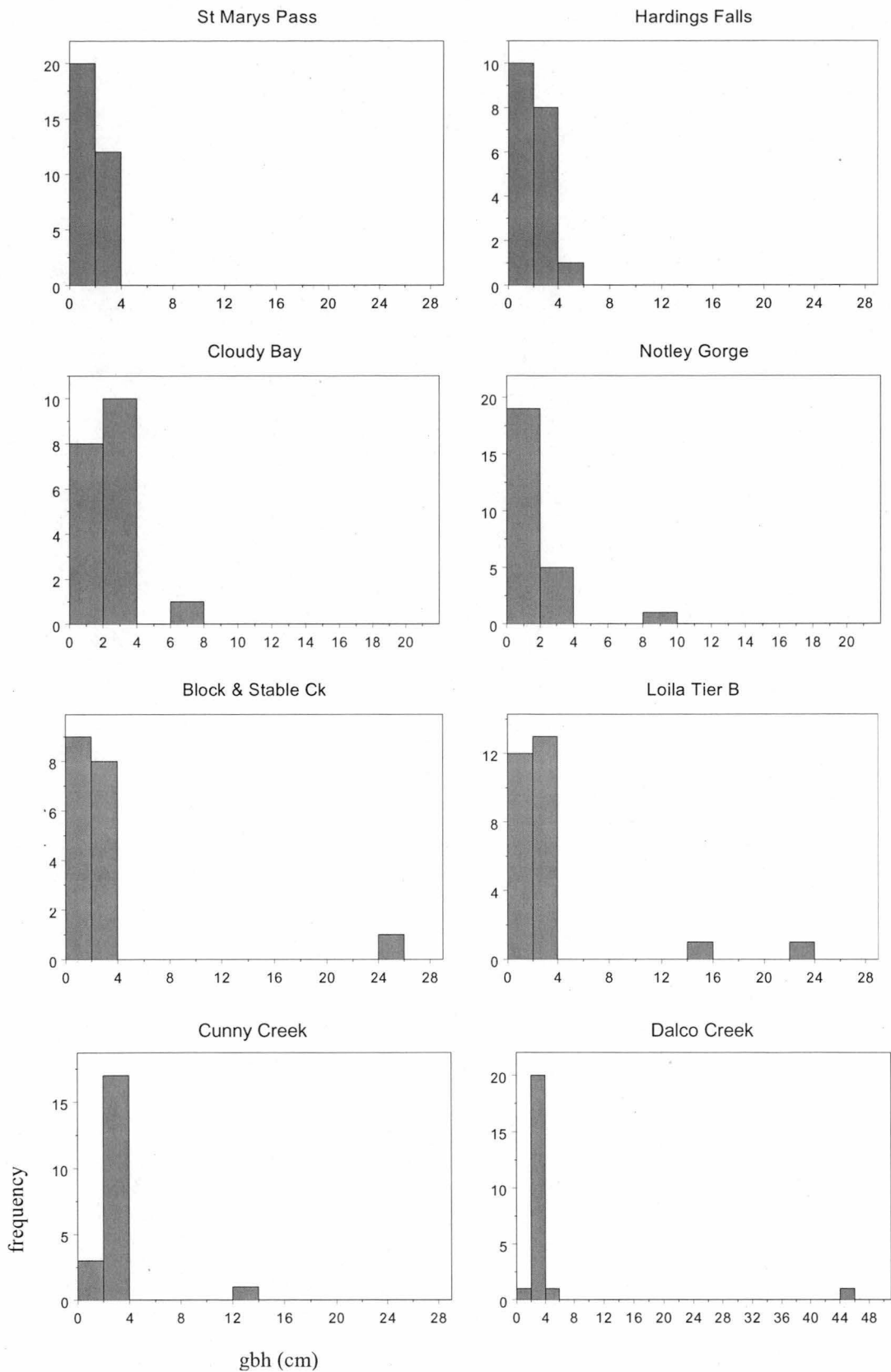
Figure 4.3 *Coprosma quadrifida* size-class distribution (continued on next page).
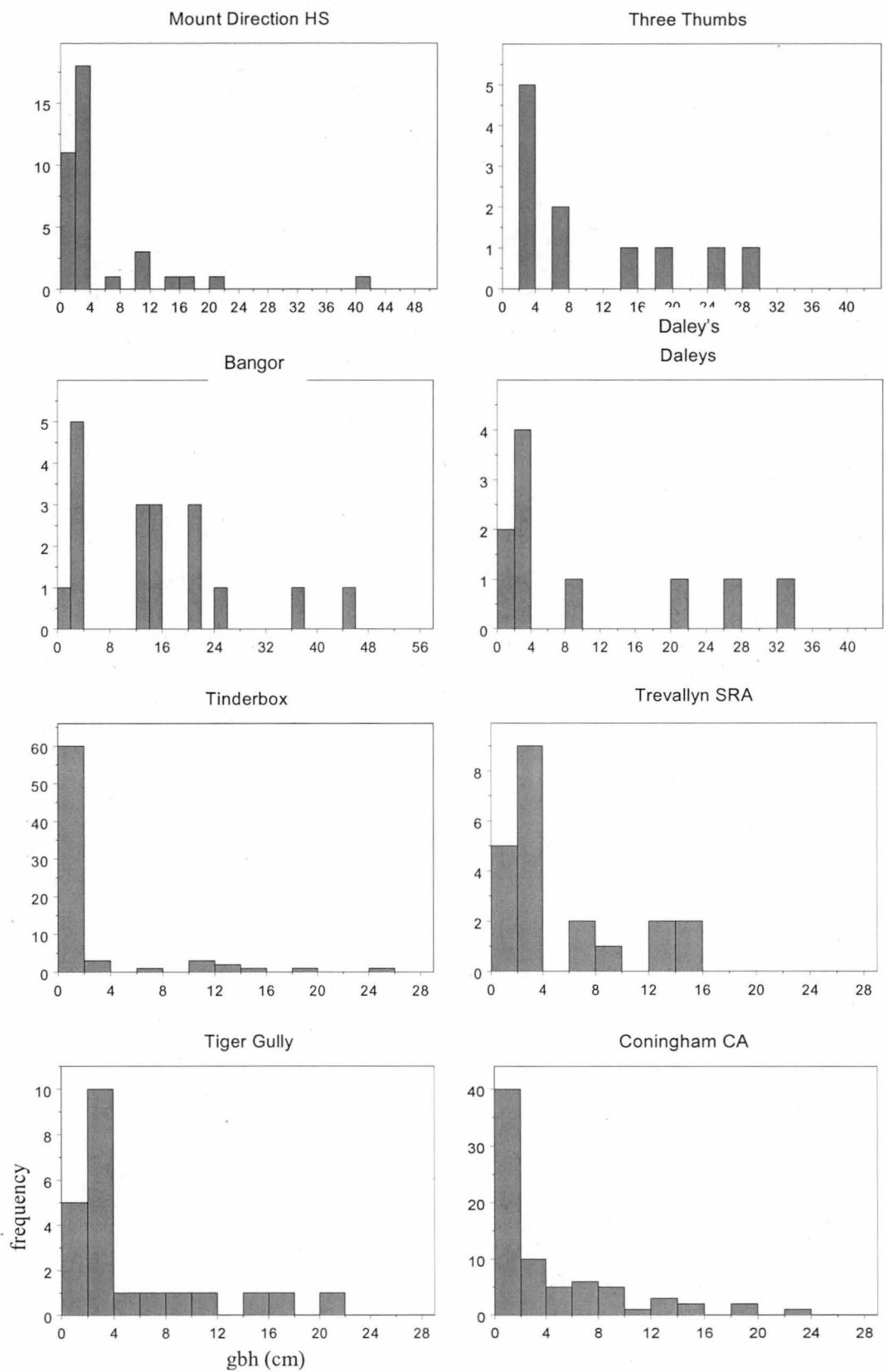
Figure 4.3 *Coprosma quadrifida* size-class distribution (continued on next page).
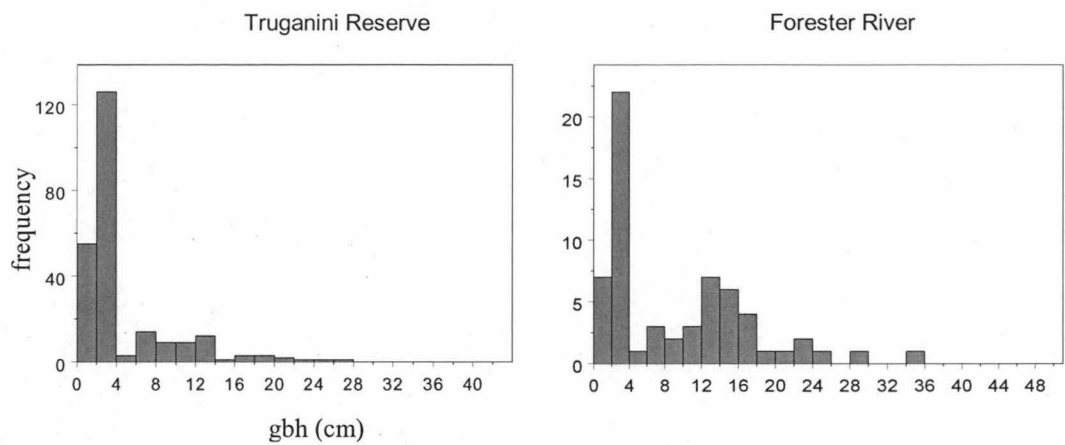
Figure 4.3 *Coprosma quadrifida* size-class distribution (continued from previous page).
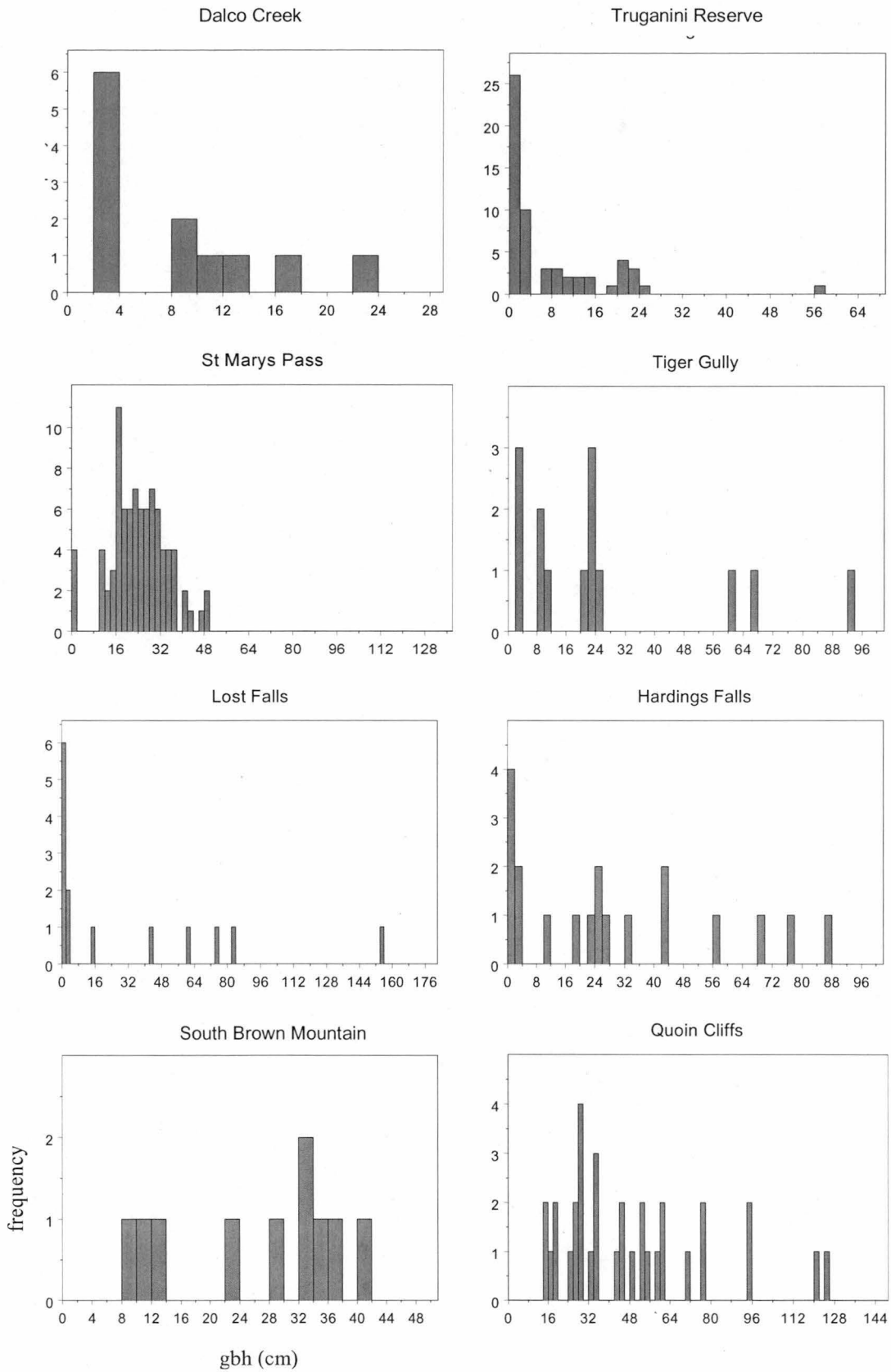
Figure 4.4 *Olearia argophylla* size-class distribution (continued on next page).
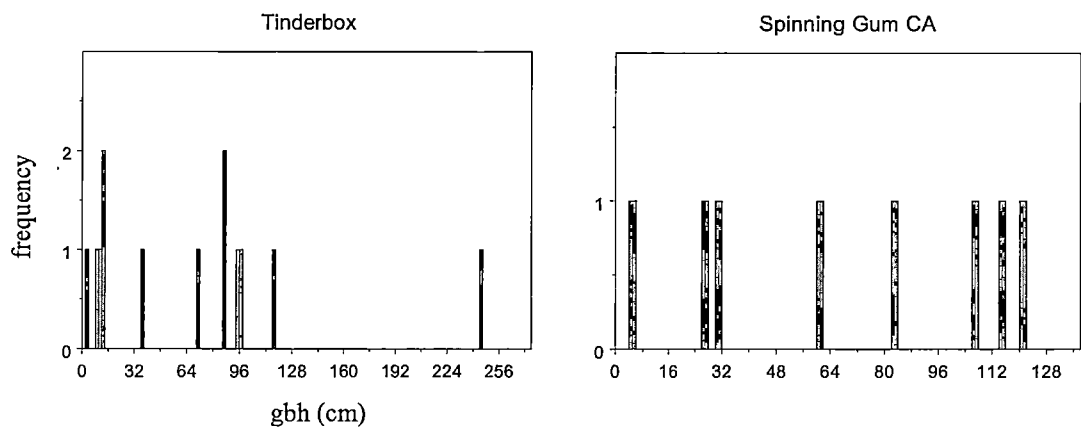
Figure 4.4 *Olearia argophylla* size-class distribution (continued from previous page).
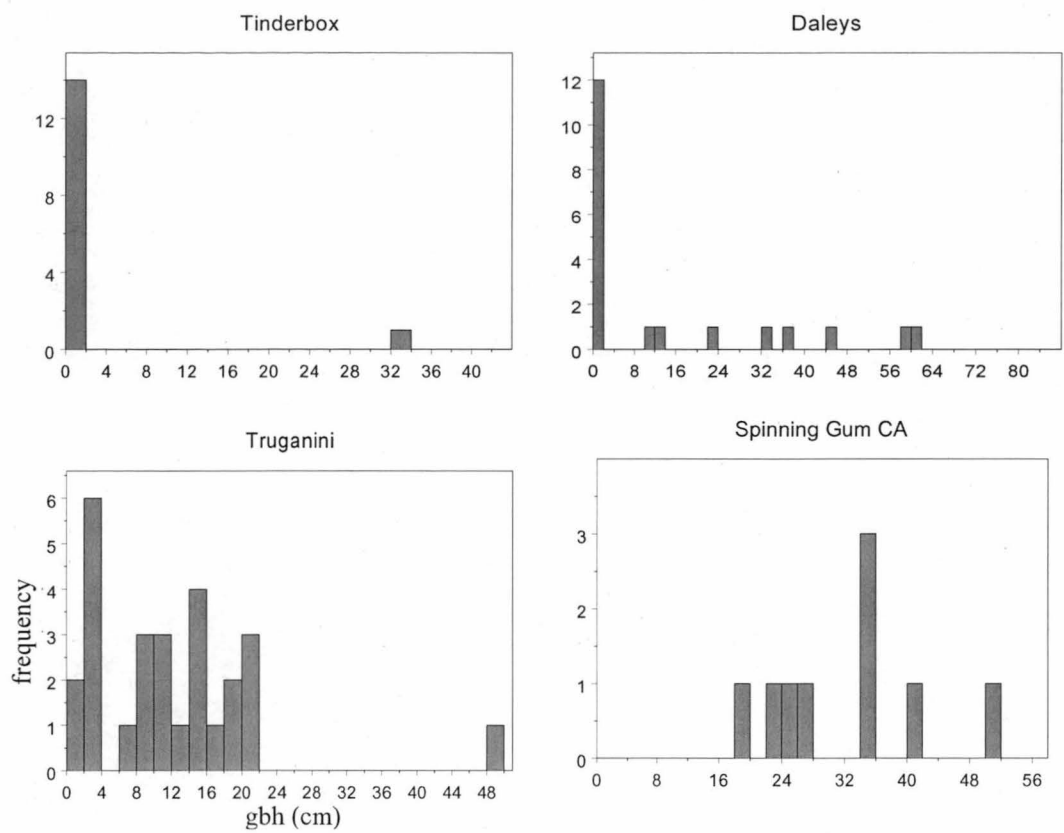
Figure 4.5 *Asterotrichion discolor* size-class distribution.
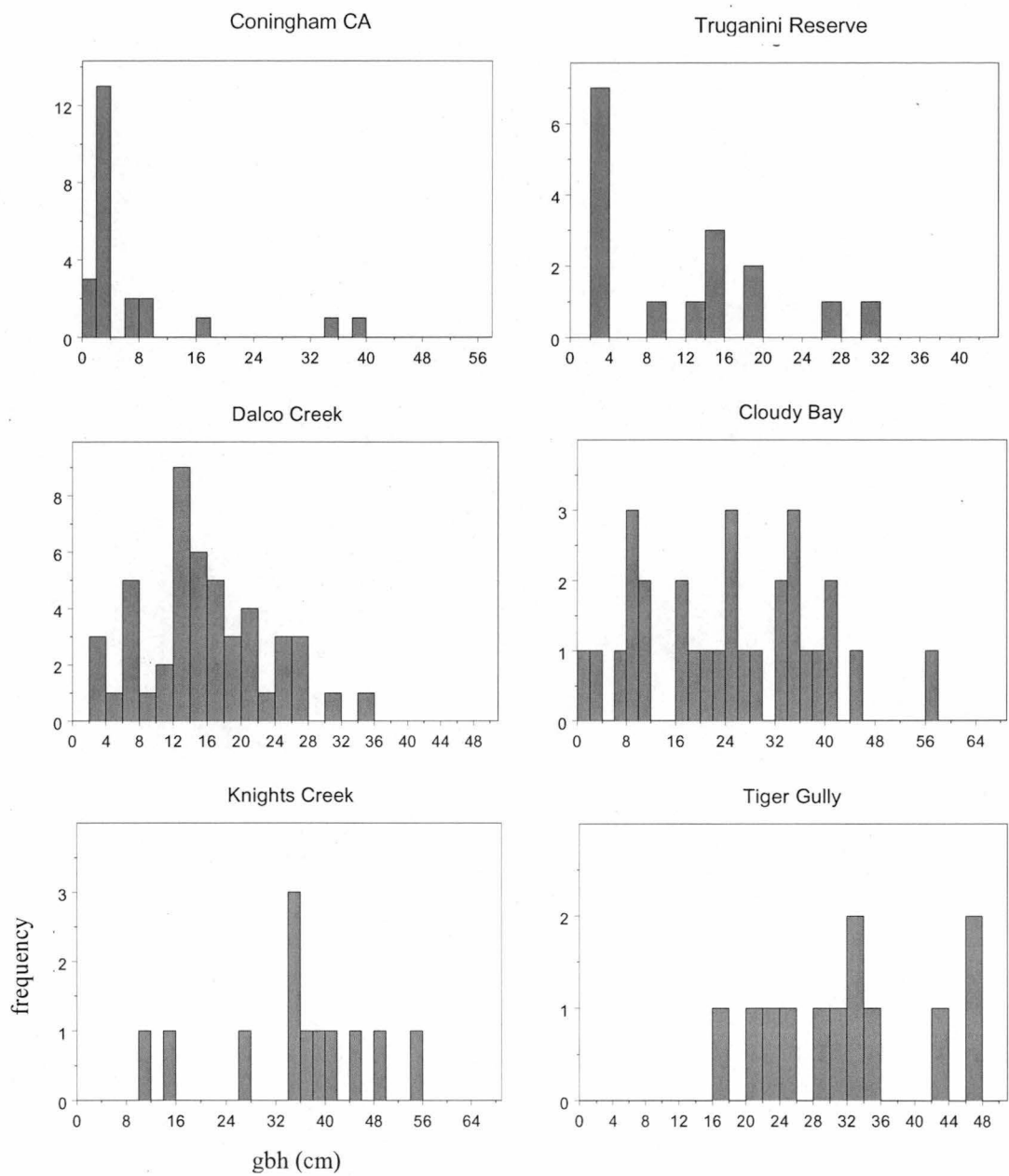
Figure 4.6 *Bedfordia salicina* size-class distribution.
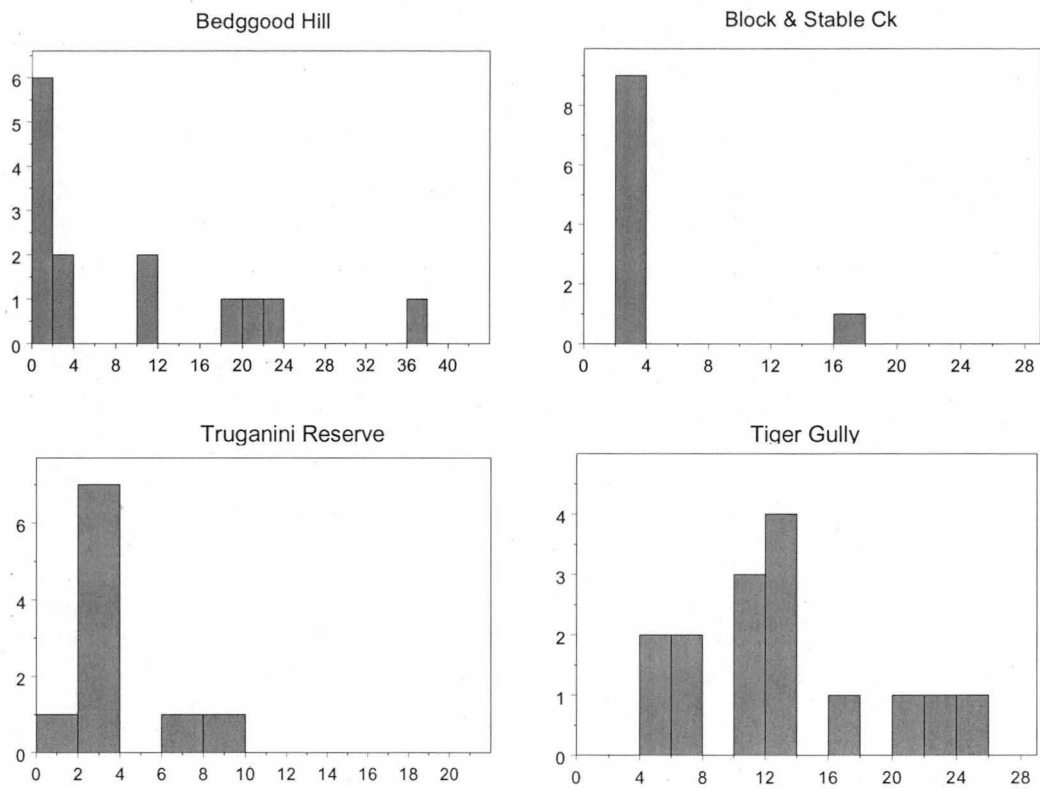
Figure 4.7 Zieria arborescens size-class distribution.
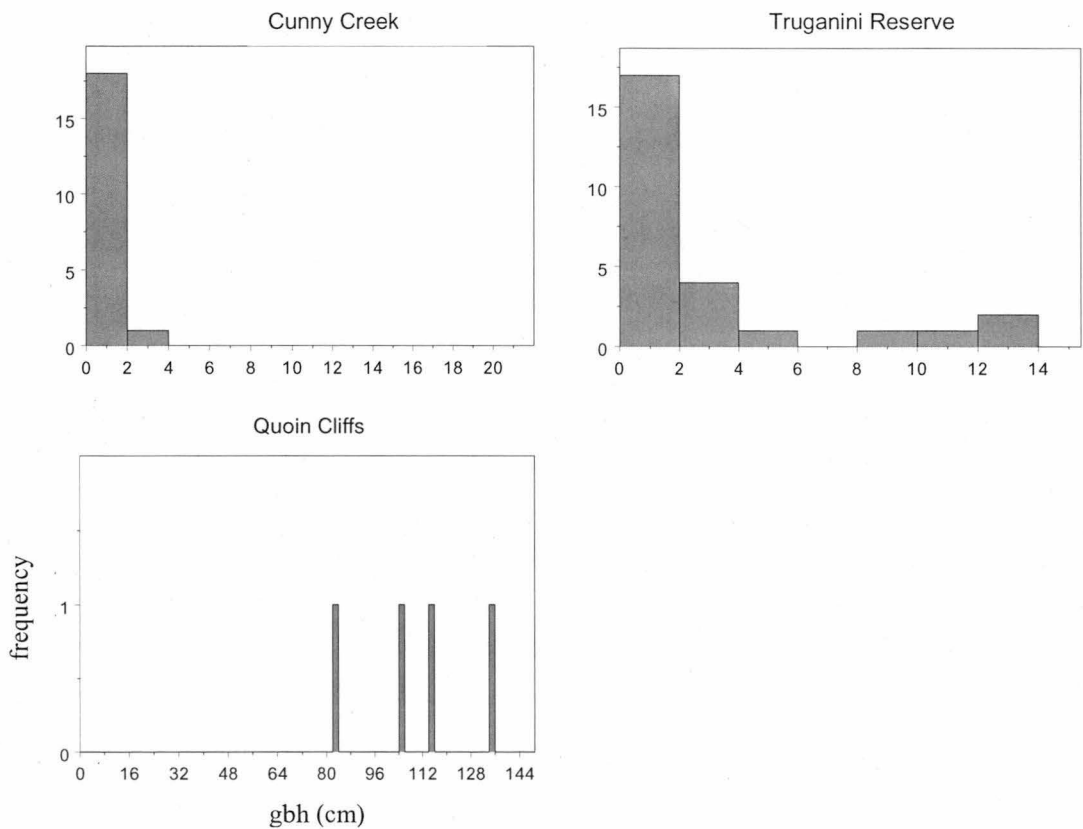
Figure 4.8 *Acacia melanoxylon* size-class distribution.

Lost Falls

Block & Stable Ck
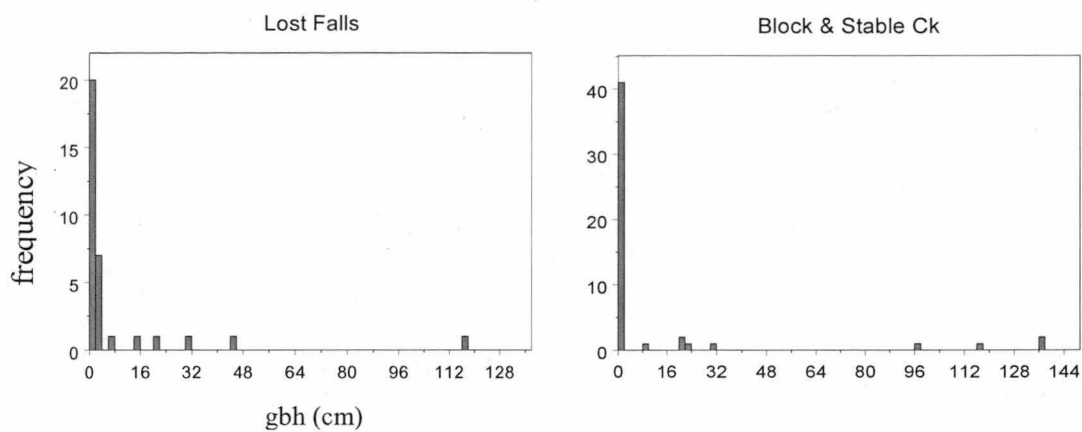
Figure 4.9 *Notelaea ligustrina* size-class distribution.

Truganini Reserve

Dalco Creek
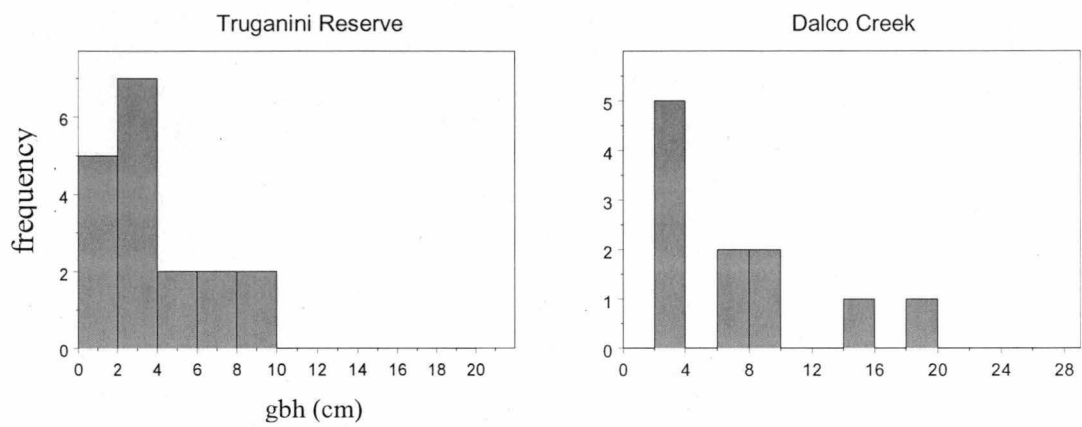
Figure 4.10 *Pittosporum bicolor* size-class distribution.

Table 4.2 Mode of dispersal and regeneration observations of major Tasmanian dry closed-forest species.

Species	Mode of dispersal of seed	Regeneration observations
Bedfordia salicina	Wind dispersed	Coppicing from base of stem and suckering from roots.
Beyeria viscosa	Bird dispersed & Soil stored seed	Coppicing from stem and suckering from roots. When leaning or fallen downslope, adventitious roots develop on the lower side of the trunk. Seedlings around the base of large trees, on matted moss and on fallen rotting trunks of *Eucalyptus*. Germinaté en masse following fire.
Pomaderris apetala	Gravity or occasionally bird-dispersed & soil-stored seed.	Coppicing from stem, forming many branches near ground level. Adventitious roots on the lower side of leaning trunk as for *Beyeria viscosa*. Vigorous lateral shoots produced along fallen trunks. Seedlings on matted moss and on fallen rotting fallen trunks of *Eucalyptus* and some clumping around the base of large trees. Germinate en masse following fire.
Zieria arborescens	Gravity or occasionally bird-dispersed & soil-stored seed (Cunningham & Cremer 1965)	Numerous branches produces from root suckering and stem coppicing, especially when individuals lean or fall over on steep ground.
Coprosma quadrifida	Bird dispersed	Coppicing from stem and suckering from roots. Vigorous lateral shoots produced along fallen and leaning trunks. Seedlings scattered around the base of large trees and on rotting fallen trunks of *Eucalyptus*. Browsed by marsupials (bonsai plants).
Olearia argophylla	Wind dispersed	Large individuals consisting of many coppice stems arising from a large swelling at the base of the trunk. Seedling germination on moss beds.
Pittosporum bicolor	Bird dispersed	Germination on rotten fallen trunks of *Eucalyptus*. Seedlings scattered around the base of large trees.
Asterotrichion discolor	Gravity dispersed?	Coppicing from the trunk near the base, and often also re-sprouting along the upper side of a leaning trunk. Most often the main trunk is heavily leaning with only a few branches up the main trunk. Germinates en masse following fire.
Acacia melanoxylon	Gravity dispersed & soil stored seed	Browsed by marsupials (bonsai plants).
Notelaea ligustrina	Bird dispersed	Seedlings scattered around the bases of large trees. Coppicing from base of trunk.

Spatial patterns

A common feature of the dry closed-forest stands was the association of seedlings with large trees. Figure 4.11 shows parts of transects at Block & Stable Creek and Hellfire Bluff where the clumping pattern of seedlings around large trees is obvious. They were also observed growing in moss or accumulated leaf litter. The moss was found either at the base of trees, or on the upper-side of living horizontal branches, while accumulated leaf-litter can be found on large flat rocks or on top of rotting eucalypt logs that had fallen into the community from upslope.
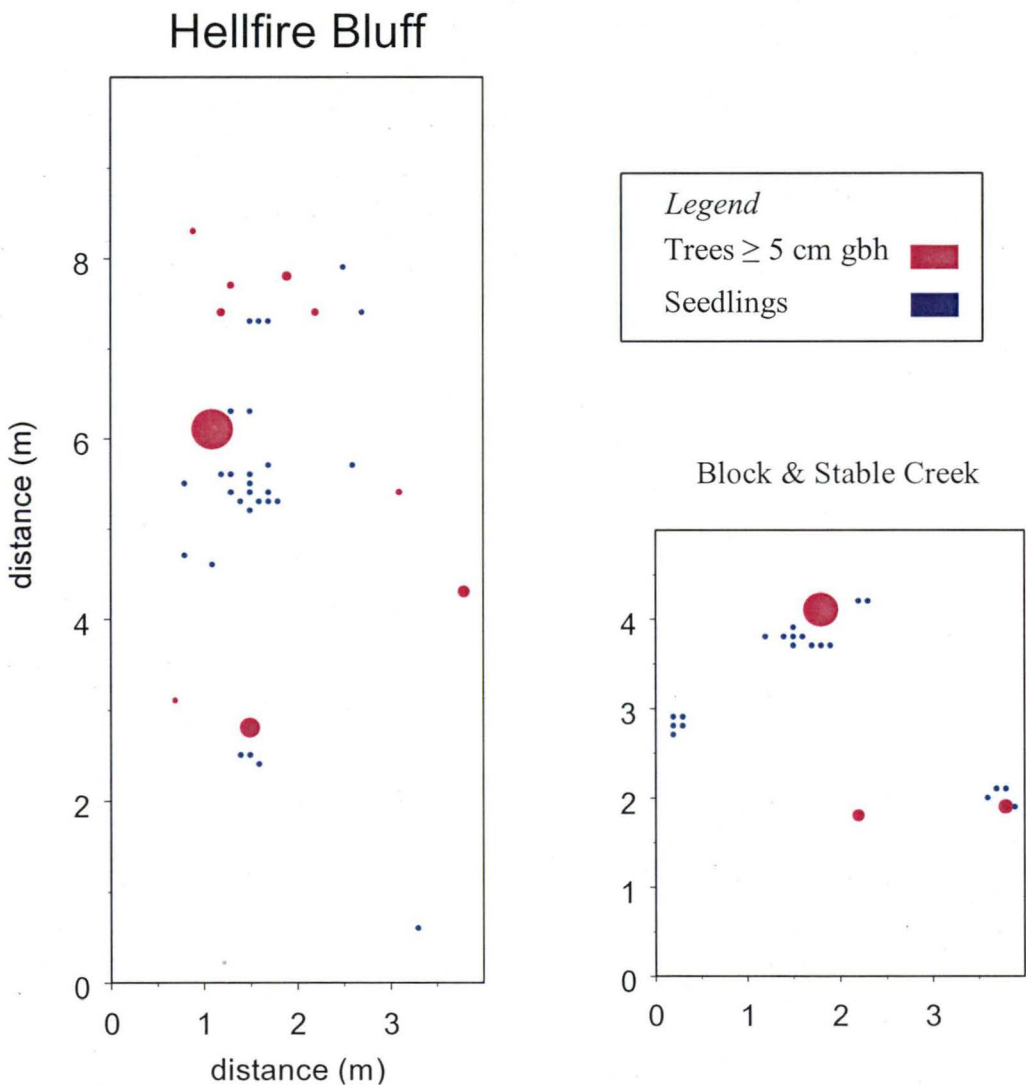
Figure 4.11 Example of clumped distribution of seedlings (all species) around large trees at Block & Stable Creek and Hellfire Bluff.

A full listing of the significant results of the spatial analysis, including values for the segregation index (S), the Z statistic and associated p-values are in

Appendix 4. Multiple instances of significant self-segregation were found for a number of species. However, each of these species showed as many or more instances where they were not significantly self-segregated (Table 4.3).

Table 4.3 Number of stands at which a particular dry closed-forest species displayed a significant (P≤0.05) level of self-segregation. Only individuals with a gbh ≥ 5 cm were included in the analysis.

Species segregated	Number of stands with significant self-segregation	Number of stands with insignificant self-segregation
Acacia dealbata	0	4
Acacia melanoxylon	1	11
Asterotrichion discolor	2	3
Bedfordia salicina	6	6
Beyeria viscosa	4	14
Coprosma quadrifida	2	15
Notelaea ligustrina	4	21
Olearia argophylla	2	12
Pittosporum bicolor	4	12
Pomaderris apetala	6	18
Zieria arborescens	0	4

For associations between individuals of one species and individuals of another species (Table 4.4), there was a similar trend in segregation as was found for self-segregation of species. Although some segregation was observed between species this was generally outweighed by the large number of instances where segregation was not observed.

Table 4.4 Summary of significant tests (p > 0.05) of species segregation for major dry closed-forest species following the method of Dixon (2002). The equations for deriving the Z-statistic and deriving a p-value from z-tables are found in the methods section of this chapter. Full results for all species and all stands are in Appendix 4.

From Species	To species	Number of stands with significant segregation	Number of stands with insignificant segregation
Acacia dealbata	Acacia melanoxylon	0	1
	Asterotrichion discolor	0	2
	Bedfordia salicina	1	3
	Beyeria viscosa	0	3
	Coprosma quadrifida	0	3
	Notelaea ligustrina	0	1
	Olearia argophylla	2	3
	Pittosporum bicolor	1	0
	Pomaderris apetala	1	3
	Zieria arborescens	0	2
Acacia melanoxylon	Acacia dealbata	0	1
	Asterotrichion discolor	0	2
	Bedfordia salicina	0	4
	Beyeria viscosa	0	6
	Coprosma quadrifida	0	9
	Notelaea ligustrina	0	6
	Olearia argophylla	1	10
	Pittosporum bicolor	0	8
	Pomaderris apetala	0	12
	Zieria arborescens	0	1
Asterotrichion discolor	Acacia dealbata	0	1
	Acacia melanoxylon	0	3
	Bedfordia salicina	0	2
	Beyeria viscosa	0	3
	Coprosma quadrifida	0	4
	Notelaea ligustrina	0	2
	Olearia argophylla	0	6
	Pittosporum bicolor	0	4
	Pomaderris apetala	1	4
	Zieria arborescens	0	1
Bedfordia salicina	Acacia dealbata	0	3
	Acacia melanoxylon	1	5
	Asterotrichion discolor	0	2
	Beyeria viscosa	2	7
	Coprosma quadrifida	1	8
	Notelaea ligustrina	0	5
	Olearia argophylla	0	12
	Pittosporum bicolor	0	6
	Pomaderris apetala	2	10
	Zieria arborescens	0	3

Table 4.4 continued.

From Species	To species	Number of stands with significant self-segregation	Number of stands with insignificant self-segregation
Beyeria viscosa	*Acacia dealbata*	0	2
	Acacia melanoxylon	0	7
	Asterotrichion discolor	0	3
	Bedfordia salicina	1	8
	Coprosma quadrifida	3	11
	Notelaea ligustrina	0	11
	Olearia argophylla	1	15
	Pittosporum bicolor	0	11
	Pomaderris apetala	2	11
	Zieria arborescens	0	3
Coprosma quadrifida	*Acacia dealbata*	0	2
	Acacia melanoxylon	0	9
	Asterotrichion discolor	0	4
	Bedfordia salicina	1	8
	Beyeria viscosa	2	13
	Notelaea ligustrina	0	13
	Olearia argophylla	1	18
	Pittosporum bicolor	0	14
	Pomaderris apetala	1	16
	Zieria arborescens	0	3
Notelaea ligustrina	*Acacia dealbata*	0	1
	Acacia melanoxylon	0	7
	Asterotrichion discolor	0	3
	Bedfordia salicina	0	6
	Beyeria viscosa	1	11
	Coprosma quadrifida	0	14
	Olearia argophylla	1	12
	Pittosporum bicolor	3	8
	Pomaderris apetala	0	12
	Zieria arborescens	0	3
Olearia argophylla	*Acacia dealbata*	2	2
	Acacia melanoxylon	2	8
	Asterotrichion discolor	0	5
	Bedfordia salicina	0	11
	Beyeria viscosa	2	13
	Coprosma quadrifida	1	16
	Notelaea ligustrina	2	11
	Pittosporum bicolor	0	15
	Pomaderris apetala	2	17
	Zieria arborescens	0	4

Table 4.4 continued.

From Species	To species	Number of stands with significant self-segregation	Number of stands with insignificant self-segregation
Pittosporum bicolor	Acacia dealbata	0	0
	Acacia melanoxylon	0	9
	Asterotrichion discolor	0	4
	Bedfordia salicina	0	6
	Beyeria viscosa	0	11
	Coprosma quadrifida	0	14
	Notelaea ligustrina	3	8
	Olearia argophylla	1	14
	Pomaderris apetala	0	14
	Zieria arborescens	1	2
Pomaderris apetala	Acacia dealbata	0	3
	Acacia melanoxylon	1	13
	Asterotrichion discolor	0	5
	Bedfordia salicina	2	10
	Beyeria viscosa	2	12
	Coprosma quadrifida	1	15
	Notelaea ligustrina	0	11
	Olearia argophylla	2	19
	Pittosporum bicolor	0	14
	Zieria arborescens	1	3
Zieria arborescens	Acacia dealbata	0	1
	Acacia melanoxylon	0	2
	Asterotrichion discolor	0	1
	Bedfordia salicina	0	3
	Beyeria viscosa	1	2
	Coprosma quadrifida	0	4
	Notelaea ligustrina	0	3
	Olearia argophylla	0	4
	Pittosporum bicolor	2	1
	Pomaderris apetala	0	4

Plate 4.3 Enlarged coppiced base of *Olearia argophylla* at Spinning Gum Conservation Area, southern Midlands.
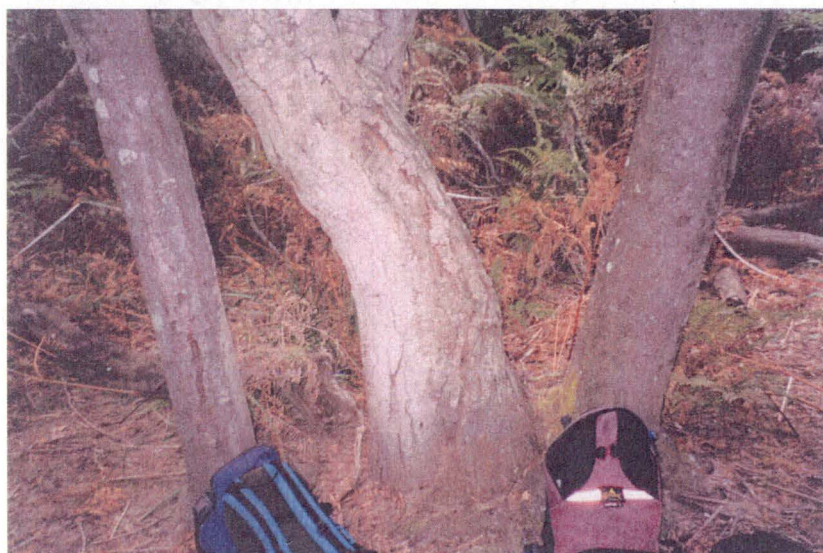
Plate 4.4 *Pittosporum bicolor* growing around the base of *Banksia marginata* (centre) at Bangor, southern Tasmania.
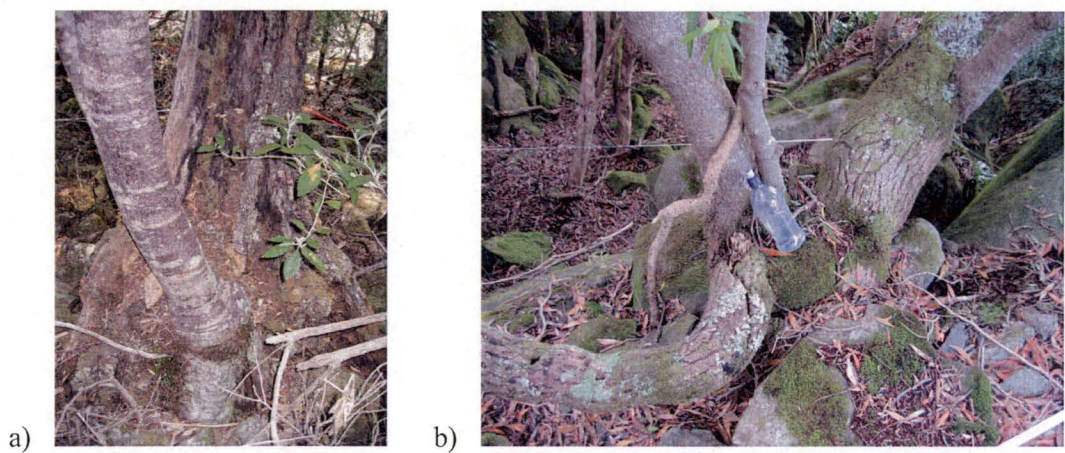
Plate 4.5 *Pittosporum bicolor* growing from the base of *Notelaea ligustrina* at (a) Hellfire Bluff, and (b) Trevallyn State Recreation Area (*P. bicolor* on the left in both images).

Discussion

Vegetation structure

There is considerable variability in the basal area of Tasmanian dry closed-forest stands. Stands for which a high basal area was recorded consisted mainly of large individuals, especially of *Acacia melanoxylon*, *Acacia dealbata*, *Olearia argophylla* and *Notelaea ligustrina*. In contrast to this, the two localities that recorded the lowest stand basal areas (Coningham CA and Truganini Reserve) consisted of dense stands of small individuals. It appears that these differences in stand basal area reflect time since the last fire disturbance. Stands with large scattered trees above an open understorey devoid of regenerating young individuals do not seem to have experienced fire for a considerable period. In contrast, dense stands with a predominance of small individuals, such as Coningham CA and Truganini Reserve, indicate the occurrence of a relatively recent bushfire, which has killed large individuals and opened up the canopy, allowing dense regeneration of species such as *Beyeria viscosa*, *Pomaderris apetala*, and *Bedfordia salicina*.

Beyeria viscosa was consistently well represented by large numbers of saplings and/or seedlings in dry closed-forest stands. Sites that had a high proportion of *B. viscosa* as larger individuals had size-class distributions that approached the expected pattern for self-replacing vegetation. A dip in numbers of individuals slightly larger than sapling size seems to indicate self-thinning of dense stands of these saplings as individuals compete for light, soil moisture and nutrients. The most successful regeneration event for *B. viscosa* appears to be disturbance by fire, after which dense regeneration occurs. *B. viscosa* was commonly observed densely filling the dry closed-forest-eucalypt forest ecotone following a breach in the rainforest boundary by fire. In such situations *B. viscosa* self-thinned as the individuals competed with one another for canopy space. However, *B. viscosa* also appears to be able to regenerate continuously between disturbance events. For stands that have not had recent exogenous disturbance the size-class distribution of *B. viscosa* is that of a self-replacing species.

Pomaderris apetala more clearly showed a size-class distribution that indicates regeneration following fire disturbance. This disturbance event diminished the

canopy cover enough to allow *P. apetala* to establish itself in these stands. Cunningham and Cremer (1965) also observed dense regeneration of *P. apetala* from soil-stored seed in wet eucalypt forest following fire.

Coprosma quadrifida was most common as small individuals in dry closed-forest stands, and this reflects its normal growth habit as an understorey shrub. This species is probably self-replacing because in most instances there were adequate numbers of seedlings and/or saplings in the understorey capable of reaching maturity in small canopy gaps. Being an understorey element in dry closed-forest it is expected that *C. quadrifida* would be somewhat tolerant of low-light conditions. Ashton & Turner (1979) recorded a light compensation point for *C. quadrifida* that was relatively low when compared with the other understorey species of Victorian wet sclerophyll forest.

Olearia argophylla displayed a size-class distribution pattern that indicates this species is opportunistic in its regeneration strategies. Being wind dispersed, *O. argophylla* is able to regenerate densely following fire disturbance from seed derived from adjacent intact forest (Cunningham and Cremer 1965). The key to *O. argophylla* dominating a stand appears to be related to its ability to form an extensive canopy through coppicing. Large multi-stemmed specimens of this species are the result of this vegetative perpetuation, which is in contrast to some of the other common species of dry closed-forest such as *B. viscosa* and *P. apetala* which use mass recruitment of large numbers of individuals to dominate a stand. Large specimens of *O. argophylla* possess a hemispherical swollen base from ground level (Plate 3.3), from which coppices emerge after a bushfire (Ashton 1981). In addition, *O. argophylla* was observed in the present study coppicing in the absence of fire, possibly enabling it to increase its percentage of the stand canopy cover between fire events, effectively reducing the light reaching other regenerating dry closed-forest species.

Asterotrichion discolor is largely faithful to dry closed-forest. The size-class distribution analysis reveals that *A. discolor* is well represented in the south-eastern Tasmanian stands as seedlings. A size-class distribution with only larger individuals at Tiger Gully may indicate a past fire event. *A. discolor* is a mass

regenerator following fire. This has been observed by the author at New Town Rivulet and Truganini Reserve both near Hobart, where there is very dense regeneration of small individuals in the ecotone between dry closed-forest and eucalypt forest 5-10 years after a bushfire. These stands are in the process of thinning by competition and insect defoliation.

The size-class distribution of *Bedfordia salicina* in dry closed-forest is similar to that of *P. apetala*. *B. salicina* regenerates from seed after a fire disturbance event but is capable of resprouting after a low intensity fire. Individuals of both young and mature *B. salicina* were comonly found at the margins of dry closed-forest stands. This may indicate that *B. salicina* regenerates where the fire frequency is at its greatest. Despite having a similar dispersal-mode and post-fire regeneration strategy to *O. argophylla*, *B. salicina* rarely dominates the core of stands.

Zieria arborescens was only infrequently recorded from dry closed-forest stands in contrast to the dense regeneration of this species recorded by Cunningham and Cremer (1965) in wet eucalypt forests after fire disturbance. These low numbers could relate to *Z. arborescens* preference for moister summers than are experienced in most areas that support dry closed-forest.

A. melanoxylon is most often seen as isolated emergents above the dry closed-forest. Due to this low density, *A. melanoxylon* individuals were rarely encountered in the small sample areas examined for each stand in the present study. However, the observation of large isolated individuals seems to suggest opportunistic regeneration when a gap in the canopy is created. It is possible that *A. melanoxylon* could be regenerating in gaps created by tree-fall in dry closed-forest. Jarman & Brown (1983) noted that this species had been observed regenerating in tree-fall gaps in temperate rainforest. The low frequency of *A. melanoxylon* individuals reaching maturity could also be the result of marsupial browsing. The palatability of this species to browsing marsupials is well known (Jennings 1998; Hickey & Wilkinson 1999). Dry closed-forest provides a dense protective habitat for a number of marsupials including wombats and wallabies. It was common for A. *melanoxylon* individuals to be observed as stunted "bonsai" specimens, as a result of heavy marsupial browsing. Even if *A. melanoxylon* was able to regenerate

profusely it is likely that palatability to marsupials would result in a low survival rate.

Like *A. melanoxylon*, *Notelaea ligustrina* was commonly recorded as low numbers of large individuals, and was rarely recorded from the transects because of its low density in stands. *N. ligustrina* (along with *B. viscosa*, *P. bicolor* & *C. quadrifida*) was commonly found as seedlings clumped around large trees which is indicative of depositing of seed by birds from perches. This is a feature of regeneration in rainforest boundaries such as the monsoon rainforest-savanna ecotone (Fensham & Bulter 2004) and isolated trees in disused ex-farmland surrounded by subtropical rainforest (Toh *et al.* 1999). *N. ligustrina* probably regenerates in gaps when a seed is excreted by a bird and the seed lands where the canopy is open enough above to allow for growth. *N. ligustrina* displayed a strong affiliation with rock, commonly growing as mature individuals on rocks at the bottom of a gully or on rock scree. This affiliation with rock is probably related to the protection from birds and other seed-eating creatures that crevices between rocks afford. However, *N. ligustrina* was observed re-sprouting following fire, which indicates that growing in rocky situations is not implicitly related to fire-avoidance. Despite this, occurrence with rock does equate to a low fire-frequency, and therefore by default, stands containing large *N. ligustrina* could represent a late-successional stage of dry closed-forest that has developed in the absence of recent fire disturbance.

The regeneration strategy of *P. bicolor* is very similar to that of *N. ligustrina*, and like this species is capable of regeneration without exogenous disturbance. A fuller account of the regeneration mode of this species follows in the next section.

Spatial patterns

One ecologically interesting feature of *P. bicolor* regeneration is its propensity for establishing on the base of other large trees. This was observed at Bangor where *P. bicolor* is growing from the base of *Banksia marginata* in a woodland converting to dry closed-forest under an infrequent fire regime (Plate 4.4), and at Hellfire Bluff and Trevallyn SRA where it can be seen growing from the base of *N. ligustrina* (Plate 4.5). The reason for *P. bicolor* germinating in this way is that its fruit is bird dispersed and contains its seeds in a very sticky pulp. As the large trees are

preferred perching sites for birds, bird excrement falls directly to the base of the large tree and the seeds germinate in the moist leaf litter at the base of the large trees. Gleadow and Rowan (1982) suggested that the clumping of seedlings of the related species *Pittosporum undulatum* around the base of mature trees is partly due to uneven dispersal by birds. They suggest that this clumping pattern is reinforced by the moderating effects of the shady location on high summer temperatures and photon flux densities; both important factors that influence drought tolerance in *P. undulatum*.

Beyeria viscosa and *Pomaderris apetala* also displayed patterns of seedling distribution associated with large trees, a pattern most easily explained by their being bird-dispersed. However, these species did not have as much success in germinating in the relatively dark conditions under the canopy of a large tree, unlike *N. ligustrina* and *P. bicolor*. Continuous regeneration of *B. viscosa* does occur, but establishment seems to only take place in open areas of stands, such as near the boundary or in tree-fall gaps, rather than around large trees. This suggests that *N. ligustrina* or *P. bicolor* have lower light compensation points than *B. viscosa* and *P. apetala*. This assertion is supported by the fact that both *P. bicolor* and *N. ligustrina* can also be found growing in the low-light environment of temperate rainforest. The large numbers of *B. viscosa* and *P. apetala* seedlings around large trees presumably die off because of a lack of light, and would only be successful in reaching a larger size if the canopy above them was breached by the large tree falling or dying of old age. Another possible combining factor that could cause this seedling death is a lack of soil moisture, caused by regular water deficit during summer in the east of Tasmania or difficulty in reaching sub-surface water on rocky sites. However, one would also expect death of *P. bicolor* and *N. ligustrina* seedlings if moisture was limited, which does not seem to occur. Beneath the dry closed-forest canopy the ground is commonly covered in a thick layer of rock mulch, the surface of which retains little moisture. This means that for a seedling to survive it needs to be in thick leaf-litter or moss, or in a gap between rocks.

The finding that there are comparatively few examples of established individuals of dry closed-forest species that display significant spatial segregation indicates

that, in the majority of stands, established individuals of dry closed-forest species are randomly distributed.

The present study identified a number of dry closed-forest species with vegetative recovery mechanisms. *O. argophylla* was shown to recover from fire disturbance by vigorous coppicing, as has also been reported by Ashton (1981). The present study also documented a number of species sprouting along stems that had fallen down on steep, rocky unstable slopes. This is in agreement with observations made by Woolward (1983) in dry closed-forests in the Hobart area. The steep scree slopes on which dry closed-forest commonly grows are extremely prone to rock movement, and inevitably trees end up leaning downslope. Most dry closed-forest species showed the capacity to vegetatively recover from such an incident by sprouting new stems along the leaning or fallen trunk and forming new roots where the trunk contacts the soil. Sometimes, as exemplified by *Pomaderris apetala*, this conferred an advantage because the regrowth along the stem was very dense and the individual ended up with a much greater leaf area in the canopy than before the fall.

The definition of a rainforest tree species of Lynch & Neldner (2000) focuses on the ability to regenerate vegetatively or by seed under a closed canopy or in an area of small-scale disturbance caused by a natural rainforest ecosystem process, such as a single tree-fall. It would seem therefore that the dry closed-forest species *Beyeria viscosa*, *Coprosma quadrifida*, *Notelaea ligustrina*, *Pittosporum bicolor* and possibly *Acacia melanoxylon* fulfil the specifics of Lynch & Neldner's definition, as has been suggested previously by Kirkpatrick (1989, 1992). Despite many of the Tasmanian dry closed-forest species obviously not being gap-phase regenerators, the community as a whole shows ecological and structural similarities to other dry closed-forests across Australia, most obviously in occupying sites that exclude fire (Chapter 2) and by occurring as small isolated patches in an otherwise eucalypt-dominated landscape (Chapter 4). Some species in the community take advantage of the opportunities created by a severe fire event, while others take advantage of smaller chance endogenous disturbance events.

The results of the size-class analysis of individuals of dry closed-forest species

indicated that *Beyeria viscosa, Pomaderris apetala, Asterotrichion discolor, Bedfordia salcicina,* and *Zieria arborescens* regenerate primarily following disturbance, and that *Beyeria viscosa, Coprosma quadrifida, Notelaea ligustrina, Pittosporum bicolor, Acacia melanoxylon,* appear to be able to continuously regenerate in the absence of disturbance. *Olearia argophylla* seems to be a special case in that it requires disturbance for seedling establishment, but can persist in the long-term by vegetative regeneration.

The major management issue concerning dry closed-forest is that of fire. Any change in the fire frequency will shift dry closed-forest backwards or forwards in its successional sequence. A greater fire frequency will favour dry closed-forest containing a higher proportion of fire-requiring regenerators, while a decrease in fire frequency will favour dry closed-forest with more gap-phase regenerators. This should be taken into account when determining fire regimes for areas containing this community.

Concluding remarks

Of the ten species studied *Beyeria viscosa, Pomaderris apetala, Olearia argophylla, Bedfordia salicina, Zieria arborescens* and *Asterotrichion discolor* show signs of regenerating in dry closed-forest after major disturbance events, usually following a bushfire. A number of species also effectively use vegetative regeneration to perpetuate themselves between disturbance events. *Coprosma quadrifida, Notelaea ligustrina,* and *Pittoporum bicolor* (all bird-dispersed) displayed the ability to self-perpetuate themselves without exogenous disturbance. *Acacia melanoxylon* could be self-replacing in dry closed-forest, but marsupial browsing of young *A. melanoxylon* individuals may make survival to adulthood rare.

Seedlings within dry closed-forest were often clustered around large trees indicating dispersal via birds perching. However, only *P. bicolor, N. ligustrina and C. quadrifida* are capable of persisting to maturity in such low-light situations. There is evidence that dry closed-forest undergoes a successional shift over time relating to an increasing fire-free interval from *B. viscosa/P. apetala* dominance to a forest with a greater component of the low-light tolerant species *N. ligustrina, P. bicolor* and *C. quadrifida. O. argophylla* also appears to dominate stands over time due to its capability for re-sprouting and vegetative spread.

Chapter 5 - *Eucalyptus* Exclusion from Dry closed-forest

Abstract

This study tested a number of hypotheses on the cause of the absence of *Eucalyptus* from the dry closed-forest vegetation of Tasmania. These hypotheses related to soil properties, competition between species, and fire effects. *Eucalyptus globulus* and the dry rainforest species *Asterotrichion discolor* and *Pomaderris apetala* were experimentally germinated and grown in a glasshouse under different soil treatments. Germination success, seedling survival and growth were measured over a 26-week period. General Linear Models were used to test for significant differences in growth in different treatments, and interactions of treatments. On the dry closed-forest soil without a heat treatment, *E. globulus* had a relatively low germination success, experiencing the most seedling deaths, but also recorded its tallest growth. *A. discolor* response to this treatment was similar to that of *E. globulus*. Soil type influences the growth of these species, with *E. globulus* having its best growth response on eucalypt forest soil, and *A. discolor* having its best growth response on dry closed-forest soil. Negative competitive effects were identified between *E. globulus* and *A. discolor*. There was a significant interactive effect of soil type and presence/absence of *A. discolor* on the growth of *E. globulus*. The results of the experiment are discussed with reference to soil chemical properties, fungal interactions, the effects of bushfire on the soil, and competition with the dry closed-forest species.

Introduction

Eucalyptus and other fire-loving species are only exceptionally a component of Australian rainforest. They are absent from, or contribute only a small amount to the overall vegetation cover of Tasmanian dry closed-forest. Similar to rainforest with Brushbox (*Lophostemon confertus*) (Turner 1984), and the "mixed-forests" of southeast Australia (Gilbert 1959), *Eucalyptus* in dry closed-forest stands is generally present as large old trees, without younger cohorts of regenerating individuals. Many species of *Eucalyptus* dominate the vegetation around dry closed-forest stands, with the most common species being *Eucalyptus globulus* and *Eucalyptus obliqua*.

Fire regimes influence soil nutrient levels. Vegetation succession from fire-requiring vegetation to fire-intolerant vegetation in western Tasmania is thought to largely depend on the accumulation of soil nutrients (Bowman *et al.* 1986). Fires deplete soil nutrients by destroying the accumulated organic matter in the topsoil (Bowman *et al.* 1986) and through volatilisation to the atmosphere (Raison 1980), resulting in early successional vegetation. A number of vegetation studies have found differences in soil nutrients between communities with contrasting fire frequencies. For instance, in Victoria, Ashton (1976a) reported lower phosphorus levels in dry sclerophyll forest (comparatively high fire-frequency) compared with wet sclerophyll *Eucalyptus regnans* forest (comparatively low fire frequency), which is consistent with, but does not prove, the suggestion that repeated fires result in nutrient loss. In northern Australia, a number of studies have found significantly higher concentrations of various nutrients in monsoon rainforest soil compared with soil from adjacent more fire-dependent vegetation communities (Bowman *et al.* 1990b; Bowman & Fensham 1991; Bowman 1992). However, it has been suggested by Bowman (1992) that soil nutrient status alone cannot explain the distribution pattern of monsoon rainforest distribution, as this community occurs across a wide range of soil nutrient levels.

Tasmanian dry closed-forest stands predominantly occur in gullies that have southerly aspects (Chapter 2). South-facing slopes experience relatively low light-levels, especially in the winter months when the sun is low on the horizon at

Tasmanian latitudes (Holland & Steyn 1975). Few dry closed-forest stands occur on sites that face north or west. The canopy of the dry closed-forest is commonly dense, especially in gully situations, further reducing light reaching the soil surface. In the absence of bushfire, the most common disturbance of dry closed-forest is tree-fall or landslide. These endogenous disturbances do not produce extensive canopy gaps. Canopy gaps of more than 30 m in diameter (well above the scale of those produced in dry closed-forest stands) may be necessary for successful long-term establishment of wet forest *Eucalyptus* species (Ashton & Chinner 1999). Death in this case may not be the direct result of low light-levels, but instead occur because of the changes these produce in soil fungi.

The establishment of two dry closed-forest species in savanna and dry closed-forest soil has been experimentally investigated in the Northern Territory (Bowman & Panton 1993). This study suggests that factors such as soil micro-biota, soil moisture, soil fertility, and ground surface temperature may influence the successful establishment of dry closed-forest species.

Interactions between seedling growth, low light-levels and soil fungi have been examined in a number of studies (Wardle 1959; Grime 1966; Ashton 1976b; Ashton & Turner 1979; Withers 1979). Enhanced growth of *Eucalyptus regnans* has been observed both in the field and the glasshouse following inoculation with a specific mycorrhizal fungus (Ashton 1976b). When light intensities were less than 20-25 % of daylight levels (for Melbourne), *Eucalyptus regnans* showed negative growth, and at 1.5 % daylight seedlings suffer considerable losses to fungal attack (Ashton & Turner 1979). Likewise, seedlings in northern hemisphere woodlands commonly perish as a result of damping-off fungi under low light conditions (Grimes 1959). Thinning out of *Fraxinus excelsior* seedlings in English woodlands primarily occurs through attack by damping-off fungi (Wardle 1959). Ashton & Turner (1979) found that, for *E. regnans*, low light-levels reduce the extent of the plants root system and the development of symbiotic mycorrhizal fungi. This in turn affects the ability of the plant to survive other stresses such as water and nutrient deficiency (Ashton & Turner 1979). Under experimental conditions, Withers (1979) found that *E. ovata* seedlings died after prolonged intense shading,

especially over the winter months, probably due to attack by the fungus *Botrytis cinerea.*

The amount of available water in the soil can also limit the potential for *Eucalyptus* germination. Bachelard (1985) found germination of three *Eucalyptus* species was reduced when negative soil matric potentials produced water stress. They found no difference relating to soil type. The reduction in germination was somewhat offset in high humidity conditions (Bachelard 1985). Water stress was shown to be more restrictive of germination than dark stress in *Eucalyptus occidentalis* (Zohar *et al.* 1975). These factors along with temperature are interrelated, and increasing light and temperature when seeds are under water stress improves germination (Zohar *et al.* 1975). Dry closed-forest plants have been widely documented as being commonly associated with rock scree (Webb & Tracey 1981; Clayton-Greene & Beard 1985; Kirkpatrick *et al.* 1987; Kirkpatrick *et al.* 1988; Ash 1988; Williams 1993; Peel 1999). It is probable that for successful seedling establishment a seed must find its way into a fissure between rocks. In comparison to the surface of rock scree, which is largely devoid of soil, fissures accumulate water and organic matter, therefore offering a favourable place for seed germination.

Limitations on *Eucalyptus* establishment may arise because of competition with dry closed-forest trees. Ashton (1976c) suggested that intense root competition occurs between thick stands of *P. aspera* (closely related to the common Tasmanian dry closed-forest tree *P. apetala)* and *E. regnans* in Victorian wet forest during the intitial 10-15 years after a fire disturbance. This competition for resources puts stress on the *Eucalyptus* saplings, and results in considerable thinning of the regenerating *Eucalyptus* stand. The presence of a dense shrub layer has been implicated in the dieback of *E. delegatensis* in long unburnt forests of the highlands of northeast Tasmania (Ellis 1964), although no particular cause was identified.

Fire is an important factor in the germination of many Australian plant species, including *Eucalyptus*. Stimulation of seed germination by smoke has been reported in a number of studies (e.g. Roche *et al.* 1997; Tien *et al.* 1999; Lloyd *et al.* 2000, Read *et al.* 2000; Tang *et al.* 2003). For some species the heat of a moderate intensity bushfire enhances germination, while in other cases it is smoke that is the

enhancing factor; these factors appear to be complementary in effect (Read *et al.* 2000). Studies of rainforest boundaries have identified that fire is the key factor in determining both the direction of shift of the boundary over time, and the relative proportions of sclerophyll and rainforest components in the boundary vegetation (Unwin *et al.* 1985; Ash 1988). Fire opens up the rainforest canopy, letting in more light, which allows *Eucalyptus* and other light-loving species to establish. In addition to germination being stimulated by fire, it is commonly observed that plant growth is also enhanced. This is known as the "ash-bed effect". This has been attributed to an increased availability of nutrients in the soil, particularly nitrogen and phosphorus (Chambers & Attiwill 1994).

The aim of the present study is to investigate why *Eucalyptus* is excluded from Tasmanian dry closed-forest. The germination and growth of *Eucalyptus globulus* and competition with the dry closed-forest species *Asterotrichion discolor* and *Pomaderris apetala* is compared between eucalypt forest soil and dry closed-forest soil. A number of hypotheses are tested concerning why *Eucalyptus* is not a substantial component of the dry closed-forest vegetation of Tasmania? These are that:

- soil properties influence the relative success of *Eucalyptus* and dry closed-forest species

- competition between *Eucalyptus* and dry closed-forest species influences the relative success of these species

- the effects of fire influence the relative success of these species

- there are interactions between these factors that influences the relative success of these species

The results of the experiment are discussed with reference to soil chemical properties, fungal interactions, the effects of bushfire on the soil, and competition with the dry closed-forest species.

Methods

The soil from a single dry closed-forest stand and the adjacent eucalypt forest was examined (Figure 5.1). This stand is representative of the majority of Tasmanian dry closed-forest stands, occurring in a gully situation and on dolerite geology. The site geo-coordinates are n 5244052, e 527555.
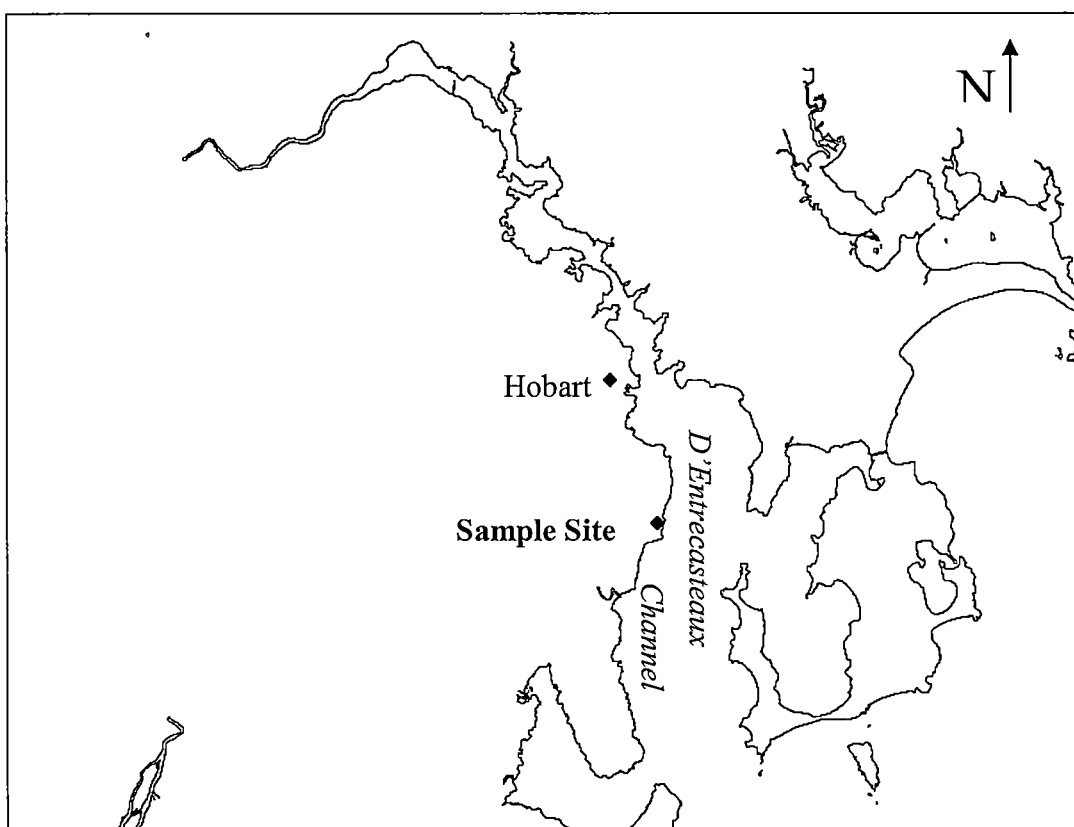
Figure 5.1 Location of the site where soil was collected from dry closed-forest and adjacent eucalypt forest (geocoordinates: n 5244052, e 527555).

Individually for the dry closed-forest stand and the adjacent eucalypt forest, leaf-litter was removed from the soil surface and the surface 10 cm of soil collected from at least 5 localities until the required volume of soil was reached. Approximately 0.5 m^3 each of dry closed-forest soil and eucalypt forest soil was collected in total. Representative leaf litter was collected from the two vegetation types. The dry closed-forest litter consisted mostly of leaves and branchlets of *Pomaderris apetala*, and the eucalypt forest litter consisting mostly of leaves and

branchlets of *Eucalyptus globulus*. In a glasshouse the dry closed-forest soil was thoroughly mixed together. A sample of the soils from each of the vegetation types was analysed for pH, EC, total nitrogen, extractable phosphorus, and organic carbon (see methods in Chapter 3 for details). One hundred and twenty pots 85 mm diameter and 150 mm tall were filled with soil (60 with dry closed-forest soil and 60 with eucalypt forest soil). Half of the dry closed-forest soil pots and half of the eucalypt forest soil pots were subjected to a heat treatment of burning leaf-litter on the soil surface. This was intended to approximate the effects of a ground-running bushfire on the soil. As the burning was carried out in the pots it was necessary to protect the plastic from the heat. The easiest way to achieve this is to insert a small protective sleeve, fashioned from a cylinder made from a modified tin can and wrapped in aluminium foil, which slips inside the top of the pot (Plate 5.1).

Plate 5.1 Example of a pot with protective tin can insert and eucalypt leaf litter ignited.

The experiment was divided into 4 treatments:

1) Dry closed-forest soil without heat treatment (30 pots)

2) Dry closed-forest soil with heat treatment (30 pots)

3) Eucalypt forest soil with heat treatment (30 pots)

4) Eucalypt forest soil with heat treatment (30 pots)

Four seeds were planted equidistant from each other in the following spatial arrangement (Figure 5.2). For half of the pots of each treatment 2 seeds of *Eucalyptus globulus* plus 2 seeds of *Asterotrichion discolor* were planted. For the other half of the pots 2 seeds of *Eucalyptus globulus* plus 2 seeds of *Pomaderris apetala* were planted.
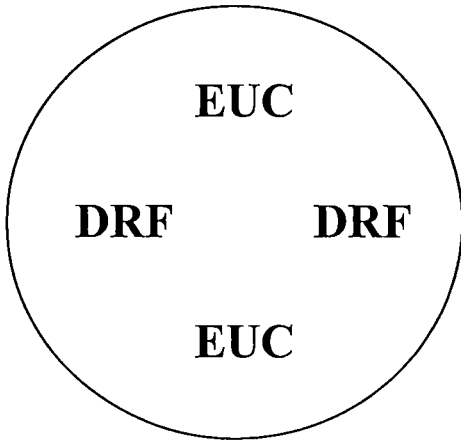
Figure 5.2 Top view of the spatial arrangement of planted seeds in a pot. Euc = eucalyptus globulus seed, and DRF = a dry closed-forest seed.

The pots were positioned randomly along a bench in the glasshouse (Plate 5.2). Pots had a deep watering once a week, and were randomly rearranged before each watering. Measurements of the height of each germinated individual and any deaths that had occurred were taken weekly over a 20 week period, with final measurements taken after 26 weeks. The emergence of any species other than the four target species was also noted. In data analysis, the heights of the tallest surviving individuals of each species from each pot were used for growth comparisons. Data were analysed with ANOVA using the GLM procedure in Minitab version 14 statistical software.

Plate 5.2 One-hundred and twenty pots containing the four soil treatments, planted with seeds of *Eucalyptus globulus*, *Asterotrichion discolor* and *Pomaderris apetala* and arranged randomly on the glasshouse bench.

Results

Table 5.1 Selected properties of dry closed-forest soil and adjacent eucalypt forest soil from the sample site of this experiment, with mean comparison values from Tasmanian dry closed-forest soil. (Along with the comparative data for the adjacent eucalypt forest at Quarry Reserve Creek, some comparative figures from two other Tasmanian wet eucalypt forests on dolerite are given).

	Total Nitrogen (%)	extractable Phosphorus (ppm)	Organic Carbon (%)	pH	Electrical Conductivity (EC) (µS/cm)
Quarry Reserve Creek dry closed-forest	0.63	13.00	11.10	7 06	39.50
Typical Tas. dry closed-forest stand (N = 60)	0.62 (SD = 0.24)	22.00 (SD = 53.2)	10.75 (SD = 4.3)	6 (SD = 0 73)	51.9 (SD = 28.0)
Quarry Reserve Creek eucalypt forest	0.28	7	-	6.37	46.47
Weilangta[1]	0.32	8	5.7	5.6	-
Manuka Road[2]	0.28 (SD = 0.08)	4.6 (SD = 3 0)	7.7 (SD = 2.3)	4.8 (SD = 0.4)	-

1. McIntosh *et al.* (2001) 0-13 cm (Colwell phosphorus extraction method)

2. Laffan, M. (2001). 0-5 cm (Colwell phosphorus extraction method)

The majority of Tasmanian closed-forest stands occur on dolerite geology (Chapter 2). A general trend from higher soil nutrients in wet eucalypt forests to lower levels in drier eucalypt forests has been noted on this substrate (Laffan & McIntosh 2005). Low nutrient levels in drier communities probably reflect higher fire-frequencies and associated nutrient losses (Ashton 1976a). This trend is apparent in the values of Table 5.1, with Quarry Reserve Creek dry closed-forest soil (relatively low fire frequency) having higher levels of total nitrogen, extractable phosphorus, organic carbon and pH than soil from the adjacent wet eucalypt forest (relatively high fire frequency). This trend is also apparent in the comparative figures from wet eucalypt forests at Weilangta and Manuka Road. The electrical conductivity (EC) does not differ greatly between dry closed-forest soil and wet eucalypt forest soil from Quarry Reserve Creek. The dry closed-forest soil from Quarry Reserve Creek has similar total nitrogen, extractable phosphorus, organic carbon and EC values to other dry closed-forest in Tasmania. However, the pH was relatively high compared with the average obtained for the other dry closed-forest sites (Table 5.1).

Table 5.2 Details of time of emergence for *Eucalyptus globulus, Asterotrichion discolor*, and *Pomaderris apetala* seeds in four different soil treatments. The exact time of the last emergence of *P. apetala* seedlings in dry closed forest soil treatments was uncertain and therefore no mean could be given.

Species	Treatment	Emergence interval (days from planting)			
		First	Last	Mean	N
Eucalyptus globulus	Dry closed-forest soil - no heat	14	49	23	24
	Eucalypt forest soil - no heat	14	28	15.2	47
	Dry closed-forest soil - with heat	14	91	20.8	38
	Eucalypt forest soil - with heat	14	105	17.1	43
Asterotrichion discolor	Dry closed-forest soil - no heat	14	35	25.7	6
	Eucalypt forest soil - no heat	14	28	15	14
	Dry closed-forest soil - with heat	14	49	19.4	13
	Eucalypt forest soil - with heat	14	98	26.1	11
Pomaderris apetala	Dry closed-forest soil - no heat	91	140-182	?	17
	Eucalypt forest soil - no heat	91	98	94.5	2
	Dry closed-forest soil - with heat	84	140-182	?	21
	Eucalypt forest soil - with heat	-	-	-	0

The vast majority of *Eucalyptus globulus* and *Asterotrichion discolor* seeds emerged within 4 weeks of planting (Table 5.2). In contrast to this *Pomaderris apetala* was slow to emerge, taking at least 84 days. An additional unplanted but commonly germinating species was *Beyeria viscosa*, a major canopy tree in dry closed-forest. This did not appear until after the last main group of measurements (after 140 days). However, by 182 days when a final set of measurements was taken, this species had 16 germinated individuals in non heat-treated dry closed-forest soil, 19 individuals in heat-treated dry closed-forest soil, and 1 individual in non heat-treated eucalypt forest soil. Other species that germinated in small numbers were *Galium australe, Hydrocotyle hirta, Stellaria flaccida, Wahlenbergia* sp., *Clematis aristata, Rubus fruticosus, Acacia* spp., *Bossiaea prostrata, Coprosma quadrifida* and unidentified monocotyledonous species.

Table 5.3 Germination success of seeds and proportion of deaths of seedlings of *Eucalyptus globulus, Asterotrichion discolor,* and *Pomaderris apetala* with and without soil heat treatment on different soil types.

Soil type	Soil heat treatment	Species	Germination success %	Deaths %	Number of germinating individuals
Dry closed-forest	no	*Eucalyptus globulus*	40	33	24
		Asterotrichion discolor	27	25	8
		Pomaderris apetala	N/A due to soil-stored seed	13	15
Dry closed-forest	yes	*Eucalyptus globulus*	62	19	37
		Asterotrichion discolor	43	08	13
		Pomaderris apetala	N/A due to soil-stored seed	0	19
Eucalypt forest	no	*Eucalyptus globulus*	78	13	47
		Asterotrichion discolor	47	0	14
		Pomaderris apetala	07	50*	2
Eucalypt forest	yes	*Eucalyptus globulus*	70	05	42
		Asterotrichion discolor	40	17	12
		Pomaderris apetala	03	100*	1

The lowest proportion of *Eucalyptus globulus* seeds germinated in untreated dry closed-forest soil (Table 5.3). The three other soil treatments produced a moderately high germination success in this species. *Asterotrichion discolor* had moderate germination success in all treatments, with the least success occurring in untreated dry closed-forest soil. *Pomaderris apetala* had a moderate number of germinating individuals in dry closed-forest soil, with few seeds germinating in eucalypt soil (Table 5.3). It was impossible to get a germination success for *P. apetala* germinated in dry closed-forest soil (note N/A entries in Table 5.3) as this soil contained soil-stored seed that subsequently germinated in addition to the seeds planted. Because the eucalypt forest soil contained no soil-stored *P. apetala* seed a measure of germination success was possible for these treatments.

Those results marked with an asterisk indicate that less than five individuals germinated, and it is thought therefore that a calculated value for the proportion of deaths in these cases is probably unreliable. The largest proportion of *E. globulus*

seedlings died in untreated dry closed-forest soil, while very few seedlings of this species died in heat-treated eucalypt forest soil. The most *A. discolor* seedlings died in untreated dry closed-forest soil followed by heat-treated eucalypt forest soil, while heat-treated dry closed-forest soil and non heat-treated eucalypt forest soil both resulted in comparatively few deaths.

Typical responses of *E. globulus* and *A. discolor* growing in the different soil treatments are shown in Plate 5.3. Note how *A. discolor* overtops *E. globulus* on the dry closed-forest soil, while it is less competitive with *E. globulus* on the eucalypt forest soil treatments

Plate 5.3 *Typical growth responses of the four primary treatments. Asterotrichion discolor and Eucalyptus globulus in (from left to right) eucalypt soil with no heat treatment, eucalypt soil with heat treatment, dry closed-forest soil with no heat treatment and dry closed-forest soil with heat treatment.*

Comparative growth of species
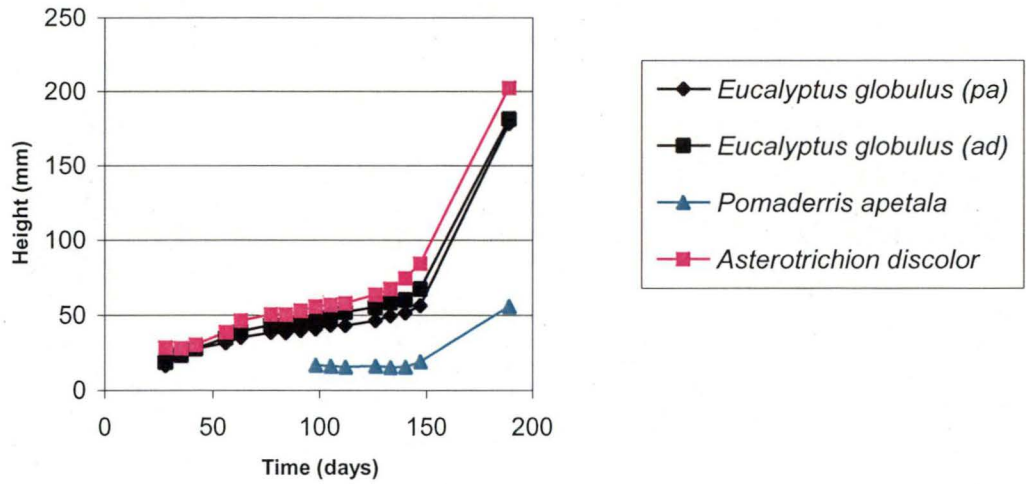
Figure 5.3 Comparative growth responses of *Eucalyptus globulus*, *Pomaderris apetala*, and *Asterotrichion discolor* in non heat-treated dry closed-forest soil (note *E. globulus* results are split into those grown alongside *P. apetala* (pa) and those grown alongside *A. discolor* (ad)). Heights are an average of the tallest surviving individuals of the species from each replicate.
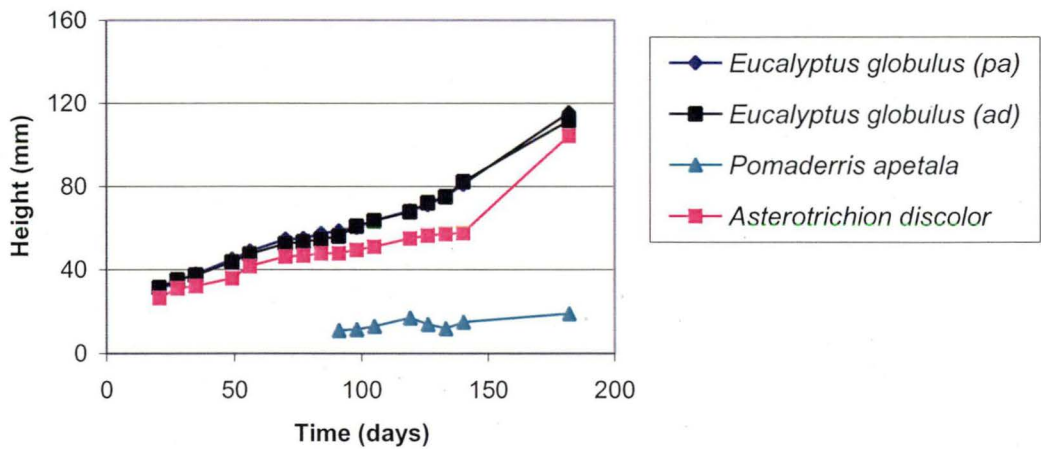
Figure 5.4 Comparative growth responses of *Eucalyptus globulus*, *Pomaderris apetala*, and *Asterotrichion discolor* in non heat-treated eucalypt forest soil (note *E. globulus* results are split into those grown alongside *P. apetala* (pa) and those grown alongside *A. discolor* (ad)). Heights are an average of the tallest surviving individuals of the species from each replicate.
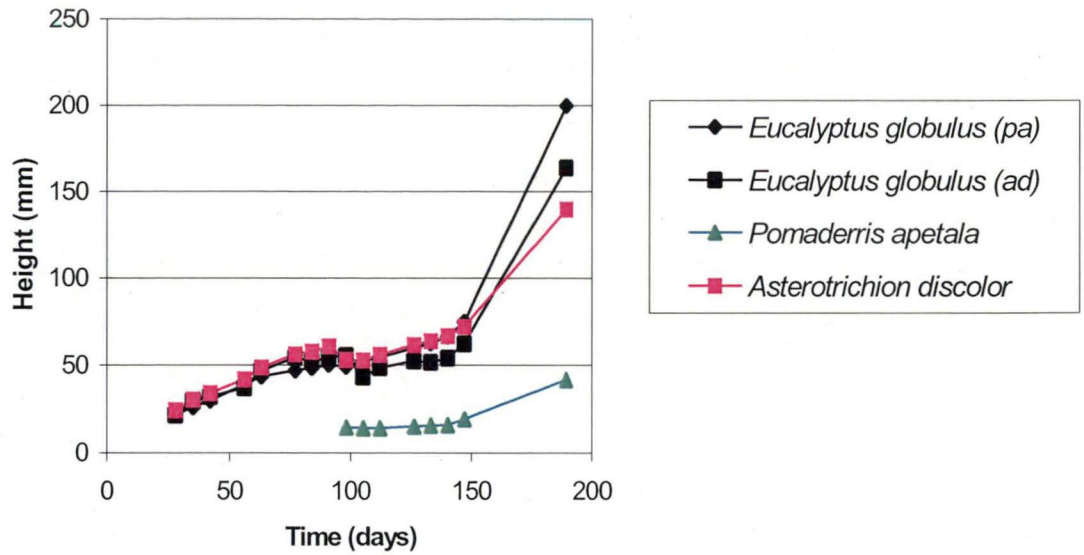
Figure 5.5 Comparative growth responses of *Eucalyptus globulus*, *Pomaderris apetala*, and *Asterotrichion discolor* in heat-treated dry closed-forest soil (note *E. globulus* results are split into those grown alongside *P. apetala* (pa) and those grown alongside *A. discolor* (ad)). Heights are an average of the tallest surviving individuals of the species from each replicate.
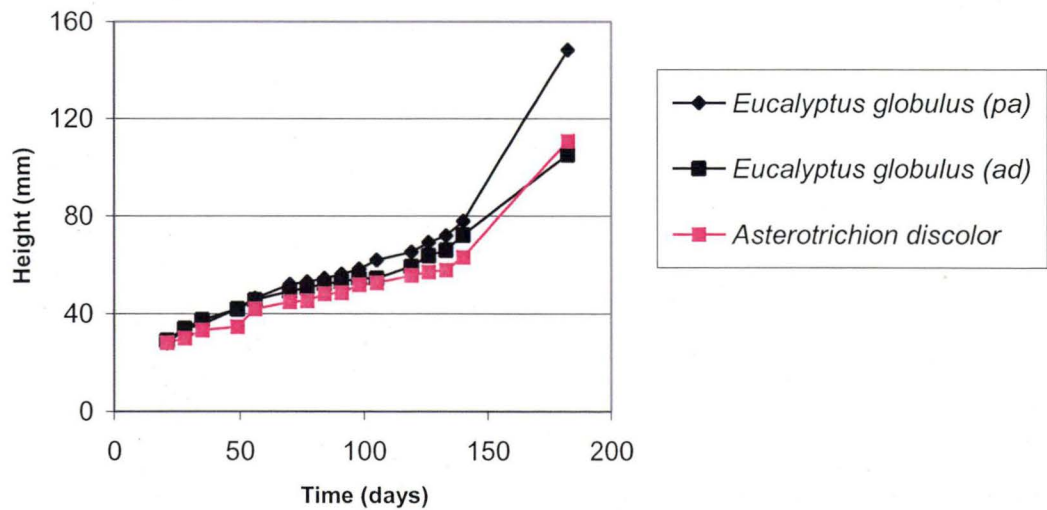
Figure 5.6 Comparative growth responses of *Eucalyptus globulus* and *Asterotrichion discolor* in heat-treated eucalypt forest soil (note *E. globulus* results are split into those germinated alongside *P. apetala* (pa) and those germinated alongside *A. discolor* (ad)). Heights are an average of the tallest surviving individuals of the species from each replicate. In this treatment no P. apetala germinated and therefore are absent from the graph.

The response in growth over time of the 3 target species germinated on the four different soil treatments is displayed in Figures 5.3, 5.4, 5.5, & 5.6. When grown on non-heated dry closed-forest soil (Figure 5.3), the mean height of *A. discolor* individuals at each measuring interval is higher than either *E. globulus* or *P. apetala*. Overall, the growth rate of *P. apetala* is relatively low, but appears to be increasing over the last two measurements. *E. globulus* individuals grown with *A. discolor* have approximately the same growth response as *E. globulus* grown with *P. apetala*. When grown on non heat-treated eucalypt forest soil (Figure 5.4), the growth response of *E. globulus* is greater than *A. discolor* and *P. apetala*. Unlike the increasing growth rate of *P. apetala* on non heat-treated dry closed-forest soil, the slow growth rate of *P. apetala* on non heat-treated eucalypt forest soil remains low throughout the experiment on this soil. When grown on heat-treated dry closed-forest soil (Figure 5.5), *A. discolor* has a mean height that is greater that *E. globulus* and *P. apetala* until the last measurement at 182 days from planting. At this time the mean height of *E. globulus* is tallest, although the growth rates of the other species is still increasing. *P. apetala* seeds did not germinate in the heat-treated eucalypt forest soil (Figure 5.6). The mean height of *E. globulus* was greater than that of *A. discolor* during the majority of the experiment. At the last measurement, *E. globulus* grown with *A. discolor* had a lower mean height than *A. discolor*.

Growth of individual species
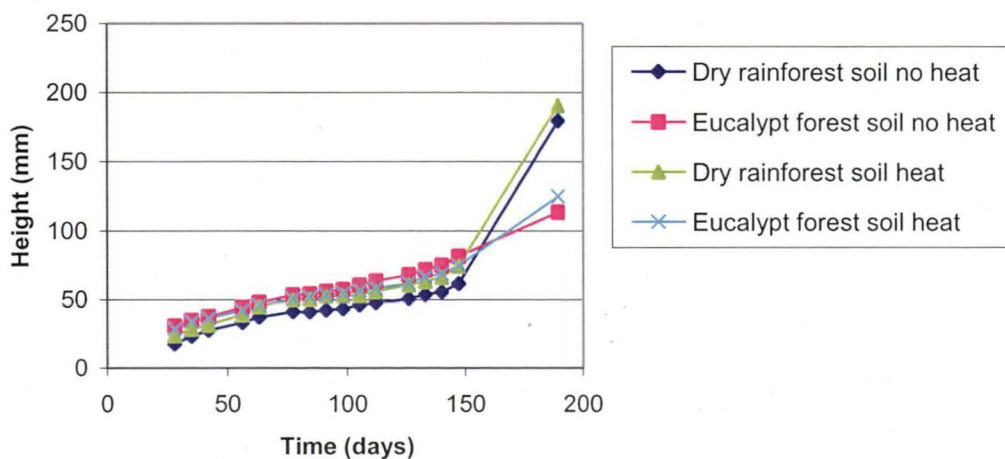
Figure 5.7 Growth of *Eucalyptus globulus* on four different soil treatments. Heights are an average of the tallest surviving individuals of the species from each replicate.

At the final measurement the mean height of *E. globulus* seedlings was greatest on the dry closed-forest soil (Figure 5.7). The mean height of *E. globulus* seedlings were 179.6 mm (StDev = 60.4 mm, N = 13) on non heat-treated dry closed-forest soil, 190.7 mm (StDev = 73.9 mm, N = 23) on heat-treated dry closed-forest soil, 113.6 mm (StDev = 25.2 mm, N = 26) on non heat-treated eucalypt forest soil, and 125.1 mm (StDev = 41.2 mm, N = 26) on heat-treated eucalypt forest soil.
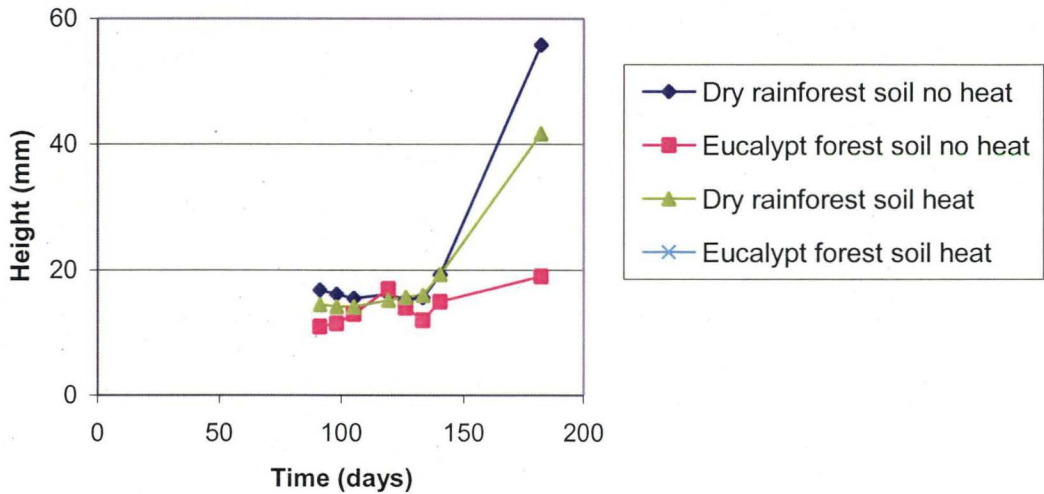
Figure 5.8 Growth of *Pomaderris apetala* on four different soil treatments. Heights are an average of the tallest surviving individuals of the species from each replicate.

The mean height of *P. apetala* at the end of the experiment was greatest on the dry closed-forest soil treatments, and relatively low on the eucalypt forest soil treatments (Figure 5.8). The mean heights of *P. apetala* are 55.8 mm (StDev = 23.1 mm, N = 6) on non heat-treated dry closed-forest soil, 41.7 mm (StDev = 19.5 mm, N = 7) on heat-treated dry closed-forest soil, and 19 mm (N = 1) on non heat-treated eucalypt forest soil. *P. apetala* had no successful germination on heat-treated eucalypt forest soil.
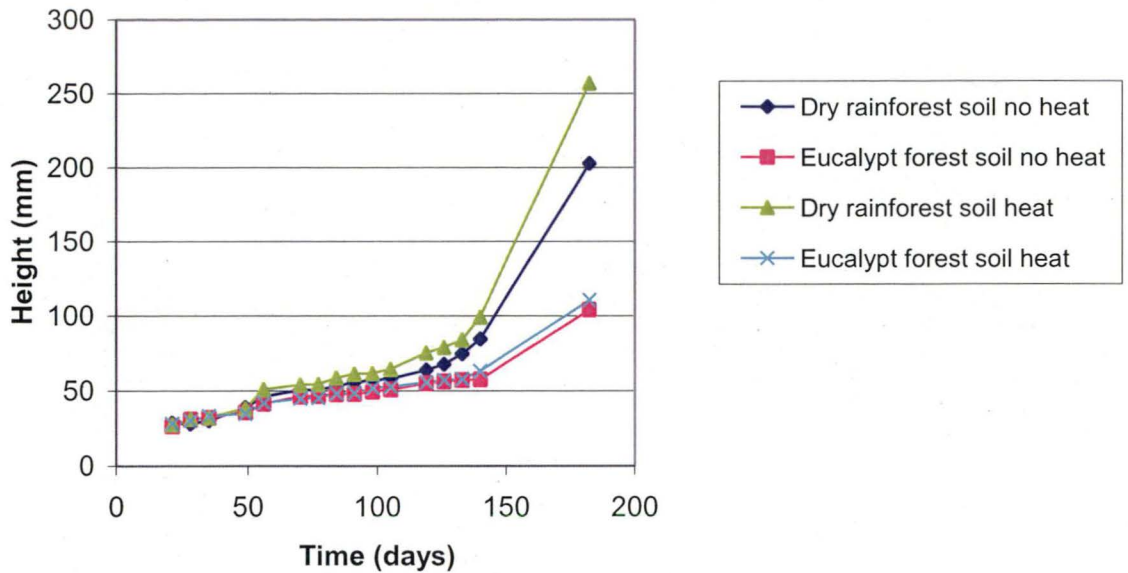
Figure 5.9 Growth of *Asterotrichion discolor* on four different soil treatments. Heights are an average of the tallest surviving individuals of the species from each replicate.

The mean height of *A. discolor* at the end of the experiment was greatest on the dry closed-forest soil treatments (Figure 5.9). The mean heights of *A. discolor* are 202.6 mm (65.7 mm, N = 5) on non heat-treated dry closed-forest soil, 257.2 mm (StDev = 76.1 mm, N = 10) on heat-treated dry closed-forest soil, 104.3 mm (StDev = 16.9 mm, N = 12) on non heat-treated eucalypt forest soil, and 110.8 mm (StDev = 33.8 mm, N = 9) on heat-treated dry closed-forest soil.

Table 5.4 ANOVA (GLM procedure) for *Eucalyptus globulus* seedling height under treatments of soil heating, soil type, presence/absence of *Asterotrichion discolor*.

Source	DF	F	P
Soil heating	1	0.42	0.521
Soil type	1	21.22	0.000
Presence/absence of *A. discolor*	1	12.32	0.001
Soil heating*soil type	1	0.00	0.965
Soil heating* Presence/absence of *A. discolor*	1	3.19	0.078
Soil type* Presence/absence of *A. discolor*	1	4.65	0.034
Soil heating*Soil type* Presence/absence of *A. discolor*	1	0.92	0.340
Error	80		

Table 5.5 ANOVA (GLM procedure) results of *Asterotrichion discolor* seedling height under treatments of soil heating, soil type, presence/absence of *Eucalyptus globulus*

Source	DF	F	P
Soil heating	1	7.99	0.008
Soil type	1	27.77	0.000
Presence/absence of *E. globulus*	1	5.88	0.022
Soil heating*soil type	1	0.75	0.393
Soil heating* Presence/absence of *E. globulus*	1	4.10	0.052
Soil type* Presence/absence of *E. globulus*	1	0.11	0.746
Soil heating*Soil type* Presence/absence of *E. globulus*	1	0.01	0.928
Error	29		

Effects on *Eucalyptus globulus* growth

The interaction of soil type x presence/absence of *A. discolor* on the height of *E. globulus* individuals was significant at $p \leq 0.05$ (Table 5.4). Further investigation with one-way ANOVA showed that when grown on dry closed-forest soil, the final height of *E.globulus* individuals was significantly greater ($F = 12.52$, $P = 0.001$) in the absence of *A. discolor* compared with those seedlings growing with *A. discolor*. However, the difference in height of *E. globulus* individuals grown on eucalypt forest soil in the presence/absence of *A. discolor* was not significant. The final height of *E. globulus* on dry closed-forest soil in the absence of *A. discolor* was 208.73 mm (StDev = 64.88 mm, N = 26) compared with a height of 130.30 mm (StDev = 41.38 mm, N = 10) on dry closed-forest soil in the presence of *A. discolor*. The interaction of soil heating x presence/absence of *A. discolor* on the final height of *E. globulus* was not significant (Table 5.4).

Effects on *Asterotrichion discolor* growth

The interaction of soil heating x presence/absence of *E. globulus* on the final height of *A. discolor* individuals was marginally insignificant (Table 5.5).

The height of *A. discolor* individuals significantly differed when grown on dry closed-forest soil compared with eucalypt forest soil (Table 5.5). The mean height of *Asterotrichion discolor* individuals grown on dry closed-forest soil was 232.7

mm (SD 77.4 mm, N = 16) compared with 107.1 mm (SD = 25.0 mm, N = 21) for individuals growing on eucalypt forest soil. There was a significant difference in the final height of *A. discolor* individuals between heat treated and non heat treated soil (Table 5.5). The final height of *A. discolor* individuals was greatest when grown on heat treated soil (mean = 186.9 mm, StDev = 92.7 mm, N = 20), and least for when grown on non heat-treated soil (mean = 131.5 mm, StDev = 58.3 mm, N = 17). There was a significant difference in the final height of *A. dicolor* seedlings growing in the presence of *E. globulus* seedlings compared with seedlings growing in the absence of *E. globulus* seedlings (Table 5.5). At the final measurement, the mean *A. discolor* height was greatest in the absence of *E. globulus* (mean = 218.22 mm, SD 100.32 mm, N = 9) and least when grown in pots containing *E. globulus* individuals (143.14 mm, SD = 68.52 mm, N = 28).

Discussion

Occurrence of *Eucalytpus* in dry closed-forest

Eucalyptus individuals present in Tasmanian dry closed-forest stands usually grow towards the boundary of the stand. There are two possibilities to explain this observation; either that the boundary has been disturbed in the past and the *Eucalyptus* has emerged following the elimination of the dry closed-forest canopy, or that the dry closed-forest boundary has gradually advanced, thereby enveloping the established eucalypt. There are some examples (Knights Creek, Cloudy Bay) of dry closed-forest stands that contain a proportion of even-aged medium-sized *Eucalyptus*. This situation suggests a previous fire disturbance, causing germination of the *Eucalyptus*, with subsequent re-colonisation of the site by dry closed-forest vegetation. Often these *Eucalyptus* individuals are in a state of decline (Plate 5.5).

Rarely, *Eucalyptus* individuals were observed growing on small landslips within a stand, where the topsoil had been removed and the subsoil exposed. A similar situation was observed where a large tree had fallen in a stand, thereby upturning the soil at the base, providing a similar situation of exposed subsoil. These situations also removed enough of the canopy to provide a gap for *Eucalyptus* emergence. The exposure of subsoil may be unfavourable for the germination of dry closed-forest seedlings, which could give *Eucalyptus* seedlings a competitive advantage. This could be a mechanism by which *Eucalyptus* becomes established in a dry closed-forest stand, and reaches a large size. Alternatively, *Eucalyptus* on landslides and upturned roots may die before they reach maturity.

Even on the edge of the dry closed-forest boundary, where disturbance is common and the light-levels are elevated, *Eucalyptus* was not prominent. An example of this can be found at Truganini Reserve near Hobart, where a moderate intensity fire in the last decade has disturbed the boundary. *Eucalyptus* is practically absent in the regrowth, which is instead dominated by a dense stand of the dry closed-forest disturbance specialists *Bedfordia arborescens* and *Asterotrichion discolor*. The formation of an ecotone between dry closed-forest and adjacent fire-prone communities is thought to be important in modifying the microclimate and soil conditions and thus aiding the establishment of dry closed-forest species

(Bowman & Panton 1993). It would seem that the options are that *Eucalyptus* fails to germinate because of an unavailability of seed, or that it germinates and is killed by fungus, or that it is out-competed by the dry closed-forest species.

Germination

The slow emergence of the species *Pomaderris apetala* and *Beyeria viscosa* reflects soil-storage of their seed. This is in contrast with the quick emergence of pioneer dry closed-forest species such as *A. discolor*. Soil-storage of *P. apetala* and *B. viscosa* seed enables a secure seed source to be present when a rare disturbance event occurs, even if the seed-bearing individuals have died of old age or are killed by fire. Cunningham & Cremer (1965) observed dense *P. apetala* regeneration following fire, even when this species was not a component of the overstorey immediately before fire. This demonstrates the long-term viability of the soil-stored seed of this species.

Soil properties

E. globulus, *A. discolor* and *P. apetala* each produced their tallest growth on dry closed-forest soils. The present study showed that dry closed-forest with a low fire-frequency is richer in soil nutrients than soil of adjacent more fire-prone eucalypt forest. Similarly, elevated nutrients on monsoon dry closed-forest soil may result in improved growth of tree seedlings grown in pot trials on monsoon dry closed-forest soil compared with soil from the adjacent savanna in northern Australia (Stocker 1969). In the present study, it was found that that *A. discolor* grows taller than *E. globulus* on the dry closed-forest soils and *E. globulus* grows taller than *A. discolor* on the eucalypt forest soils. These relative growth results may reflect long-term adaptation to their respective edaphic environments.

Very few *A. discolor* seedlings that germinated subsequently died on either soil type. This may indicate some degree of resistance by *A. discolor* to attack from damping-off fungi. Comparatively poor germination success of *E. globulus* and *A. discolor* on non-heat treated dry closed-forest soil, and comparatively better germination under the soil heat treatment, could result from the activities of damping-off fungi, as has been found in a number of studies on *Eucalyptus*

seedling establishment (Ashton & Turner 1979; Withers 1979), or from the allelopathic effects of fungal and bacterial chemical exudates (Ellis 1985; Ashton & Willis 1982). The poor germination success of *P. apetala* on all eucalypt forest soil treatments may indicate that the germination success of this species is naturally low, and the higher rate of germination in dry closed-forest soil was due to the presence of more seeds from a soil-stored seed source. Alternatively the properties of the eucalypt forest soil may be such that it is unfavourable for *P. apetala* germination.

Seedling death due to damping-off fungi has been linked to low light-levels (Ashton & Turner 1979). A limitation of the present experiment was that growth relating to variation in light conditions was not tested. However, Chapter 2 of the present thesis has identified that dry closed-forest stands typically occupy aspects that receive low light-levels. The typical disturbance setting of a Tasmanian dry closed-forest stand is a small gap caused by tree-fall and fire-disturbed boundaries. Both result in limited light conditions for germinating *Eucalyptus*. Chapter 4 of the present thesis found that disturbed areas are usually quickly occupied by fast growing vegetative regrowth of dry closed-forest species such as *Asterotrichion discolor*, *Bedfordia salicina,* and *Beyeria viscosa* (Plate 5.4), which limits the light reaching *Eucalyptus* seedlings and hence limit the potential for establishment. Only rare extreme bushfire events that extensively disturb a stand provide *Eucalyptus* with ample light for regeneration, and the greatest chance of establishment. Dry closed-forest trees are mostly less than 15 m in height, and rarely produce a gap in the canopy of large enough size for *Eucalyptus* to establish. Other studies have found that *E. obliqua* establishment is successful only in gap sizes of more than 30 m in diameter (Alcorn 2002 in Forestry Tasmania 2004). In Victoria, Ashton & Chinner (1999) have found that long-term observations of *E. regnans* regrowth in similar sized gaps have indicated that this species does not survive past 10-11 years old. In addition, any gaps that are produced in the dry closed-forest canopy are often rapidly filled by vegetative regrowth from toppled individuals. Observations documented in Chapter 4 of this thesis indicate that *Pomaderris apetala*, *Asterotrichion discolor*, *Bedfordia arborescens* and *Beyeria viscosa* are all able to sprout numerous upright shoots from a fallen stem, provided that the roots of the

main trunk are still partially attached to the ground. In this way a space cleared by a fallen tree is rapidly filled, and it is not uncommon for the produced mass of stems and leaves to be more extensive that that of the individual before the tree-fall. At wetter stands it is also common for *Histiopteris incisa* and other fern species to quickly occupy the gap and limit the potential for tree establishment, as was noted for remnant temperate rainforest stands in eastern Tasmania (Neyland & Brown 1994).

Soil heating

Results of the present study showed that significantly taller growth of *A. discolor* occurs on heat-treated soil, and may be an example of the ash-bed effect, in response to a greater nutrient availability of nitrogen and phosphorus (Chambers & Attiwill 1994). *A. discolor* was the only species that displayed a significant growth response to soil heating. However, both *A. discolor* and *E. globulus* germination was improved on dry closed-forest soil when heat-treated, even though the seed was not directly heated. As the seeds were planted in heat-treated soil, and not heat-treated themselves, this may indicate a favourable change in the soil chemical or biological properties that stimulate germination.

Competition between species

The general linear modelling in the present study also showed a significant competition effect between *A. discolor* and *E. globulus*, such that the growth of each is negatively affected by the presence of the other. Possible explanations for this are direct root competition in the pots, inhibitory root exudations or the promotion of antagonistic mycorrhizal fungi. The present study found that germination of *E. globulus* and *A. discolor* occurs relatively quickly. This reflects the regeneration strategy of these species. Both take advantage of fire-disturbed areas by producing many individuals that grow quickly to fill the disturbed area. The seeds have limited capacity for soil-storage, instead relying on mass dispersal, quick germination and quick growth to out-compete other potential site occupiers. Presence of these species in dry closed-forest is a sure sign of past fire-disturbance.

Interactions

The identification of an interactive effect between soil type and presence of *A. discolor* on the growth of *E. globulus,* where growth is enhanced on dry rainforest soil in the absence of *A. discolor,* shows that soil type and competition are important factors in determining the establishment potential of *E. globulus.* The best chance for *E. globulus* establishment appears to be when free from competition from dry closed-forest species. Although good growth will occur on the relatively rich dry closed-forest soils once established, damping-off must be avoided in early stages. In the present study survival of seedlings in dry closed-forest soil was enhanced when the soil was heated. Also low light-levels have been implicated in encouraging damping-off in *Eucalyptus* (Ashton & Turner 1979). Therefore, the most suitable location in a dry closed-forest stand, where damping-off is minimised by soil heating and relatively high light-levels, is at the stand boundary. Observations in the field in the present study support this suggestion, with *Eucalytpus* individuals rarely occurring far within the boundary of the stand.

Conclusions

Combining the implications of the results of the present study, some suggestions on the probable interplay between species in regeneration scenarios can be made.

Scenario 1 – dry closed-forest soil without a bushfire (tree-fall or landslide)

E. globulus and *A. discolor* germinate quickly, but both have limited germination success. A substantial number of both species die, especially *E. globulus*, probably due to damping-off fungi. Growth of *A. discolor* over-tops *E. globulus*, increasing the chance of death of *E. globulus* from damping-off fungi. Competition between the species works to the detriment of *E. globulus* because it is already in a secondary position. *P. apetala* and *B. viscosa* are relatively slow in emerging and subsequent growth, perhaps only reaching sapling height after the dense *A. discolor* stand naturally thins.

Scenario 2 – dry closed-forest soil with a bushfire (fire at boundary)

As in scenario 1, *E. globulus* and *A. discolor* germinate quickly. A moderate

proportion of *E. globulus* seedlings subsequently die because of damping-off fungi, compared with very few deaths for *A. discolor*. *A. discolor* growth over-tops *E. globulus* early, but this is reversed as growth continues. Competition between the species reduces the growth of both, and it is likely that dim light conditions created by dense *A. discolor* growth results in further *Eucalyptus* seedlings death due to attack from damping-off fungi. *P. apetala* and *B. viscosa* are relatively slow in emerging and subsequent growth, perhaps only reaching sapling height after the dense *A. discolor* stand naturally thins.

Scenario 3 – eucalypt forest soil without a bushfire

From the results of the present experiment, we would expect that, as in the previous scenarios, *E. globulus* and *A. discolor* germinate quickly, with excellent germination success for *E. globulus*. However, this high germination success is unlikely to be reflected in a natural setting because the ground is usually covered in thick leaf and bark mulch, not bare soil, as was the case in the present experiment. Seeds would have difficulty reaching the soil and germinating through thick litter. Of the seedlings that do germinate, few subsequently die from damping-off fungi. *E. globulus* growth exceeds that of *A. discolor*, however, unlike in the present experiment, it is unlikely that there are enough germinated individuals to have serious competitive effects. Without a substantial existing overstorey of *P. apetala* and *B. viscosa* few seedlings of these species emerge because of a lack of soil-stored seed. Without fire it is likely that the understorey changes little, as few opportunities exist for germination of new individuals.

Scenario 4 – eucalypt forest soil with a bushfire

As in the previous scenarios, *E. globulus* and *A. discolor* germinate quickly. Very few seedlings of *E. globulus* subsequently die from damping-off fungi. *E. globulus* growth over-tops *A. discolor*, and competition between the species further limits the growth of *A. discolor*. Very few *P. apetala* and *B. viscosa* seedlings emerge because of a lack of soil-stored seed. *E. globulus* is in a position to continue growth and reach a canopy position, while *A. discolor* eventually naturally thins out (pers. obs. Truganini Reserve, south of Hobart, and Lenah Valley – Plate 5.4).

Plate 5.4 Dense regeneration of *Asterotrichion discolor* and *Bedfordia salicina* approximately 5 years after a fire at Lenah Valley, near Hobart. The stand is naturally thinning as it matures.

Plate 5.5 Senile *Eucalyptus* in a dry closed-forest stand at Symons Creek, near Launceston. It is likely that these trees have been enveloped by the dry closed-forest over time.

Chapter 6 – General Discussion

The primary questions addressed in this thesis were:

9. Where does dry closed-forest occur in Tasmania and what environmental factors influence this distribution?

10. How does the floristic composition of this community vary across its range?

11. What are the modes of regeneration of the major tree species of this community and why is *Eucalyptus* absent?

12. What are the conservation management and reservation requirements of the community?

The overarching aim relating to whether the community is rainforest is also addressed and directions for future work outlined.

Question 1. Where does dry closed-forest occur in Tasmania and what environmental factors influence this distribution?

Small stands of dry closed-forest are widely distributed across the eastern half of Tasmania. Dry closed-forests, along with temperate rainforest, are one of few forest communities in eastern Tasmania that are not dominated by *Eucalyptus*. A continuum exists between the floristic composition of eucalypt forest and rainforest in Tasmania, with dry closed-forest falling somewhere between these communities. Many dry closed-forest species having distributions that encompass both communities.

Fire has an important role to play in determining the patterns of sclerophyll and rainforest vegetation that occur in western Tasmania (Jackson 1968). Fire-avoidance has also been highlighted as a primary factor that limits the distribution of remnant temperate rainforests in eastern Tasmania (Neyland 1991). In line with these previous studies, the present study provides evidence that Tasmanian dry closed-forests are distributed in those parts of the landscape of eastern Tasmania where the impact of fire is minimal.

Three primary features of Tasmanian dry closed-forest distribution were highlighted in this thesis:

- a preference for gullies

- southerly aspects, and

- rocky sites.

The fact that dry closed-forests primarily occur in gullies would seem to suggest a limitation on distribution associated with moisture supply. However, a number of other studies have shown that apparent edaphic controls on rainforest distribution may in fact reflect fire-avoidance, or at least a complex interplay between a number of factors including favourable moisture and fire-avoidance (Barrett & Ash 1992; Bowman 1992). By occupying gully locations, dry closed-forests avoid the worst effects of fires because a fire must descend to reach a stand, and thereby decrease in intensity (Unwin *et al.* 1985). Tasmanian dry closed-forests are not exclusive to gully situations. This suggests that, although gullies are an excellent geomorphic situation for fire-avoidance, other site features such as aspect and rock cover are also significant factors that influence the distribution of this community.

The predominance of dry closed-forest stands occurring on southerly aspects reflects exclusion by fire from northerly aspects in favour of more fire-tolerant vegetation. A hypothesis concerning dry closed-forest distribution tested in the present study was that dry closed-forest stands are protected from fire by the topography in a northwest direction (see Chapter 2). In Tasmania severe fire weather is associated with hot, gusty winds from the northwest. The northwest topography hypothesis appears to be supported by the findings of the present study. The presence of high northwest topography is especially important for the protection of non-gully stands, which commonly occur at the base of significant topography that impedes the path of a fire approaching from this direction.

The association between dry closed-forest stands and naturally fire-avoiding rocky situations also suggests that fire restricts the distribution of this community. Many studies have reported dry closed-forest associated with rocky situations (Webb &

Tracey 1981; Clayton-Greene & Beard 1985; Kirkpatrick *et al.* 1987; Kirkpatrick *et al.* 1988; Ash 1988; Williams 1993; Peel 1999 and others). Rock-mulch is both a physical barrier to the movement of fire and an impediment to the development of an understorey that could provide fuel for a fire (Kirkpatrick *et al.* 1987), while cliff-lines act as firebreaks for fronts moving downhill towards a stand.

The environmental factors that were identified in the present study as influencing the nature and distribution of dry closed-forest are related to the primary necessity for stands to avoid severe fires. The community occurs as small discrete stands within a landscape that is dominated by eucalypt forest. As most bushfires that occur in Tasmania are ignited as a result of human activity rather than lightning strike, as has been suggested by Jackson & Bowman (1982), then it is possible that prior to Aboriginal arrival the area occupied by this community would have been more extensive. With a lesser influence from fire, the east of Tasmania may have looked substantially different, being a complex patchwork of dry closed-forest, temperate rainforest, and eucalypt forest, with much less of a dominance of *Eucalyptus* than is seen today.

Question 2. How does the floristic composition of this community vary across its range?

Dry closed-forest contains a number of dominant species that have broad environmental tolerances and occur in both closed-forest and *Eucalyptus* communities both in Tasmania and other states. This broad environmental tolerance is reflected in the fact that dry closed-forest has a similar species composition across its range, with a relatively small number of species present that are useful in distinguishing between sub-communities. The wetter dry closed-forest sub-communities are relatively distinct,.and show some floristic affinity to temperate rainforest. Additional summer moisture lessens the risk of summer drought at sites occupied by these sub-communities. This allows more drought sensitive plants to grow alongside the typical dry closed-forest species, which occur across a wider range of moisture availability.

Fire and moisture availability are strong influences on the floristic composition of a number of the sub-communities identified in the present study. Recurrent fires,

such as those that have occurred around Hobart (sub-community C) have resulted in an increase in the contribution from fire-tolerant boundary species to the species composition of these stands. These species are useful characteristic species of this sub-community, but would probably become less prominent with a reduction in the fire-frequency around Hobart. This highlights the importance of local fire frequency in determining the relative proportions of fire-dependent regenerators and species that are discouraged by recurrent fires. Moisture availability influences the proportion of drought intolerant species contributing the species composition of a particular dry closed-forest stand. This is apparent in the species composition of the wettest dry closed-forest sub-communities D and E. It was common to observe stands from these sub-communities supporting low numbers of temperate rainforest species such as *Atherosperma moschatum* and *Nothofagus cunninghamii* on rocky creek-lines where moisture supply was greatest. These stands graded into a more typical dry closed-forest species composition upslope. The small-scale distribution pattern of these temperate rainforest species along creek-lines could also partly reflect the necessity for fire-avoidance; the most fire-protected area of a stand generally being at the bottom of a gully (Chapter 2).

Question 3. What are the modes of regeneration of the major tree species of this community and why is *Eucalyptus* absent?

The major dry closed-forest species can be broadly split into fire-dependent and fire-independent regenerators. Fire-dependent regenerators are the species *Pomaderris apetala, Olearia argophylla, Bedfordia salicina, Zieria arborescens*, and *Asterotrichion discolor*, and fire-independent regenerators are the species *Beyeria viscosa, Pittosporum bicolor, Notelaea ligustrina, Coprosma quadrifida,* and *Acacia melanoxylon. Beyeria viscosa* was unique among the major species in being able to regenerate vigorously following disturbance and also having the capacity to perpetuate itself in the absence of exogenous disturbance. Without seedling regeneration, a number of these disturbance-requiring species were observed to regrow vegetatively from small-scale disturbance, allowing them to survive within a stand between disturbance events. For instance, *P. apetala* was observed vigorously coppicing along its trunk after falling downhill.

A flow chart representing the probable successional sequence of dry closed-forest was produced (Figure 6.1). In the early stages of post-fire recovery dry closed-forest is likely to be dominated by combinations of the species *Pomaderris apetala, Beyeria viscosa, and Bedfordia salicina*. As the fire-free interval increases the proportion of the late successional rainforest species such as *Pittosporum bicolor* and *Notelaea ligustrina* is likely to increase. These species are shade-tolerant and bird-dispersed. Another possible outcome occurs when an area in inundated with *Olearia argophylla* seed. This species initially takes advantage of the area disturbed by fire, and with its ability to vegetatively re-sprout, can form an extensive canopy and occupy a site over a relatively long fire-free interval. Ashton (2000) suggests that *O. argophylla* replaces *Pomaderris aspera* (closely related to *P. apetala*) over time in the understorey of Victorian wet eucalypt forest. *O. argophylla* dominance in this setting is primarily achieved by vegetative regeneration, in this case by layering of decumbent branches (Ashton 2000).

Observations of the spatial arrangement of seedlings of a number of the major dry closed-forest species being clumped around the base of large individuals (see Chapter 4) suggests that uneven bird-assisted dispersal of seeds was occurring. A similar association has been reported between establishing rainforest regeneration and large trees (Toh *et al.* 1999; Fensham & Butler 2004) and this spatial pattern has been linked to seed-dispersal by birds from perches. The present study found that many of these bird-dispersed species are self-replacing and dominate dry closed-forest stands that have remained unburnt for long periods. Seedlings of the sometimes bird-dispersed species *B. viscosa* and the occasionally bird-dispersed species *Pomaderris apetala* were commonly observed around the base of large trees, but established individuals were not. Established individuals of these species were located in relatively high light areas of a stand, such as in small gaps or at the stand boundary. Both are soil-stored and regenerate densely following fire, suggesting that bird-aided dispersal is not their primary mechanism of regeneration. These results suggest that the development of late-successional self-replacing dry closed-forest vegetation (rainforest vegetation) relies on bird-aided dispersal.

Developing dry closed-forest

Mixed stands of
Beyeria viscosa
Pomaderris apetala
Asterotrichion discolor
Bedfordia salicina
Zieria arborescens

decreasing fire-frequency

increasing fire-frequency

Typical mature dry closed-forest

Mixed stands of
Beyeria viscosa
Notelaea ligustrina
Pittosporum bicolor
Coprosma quadrifida
Acacia melanoxylon

increasing fire-frequency

decreasing fire-frequency

Olearia argophylla-dominated mature dry closed-forest

Olearia argophylla-dominated with a lesser component of typical mature dry closed-forest species

Figure 6.1 Flow chart of dry closed-forest succession relating to fire frequency.

Although eucalypt forests surround Tasmanian dry closed-forests, *Eucalyptus* is only rarely found inside the boundary of dry closed-forest stands. When present, it usually occurs as isolated, mature individuals, and in many instances is in a state of decline. Rarely, *Eucalyptus* regeneration was observed in small disturbances within a stand, such as on landslips and the upturned root masses of fallen trees. Whether these individuals reach maturity is uncertain. Observations of the eucalypt forest-dry closed-forest boundary indicate that *Eucalyptus* is not a prominent component of regenerating vegetation.

The present study identified damping-off fungi and competition with dry closed-forest species as having a negative influence on *Eucalyptus* establishment in the dry closed-forest environment (Chapter 5). Discussion was also made of the role that other factors such as soil heating and light availability have on *Eucalyptus* establishment. Scenarios showing the probable outcome of *Eucalyptus* establishment on dry closed-forest soil are displayed in Figure 6.2. Low light-levels and damping-off fungi preclude *Eucalyptus* establishment on dry closed-forest soil without the effects of a bushfire (scenario 1), while with a moderate/high intensity fire (scenario 2) increased light-levels and partial soil sterilisation allow some establishment success for *Eucalyptus*. This success may be short-lived however, as competition with a dense understorey of broad-leaved species can result in *Eucalyptus* dieback, as has been reported in Ashton (1976c) and Ellis (1964).

The experiment of Chapter 5 of this thesis provided some insights into the probable interplay between species in regeneration scenarios. These scenarios suggest that the regular successful establishment of *E. globulus* only occurs on eucalypt forest soil that has experienced a bushfire. *Eucalyptus* can occasionally succeed in establishing at the periphery between dry closed-forest and eucalypt forest, but this is not a common occurrence. The nature of dry closed-forest distribution results in relatively low light-levels and low fire-frequencies, both of which produce a negative influence on *Eucalyptus* establishment.
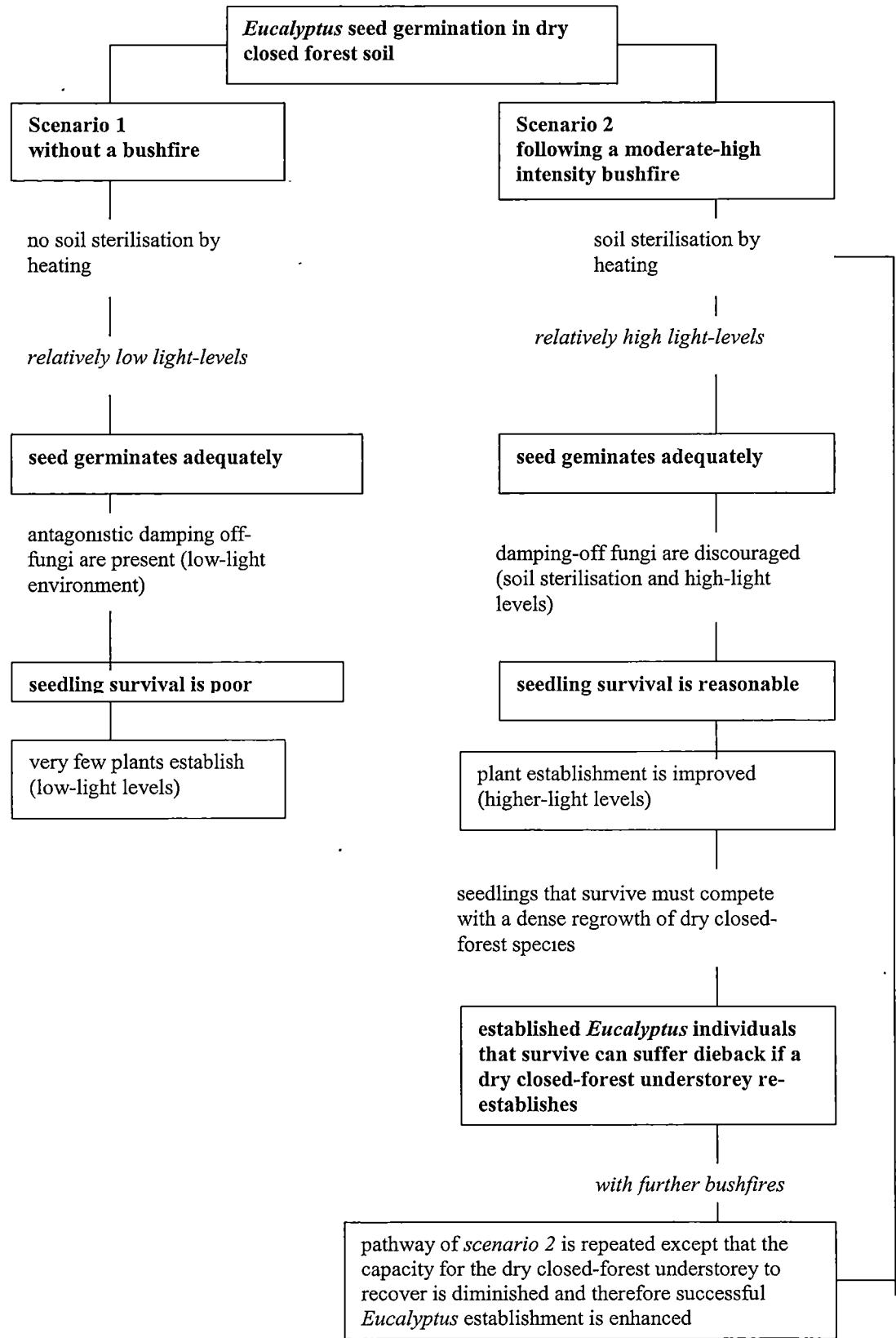
Figure 6.2 Scenarios of Eucalyptus establishment in the dry closed-forest environment

Question 4. What are the conservation management and reservation requirements of the community?

The most obvious risk to the degradation of dry closed-forest stands is from fire. An increase in the frequency and intensity of fires threatens late successional dry closed-forest. At the other extreme, maintaining an inadequate fire-frequency will convert many early successional dry closed-forest stands to a late successional species composition. The fact that Tasmanian dry closed-forest exists in a considerable variety of successional stages would seem to suggest that at present the fire-regime is not having a detrimental effect on any of these successional stages. It is likely that stand locations in deep gorges and on very rocky ground are by their very nature fire-excluding, and therefore should maintain refuge for the late-successional stage of dry closed-forest regardless of changes in fire-regime. However, a cessation of burning altogether is likely to be just as detrimental to the conservation of dry closed-forest as an increase in fire frequency. Adequate levels of burning in adjacent eucalypt communities for fuel reduction purposes are required to discourage less frequent severe fires in areas supporting dry closed-forest stands.

Riparian dry closed-forest stands and stands that occur adjacent to rivers in the gorge country of the Eastern Tiers could potentially be at risk from new water storage developments. A large number of dry closed forest-stands occur in the upper reaches of catchments, and therefore the community as a whole is not is not at risk from this type of disturbance. However, the main area of occurrence of stands of sub-communities A and F is in the Eastern Tiers, placing these these sub-communities at particular risk.

Weed invasion is a management concern for sub-community C on the outskirts of Hobart. A considerable number of garden escapees were recorded from this sub-community and it is expected that more will become established in gully dry closed-forest stands in the future. These weeds mainly invade disturbed areas. Therefore, any activities that disturb the integrity of stands in sub-community C, such as a degrading fire-regime, may have the added impact of encouraging the establishment of weeds. Weed invasion has the potential to change the floristic

composition and structure of the dry-closed forest stands around Hobart, and may have unforeseen impacts such as causing changes in the fire-regimes.

Status of Tasmanian dry closed-forest as rainforest

Tasmanian dry closed-forest displays some characteristics that are in agreement with accepted rainforest definitions. The community is structurally a closed forest, having a projected foliage cover of 70-100% as specified by Specht (1970), although more open canopy covers are not excluded from the Tasmanian rainforest definition (*sensu* Jarman & Brown 1983). The community does not tolerate recurrent severe fires, and therefore fits the definition of rainforest as a fire-sensitive vegetation type (*sensu* Cameron 1992). Sub-communities D and E (the two wettest communities) have significant floristic similarity to cool temperate rainforest. These sub-communities occupy the mid-section of a gradient between dry closed-forest and cool temperate rainforest. As a whole, however, it is the floristic specification of the Tasmanian rainforest definition (*sensu* Jarman & Brown 1983) that excludes dry closed-forest from inclusion as rainforest vegetation, despite having a significant proportion of species that are acknowledged rainforest species. For instance, Jarman & Brown (1983) include in their list of rainforest species the common dry closed-forest species *Notelaea ligustrina*, *Pittosporum bicolor*, *Coprosma quadrifida* and *Zieria arborescens*. Likewise, Cameron (1992b) considers *N. ligustrina*, *P. bicolor* and *Beyeria viscosa* to be important primary rainforest species of Victoria, and *Acacia melanoxylon* and *Prostanthera lasianthos* to be significant secondary rainforest species. Floyd (1989) considers the species *B. viscosa, P. bicolor, and N. ligustrina (syn. Negistis ligustrina), Bedfordia arborescens* (closely related to *B. salicina)*, and *Olearia argophylla* to be rainforest trees of southeast Australia. Among the 'doubtful rainforest species' of Jarman & Brown (1983) are *O. argophylla, Prostanthera lasianthos, Pomaderris apetala,* and *Acacia* spp..

This floristic affinity between dry closed-forest and remnant eastern Tasmanian temperate rainforest suggests that there is no clear boundary between these two communities, but rather that they exist as a continuum along a moisture gradient. An example of this is found along the streams of the Eastern Tiers, where dry

closed-forest occupy protected slopes of rain-shadow valleys, while further upstream at the head of streams where rainfall is higher, temperate rainforest elements such as *Atherosperma moschatum* dominate the closed-forests. Tasmanian dry closed-forest also shows floristic similarity with Victorian dry rainforest and fern-gully flora. This reflects the fact that many Tasmanian dry closed-forest species also occur in Victoria, and having broad environmental tolerance, inhabit a range of communities including wet sclerophyll forest, fern gullies, temperate rainforest, and dry closed-forest. These species include the common dry closed-forest trees and shrubs *Acacia melanoxylon, Bedfordia arborescens* (closely related to *Bedfordia salicina*), *Coprosma quadrifida, Notelaea ligustrina, Olearia argophylla, Olearia lirata, Pomaderris apetala, Prostanthera lasianthos, Pittosporum bicolor,* and *Zieria arborescens.*

Lynch & Neldner (2000) stated that a rainforest species has the ability to regenerate vegetatively or by seed under a closed canopy or in an area of small-scale disturbance caused by a natural rainforest ecosystem process such as a single tree-fall. The present study showed that a number of dominant dry closed-forest species are self-replacing in the absence of exogenous disturbance, which qualifies them as rainforest species according to this definition. However, the present study also found that another suite of dry closed-forest species rely on exogenous disturbance for regeneration. The relative proportions of species that are fire-dependent and non-fire-dependent for regeneration apparently depend on the time since the last fire disturbance. Those dry closed-forest stands that have avoided fire for a considerable period have a higher proportion of rainforest species than more frequently burned stands, which are mostly dominated by species requiring fire for regeneration. The less frequently burned stands could be considered rainforest vegetation because the constituent tree species display a capacity for self-perpetuation without fire disturbance. However, the fact that, in the majority of dry closed-forest stands, a significant number of major dry closed-forest tree species rely on catastrophic disturbance for regeneration excludes the community as a whole from classification as rainforest.

Future directions for studies in Tasmanian dry closed-forest

This thesis results from a broad ecological investigation into the little-known Tasmanian dry closed-forests. There are a number of avenues for more specific studies of this community that have been identified in the thesis. A more intensive quantitative study of the relationship between the community, fire, and rock would be useful. An extension of the experiment examining mechanisms of *Eucalyptus* exclusion would also be beneficial, involving an investigation of the effect of light-supply and controlled soil sterilisation on *Eucalyptus* establishment. More work could also be done on the endogenous regeneration dynamics of dry closed-forest species in the absence of fire-disturbance, specifically focusing on tree-fall gaps and the boundaries of stands.

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Appendices

Appendix 1 TWINSPAN ordered table of stands versus vascular plant species at 61 Tasmanian dry closed-forest stands (corresponding site names for stand numbers follows).

Sub-community	. F	D	E	A	B	C
Stand no.	45233442431	4 3	244522245 1	1215 161565 2	1 55113343452	123335
	44756018270	7868	439862376	1124531861200590	9323583964571	45790129

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Callistemon pallidus         1---1------- ----  ---------- ---------------- -------------- --------
Leptospermum lanigerum       -1-------1-- ----  ---------- ---------------- -------------- --------
Euchiton sp. A               -11--------- ----  ---------- ---------------- -------------- --------
Nematolepis squamea          ----1------- -1--  ---------- -------------1-- --1----------- --------
Wahlenbergia sp.             -------1--- ----  ----1---- ---------------- -------------- --------
Luzula spp.                   1------11-- 1--- --11---1- --1------------1 -------------- -1-1----
Huperzia varia               -1--------- --11  ---------- ---------------- -------------- --------
Aristotelia peduncularis     -1--------- --11  ---------- ---------------- -------------- --------
Acacia riceana               ----------- -11-  ---------- ---------------- -------------- --------
Nothofagus cunninghamii      ----------- 111-  ---------- ---------------- -------------- --------
Gaultheria hispida           ----------- 111- ---1------ ---------------- -------------- --------
Hymenophyllum australe       ----------- -111 --1------- ---------------- -------------- --------
Cyathodes glauca             11--11-11-1 11-1 1--------- 1-1------------- --1----------- 1-------
Ctenopteris heterophylla     11111-11--- --11 1-1-1---- 11111----------- 1------------- 1-------
Atherosperma moschatum       -1-11------- 1111 11111-1-- 1--------------- -------------- 1-------
Pimelea drupacea             11-1111111- 1111 111111111 1----1-----111-- -------------- 1-------
Grammitis billardierei       ----1-1---- -111 111-1---- ----1----------- -------------- --------
Pteris tremula               ----------- ---- -----11-1 ----------------- -------------- --------
Blechnum nudum               -----------1 -1-- 1---111-- ---------1-1----- --11--------- --------
Histiopteris incisa          1--1-------- -1-1 111111111 -1---11--------- -1------------ --------
Rumohra adiantiformis        1---------- --1- 111111111 1111-1---------- -------------- 1-1-----
Asplenium bulbiferum         -1-11------- -1-- 1-111-11- --1------------- -------------- -1---111
Parsonsia brownii            ----------- ---- 1---11-11 -1--1--1-------- 1------------- --------
Polyphlebium venosum         -1--1------- ---- 1-1-1-11- ---------------- -------------- --------
Hymenophyllum cupressiforme  1-11-------- --1- -1--11--1 11111--111-----1 ---11--------- 1-1-----
Pellaea falcata              ---1--------1 ---- -----111- --1-11---1------ -------------- 1-------
Lepidosperma gunnii          ------------ ----- ---------- ----11-1111----- -------------- -1------
Olearia stellulata           1---------- -1-- ---1------ ---------------- -------------- --------
Olearia phlogopappa          -1--------- -1-- ---------- --------------1----- -------------- --------
Poa tenera                   --11-1----- ---1 ------1-- ---------------- 1------------- --------
Tasmannia lanceolata         ------1---- 1--- --1------ 1------1-1------ --1---------- --------
```

Sub-community	F	D	E	A	B	C
Stand no.	45233442431 44756018270	4 3 7868	244522245 1 439862376	1215 161565 2 1124531861200590	1 55113343452 9323583964571	123335 45790129

```
Correa lawrenceana              11------1-- 1--- ------1-- ----------------- -------------- --------
Hymenophyllum flabellatum       --------1-- ---- -1----1-- ----------------- -------------- --------
Euchiton sp. B                  11------1-- ---- --------- -----------1----- -------------- --------
Wahlenbergia quadrifida         -------1--- ---- -------1- ----------------- -------------- --------
Cyathodes divaricata            1---11----- --11 --------- -1--------------- -----------1- -1------
Blechnum chambersii             ----------- 11-- -----1--- ----1----------- -------------- --------
Eucalyptus delagatensis         ----------- 1--- --------- 1-1------------- -------------- --------
Gahnia grandis                  ----------- 1-1- --------- -----1---------- -------------- --------
Sambucus gaudichaudiana         ----------- 1--- -------1- ----------------- -------------- --------
Tmesipteris obliqua             ----------- ---- 1---1---- ----------------- --------------- --------
Callitris rhomboidea            1---------- ---- --------- ---1-----1------ -------------- --------
Coprosma hirtella               -1--------- ---- --------- -------1-------- -------------- --------
Sarcochilus australis           --1-------- ---- 1-----1-- -1--1--------1-- -------------- --------
Drymophylla cyanocarpa          -----11-1-- ---- -1-1------ ----------------- 1------------- --------
Monotoca glauca                 -----1----- -1-- 1-------- ----------------- -------------1 --------
Hymenophyllum rarum             -1----1---1 ---- 1----1--1 1-----1--------- -----------1- --------
Acacia mucronata                1-1-------- ---- --------- -1-----1-1------ -------------- --------
Deyeuxia spp.                   ------1-1-- 1--- ---1------ --1------------- ----------1--- --------
Acacia verniciflua              ---1------- -1-- --------1 ----------------- -------------- -------1
Stellaria flaccida              -1--------- ---- -------1-- ---------1------ -11----------- -------1
Myosotis australe               ----------1 ---- ----1----- ----------------- -------------- --------
Eucalyptus globulus             ----------- --1- ----1---- -1-1------------ ----1-------- 11------
Cyathea australis               ----------- ---- --------- -------------1-- 1------------- --------
Pteris comans                   ----------- ---- --------- ----1--------1-- -------------- --------
Leucopogon lanceolatus          ----------- ---- --------- ---1------1----- -------------- --------
Melaleuca ericifolia            ----------- ---- --------- --------1-11--- 1------------- --------
Solanum laciniatum              ----------- ---- -------1-- ---------1----- -------------- --------
Eucalyptus obliqua              ----------1 ---- ----1---- ----------------- ------1------- --------
Ozothamnus thyrsoideus          ----------- --1- --------- ---------1------ -------------- -------1
Phylanthus gunnii               ----------- ---- -------1- ----------------- 1--1--------- --------
Isolepis spp.                   ----------1- -1-- --------- ----------------- ------------1 ------
Ehrharta stipoides              ---------11 ---- --------- ----------------- -------------1 -------1
Cheilanthes austrotenuifolia    ----------1 ---- --------- ------------1-1- -------------- --------
Carex spp.                      11-1---1-1- ---- --------- -------1------1-- -------------- ------1-
Juncus spp.                     -------1-1- ---- -------1- ----------------- ---1--------- --------
```

Appendix 1 continued.

Sub-community	F	D	E	A	B	C
Stand no.	45233442431	4 3	244522245	1 1215 161565 2	1 55113343452	123335
	44756018270	7868	439862376	1124531861200590	9323583964571	45790129

Geranium potentilloides	11-111-1111	1---	----11---	--11----------11	111-----1------	-11-----
Acaena novae-zelandiae	11--1--111-	11--	----1-1--	1---111-1--11---	--1----1-----	-1---1-1
Dicksonia antarctica	111111-1--1	1111	111111111	111-111111-111--	1111-11-1-1--	111-----
Clematis aristata	1111-1-1111	1111	11-111111	1---11-1-1-11--1	11-11-111-1---	11111111
Coprosma quadrifida	1-111111111	1111	111111111	11-11111111111-1	1111111111111	11111111
Olearia argophylla	--11-1--1-1	----	----1-11-	----1------1----	-11----1-11-1	--------
Polystichum proliferum	11111111111	1111	111111111	111111111--11111	111111111-11	111--111
Pomaderris apetala	11111111111	1111	111111111	11111111111111111	111111111111-	11111111
Urtica incisa	1---1----11	----	11111-111	111---1-1-11-111	-111-111-----	111-1---1
Acacia dealbata	111111-1111	1111	-1-111111	-11---1-1---1--1	-11-1--1111--	1------1
Microsorum pustulatum	11-111----1	1-11	111111111	1111111111-11111	1-1-----1----	11111111
Olearia lirata	1111-1111-1	1111	111111111	1111111111----1-	111-11-11-111	11111111
Pittosporum bicolor	-111------1	1111	1-11111-1	11111111111-1--1	1---1-1-1---1	1-111--1
Pteridium esculentum	-1111111111	-111	111111111	-1--1111-1-1-111	111-1-111-111	1------1
Asplenium bulbiferum	111111-1-11	1---	1---11-1-	11111-11111-1111	-11-11-111-1-	11111-11
Beyeria viscosa	11--1111111	11-1	1-11111-1	11111-11111-1111	1--111-11111-	11-11111
Acacia melanoxylon	--1--1---1-	-1--	1-1-11111	----111111-11111	1-11111-1--1-	111--111
Hydrocotyle hirta	11-11-11111	1111	-111111--	1--11-11111111	11-11111111-1	11111111
Notelaea ligustrina	11-111-1111	-1-1	111------	11111111111-1111	1--11--1-1111	1-11111-
Oxalis perennans	----1--1111	11--	1-111--1-	---1-11--1-11111	1-1111--111--	1111-111
Viola hederacea	11-11-1111-	111-	--11-----	-------1-1111---	-11--1-1-11-1	-1111111
Galium australe	---11--1111	1--1	1-11-----	-1--1----------1	---------1----	-1111111
Lepidosperma laterale	1-1-111111-	-111	1-11-----	-----------11--	1--1-1111111-	-----1-1
Bedfordia salicina	1111---1111	11-1	-111111-1	111-11-1--------	----11-1-111-	11111111
Zieria arborescens	11--1111111	1--1	11-------	111-1-1-11---1--	11-111111111-	1---1111
Pelargonium australe	-----------	1---	---------	--------------1-	------------1	--------
Lomatia tinctoria	--------1--	----	---------	----------------	1-----1--11--	--------
Prostanthera lasianthos	1-11----1--	--1-	--1------	-1----------	-----1---111--	-1-11--1
Exocarpos cupressiformis	-------111-	-1-1	--------1	-1-1----1----1-1	--1---111111-	--111111
Acacia verticillata	--------11-	-1-1	---11----	-----1------1---	1--1--1111--1	---11111
Olearia viscosa	---1---1-1-	11--	--11----1	--------1-----1-	------1---1--	11111111
Asterotrichion discolor	--------1-1-	----	---------	---1----1-------	-11-11111-1--	-111-111
Lomandra longifolia	--------1---	----	---------	------------1-1	---1-11-111-1	1-111111
Billardiera longiflora	-------1---	1---	-----1---	----------------	----------1---	-1---1-1
Dianella tasmanica	----1--11--	----	---------	-----------1----	---------1-----	--11-111
Poa labillardierei	----1----11-	1---	---------	----------------	---1---11----	1111--11
Dianella revoluta	--------1--	-1-1	----1----	-----1----------	------------1	11--1-1-

Sub-community	F	D	E	A	B	C
Stand no.	45233442431	4 3	244522245 1	1215 161565 2	1 55113343452	123335
	44756018270	7868	439862376	1124531861200590	9323583964571	45790129

Senecic linearifolius	---1-------	----	--1-1-1--	------1----------	-11----------	-1-1-111
Goodenia ovata	----1------	--11	---------	----------------	--------------	-1-11111
Banksia marginata	-----------	----	---------	--------1------	---------1-11	-----1-1
Bursaria spinosa	-------1-1-	----	----11--1	------1------11-	---1---------	-111111-
Senecio minimus	-----------	----	-----11--	---------------1	-1---1-------	-1-111-1
Correa reflexa	-----------	----	---------	----------------	--------------	---1111-
Cardamine lilacina	-----------	----	---------	----------------	--------------	111-----
Leptospermum scoparium	-----------	----	---------	---------1----	---------11--	--------
Dodonaea viscosa	-----------	----	---------	---------1----1-	--------------	-1-----1`
Allocasuarina verticillata	-----------	----	---------	------------1--1	---1---------	-----11-
Stellaria pungens	-----------	----	---------	---------------1	--------------	1-------
Cassinia aculeata	-----------	----	---------	----------------	--------------	--1----1

Appendix 1 continued.

Site Name	Site Number
Block & Stable Creek	1
Lost Falls	2
Spinning Gum CA	3
South Brown Mountain	4
Coningham CA	5
Dalco Creek	6
Knights Creek	7
Hardings Falls	8
Quoin Cliffs	9
Mount Henry	10
Three Thumbs	11
Roaring Beach	12
Cloudy Bay	13
Hellfire Bluff	14
Tiger Gully	15
Daley's	16
Tinderbox	17
Cunny Creek	18
Mount Direction HS	19
Trevallyn SRA	20
Bangor	21
Loila Tier B	22
St Marys Pass	23
Forester River	24
Bedggood Hill	25
Notley Gorge	26
Clements Creek	27
Jonathans Gully	28
Quarry Reserve Creek	29
Hinsby Beach south	30
Hinsby Beach north, north tributary	31
Hinsby Beach north, south tributary	32
Mount Phipps	33
Iles Tier	34
Razorback gully	35
Diamond Tier	36
Saddle Rock Creek	37
Spring Creek	38
Wilsons Ridge north	39
Mountain Gully	40
Waterfall Bay	41
Tater Garden Creek	42
Big Sassy Creek	43
Goatrock Creek	44
Carlton River	45
Morrison Sugarloaf	46
Cluan Tiers	47
Snug Falls	48
Parrs Rivulet	49
Teagardens	50
North Esk River	51
Bluff River Gorge	52
Symonds Creek	53
Meetus Falls	54
Tippogoree Hills north	55
Loila Tier A	56
Bicheno	57
Fern Tree	58
Truganini Reserve	59
Casuarina Highway	60
Douglas Apsley NP	61

Appendix 2 Mean frequencies of vascular species by sub-community group. Characteristic species of a particular sub-community are shown in bold. These characteristic species are those species that occur at 1/3 or more of the stands in a sub-community with the limitation that no more than 2 of the sub-communities record this species in that frequency.

Species	sub-community					
	A	E	D	B	C	F
Lepidosperma gunnii	**0.38**	0 00	0.00	0.00	0.13	0.00
Blechnum pattersonii	0.06	0.00	0.00	0.00	0.00	0.00
Pteris comans	0.13	0.00	0.00	0.00	0.00	0.00
Leucopogon lanceolatus	0.13	0.00	0 00	0.00	0.00	0.00
Hydorocotyle callicarpa	0.06	0.00	0.00	0.00	0.00	0.00
Dockrillia striolata	0.06	0.00	0.00	0.00	0.00	0.00
Cerastium sp	0.06	0.00	0.00	0.00	0.00	0.00
Cassytha pubescens	0.06	0.00	0.00	0.00	0.00	0.00
Hymenophyllum cupressiforme	**0.56**	**0.44**	0.25	0.15	0.25	0.27
Solanum laciniatum	0.06	0.11	0.00	0.00	0.00	0.00
Picris angustifolia	0.00	0.11	0 00	0.00	0.00	0.00
Australina pusilla	0.00	0.11	0.00	0.00	0.00	0.00
Diplazium australe	0.00	0.11.	0.00	0.00	0.00	0.00
Muehlenbeckia gunnii	0 00	0.11	0.00	0 00	0.00	0.00
Tmesipteris obliqua	0.00	0 22	0.00	0.00	0.00	0.00
Hymenophyllum rarum	0.13	**0.33**	0.00	0.08	0.00	0.27
Pellaea falcata	0.25	**0.33**	0.00	0.00	0.13	0 18
Blechnum nudum	0.13	**0.44**	0.25	0.15	0.00	0 09
Parsonsia brownii	0.19	**0.56**	0.00	0.08	0.00	0 00
Rumohra adiantiformis	0.31	**1.00**	0.25	0.00	0.25	0.09
Pteris tremula	0.00	**0.33**	0.00	0.00	0.00	0.00
Polyphlebium venosum	0.00	**0.56**	0.00	0.00	0.00	0.18
Atherosperma moschatum	0 06	**0.67**	**1.00**	0.00	0 13	0.27
Grammitis billardierei	0.06	**0.44**	**0.75**	0.00	0.00	0.18
Histiopteris incisa	0.19	**1.00**	**0.50**	0.08	0.00	0.18
Asplenium bulbiferum	0.06	**0.67**	0.25	0.00	**0.50**	0.27
Bursaria spinosa	0.19	**0.33**	0.00	0.08	**0.75**	0.18
Blechnum watsii	0.13	0.44	1.00	0.15	0.00	0.55
Cheilanthes austrotenuifolia	0.13	0 00	0.00	0.00	0.00	0.09
Sambucus gaudichaudiana	0.00	0.11	0 25	0.00	0.00	0 00
Aristotelia peduncularis	0.00	0 00	**0.50**	0.00	0.00	0.09
Huperzia varia	0 00	0 00	**0.50**	0 00	0.00	0.09
Nothofagus cunninghamii	0.00	0 00	**0.75**	0 00	0.00	0.00
Hymenophyllum australe	0 00	0.11	**0.75**	0 00	0.00	0.00
Gahnia grandis	0.06	0.00	**0.50**	0.00	0.00	0.00
Cyathodes divaricata	0.06	0.00	**0.50**	0.08	0.13	0.27
Gaultheria hispida	0 00	0.11	**0.75**	0.00	0.00	0 00
Blechnum chambersii	0.06	0 11	**0.50**	0.00	0.00	0.00
Acacia riceana	0.00	0 00	**0.50**	0.00	0.00	0.00
Prostanthera lasianthos	0.06	0 00	**0.75**	0.31	**0.50**	0 27
Cyathodes glauca	0.13	0.11	**0.75**	0 08	0.00	**0.64**
Anopterus glandulosus	0.00	0.00	0.25	0 00	0.00	0.00

Appendix 2 continued.

Species	sub-community					
	A	E	D	B	C	F
Sticherus tener	0.00	0.00	0.25	0.00	0.00	0.00
Leptospermum scoparium	0.06	0.00	0.00	0.15	0.00	0.00
Callitris rhomboideae	0.13	0.00	0.00	0 00	0 00	0.09
Phylanthus gunnii	0.00	0.11	0.00	0.15	0.00	0.00
Acacia verniciflua	0.00	0.11	0.25	0.00	0.13	0.09
Sarcophillus australis	0.19	0.22	0 00	0.00	0.00	0.09
Tasmannia lanceolata	0 19	0.11	0.25	0.08	0.00	0 09
Pittosporum bicolor	0 81	0.78	1.00	0.38	0.63	0.36
Acacia dealbata	0.38	0.78	1.00	0.54	0.25	0.91
Acacia melanoxylon	0.69	0.78	0.50	0.62	0.75	0.18
Acacia mucronata	0.19	0.00	0 00	0.00	0.00	0.18
Acaena novae-zelandiae	0.44	0.22	0.50	0.15	0.38	0.55
Acacia verticillata	0.13	0.11	0.25	0.54	0.63	0.36
Ctenopteris heterophylla	0 31	0 33	0.50	0.08	0.13	0 64
Clematis aristata	0.50	0.89	1.00	0 62	1 00	0 82
Asplenium flabellifolium	0.88	0.44	0.25	0 62	0.88	0.82
Dicksonia antarctica	0.75	1.00	1.00	0.62	0.38	0.73
Bedfordia salicina	0.38	0.56	0.75	0 46	1.00	0.91
Microsorum pustulatum	0.94	1.00	0 75	0.23	1.00	0.55
Beyeria viscosa	0.88	0.78	0 25	0 69	0.88	1.00
Coprosma quadrifida	0.88	1.00	1 00	1 00	1 00	0.91
Oxalis perennans	0.56	0.33	0.25	0.62	0 88	0.73
Polystichum proliferum	0.88	1.00	1 00	0 92	0.75	1.00
Hydrocotyle hirta	0.75	0 56	0.75	0.85	1 00	1 00
Notelaea ligustrina	0.94	0.33	0 50	0 62	0 75	0.82
Olearia argophylla	0.69	1.00	1 00	0 77	1 00	0.82
Pteridium esculentum	0.63	1.00	0 75	0.77	0.25	0 91
Pomaderris apetala	1.00	1 00	1.00	0.92	1 00	1 00
Pimelea drupacea	0.31	1.00	1.00	0 00	0.13	0.82
Zieria arborescens	0.50	0.44	0 00	0.85	0.63	0 82
Exocarpos cupressiformis	0.31	0.11	0.25	0.54	0.75	0 36
Urtica incisa	0 63	0 89	0.00	0.46	0 63	0.36
Viola hederacea	0.31	0.11	0.75	0.54	0.88	0.82
Lepidosperma laterale	0.13	0 33	0.75	0.69	0 25	0.73
Olearia lirata	0.13	0.33	0.00	0 46	0.00	0.45
Stellaria flaccida	0.06	0.11	0.00	0 15	0.13	0.09
Actites megalocarpa	0.00	0.00	0.00	0 08	0.00	0.00
Agropyron pectinatum	0.00	0.00	0.00	0 08	0 00	0.00
Cyathea australis	0.06	0.00	0.00	0 08	0 00	0.00
Senecio linearifolius	0 06	0 22	0.25	0.15	0.63	0.09
Poa tenera	0.00	0 11	0.25	0 08	0.00	0.27
Nematolepis sqaumea	0.00	0 00	0.25	0 08	0.00	0.09
Lomatia tinctoria	0.00	0.00	0.00	0.31	0.00	0.09
Melaleuca ericifolia	0.19	0 00	0 00	0.08	0.00	0.00
Monotocha glauca	0.00	0 11	0 25	0.08	0.00	0.09
Myosotis australe	0.00	0.11	0.00	0 00	0.00	0.09

Appendix 2 continued.

Species	sub-community					
	A	E	D	B	C	F
Olearia phlogopappa	0.06	0.00	0.25	0.00	0.00	0.09
Hymenophyllum flabellatum	0.00	0.22	0.00	0.00	0.00	0.09
Isolepus spp.	0.00	0.00	0.25	0.08	0.00	0.09
Juncus spp.	0.00	0.11	0.00	0 08	0.00	0.18
Eucalyptus delegatensis	0.13	0.00	0.25	0.00	0.00	0.00
Eucalyptus globulus subs *globulus*	0.13	0.11	0.25	0.08	0.25	0.00
Eucalyptus obliqua	0.00	0.11	0.00	0.08	0.00	0.09
Euchiton sp. B	0.06	0.00	0.00	0 00	0.00	0.27
Olearia stellulata	0.00	0.11	0.25	0.00	0.00	0.09
Senecio minimus	0.06	0.22	0.00	0.15	0 63	0 00
Deyeuxia spp	0.06	0.11	0.25	0.08	0.00	0.18
Cystopteris tasmanica	0.00	0.11	0.00	0.00	0.00	0.00
Agrostis billardierei	0.00	0.00	0 00	0.08	0.00	0.00
Ozothamnus thyrsoideus	0 06	0.00	0.25	0.00	0.13	0.00
Dodonea viscosa	0.13	0.00	0 00	0.00	0.25	0.00
Drymophylla cyanocarpa	0.00	0 22	0.00	0.08	0.00	0.27
Pelargonium australe	0.06	0.00	0 00	0.08	0.00	0.09
Austrofestuca littoralis	0.00	0.00	0.00	0.08	0.00	0.00
Wahlenbergia quadrifida	0.00	0.11	0.00	0.00	0.00	0 09
Wahlenbergia sp.	0.00	0.11	0.00	0.00	0 00	0.09
Ehrharta stipoides	0.00	0.00	0.00	0.08	0.13	0.18
Coprosma hirtella	0.06	0.00	0.00	0.00	0.00	0.09
Correa lawrenceana	0.00	0.11	0.25	0 00	0.00	0.27
Banksia marginata	0.06	0.00	0.00	0 23	0.25	0.00
Olearia viscosa	0.13	0.11	0.50	0.15	1 00	0.45
Spinifex sericeus	0.00	0.00	0.00	0.08	0.00	0 00
Epacris impressa	0.00	0.00	0.00	0.08	0.00	0.00
Selliera radicans	0.00	0.00	0.00	0 08	0 00	0.00
Poa rodwayi	0.00	0.00	0.00	0 08	0.00	0.00
Dichondra repens	0.00	0.00	0.00	0.08	0 00	0.00
Goodenia lanata	0.00	0.00	0.00	0 08	0 00	0.00
Asterotrichion discolor	0.13	0.00	0.00	**0.62**	**0.75**	0.18
Lomandra longifolia	0.13	0.00	0.00	**0.54**	**0.88**	0.09
Allocasuarina verticillata	0 13	0.00	0.00	0 08	0 25	0.00
Stellaria pungens	0.06	0.00	0.00	0 00	0.13	0.00
Agrostis parviflora	0.00	0.00	0.00	0.00	0.13	0 00
Echinopogon ovatus	0.00	0.00	0.00	0.00	0.13	0.00
Derwentia derwentiana	0 00	0.00	0.00	0.00	0.13	0.00
Senecio quadridentatus	0.00	0.00	0.00	0 00	0.13	0.00
Cassinia aculeata	0.00	0.00	0.00	0 00	0.25	0.00
Dianella revoluta	0.06	0 00	0 00	0.08	**0.63**	0.27
Dianella tasmanica	0.06	0.11	0 25	0 08	**0.50**	0.18
Correa reflexa	0.00	0 00	0 00	0.00	**0.50**	0.00
Goodenia ovata	0.00	0.00	0 25	0.00	**0.75**	0.18
Billardiera longiflora	0.00	0 11	0.00	0.08	**0.38**	0.18
Cardamine lilacina	0.00	0 00	0.00	0.00	**0.38**	0.00
Galium australe	0.19	0 00	0 25	0 08	**0.88**	**0.82**

Appendix 2 continued.

Species	sub-community					
	A	E	D	B	C	F
Poa labillardierei	0.00	0.00	0.00	0.23	**0.75**	**0.36**
Geranium potentilloides	0 25	0.22	0.25	0.31	0.25	**0.82**
Luzula spp.	0 13	0.11	0.00	0.00	0.25	**0.55**
Carex spp.	0.13	0.00	0.25	0 00	0.13	**0.36**
Danthonia spp.	0.00	0.00	0.00	0.00	0.00	0.09
Epilobium spp	0.00	0.00	0.00	0.00	0 00	0.09
Euchiton collinus	0.00	0.00	0.00	0.00	0.00	0.09
Goodia lotifolia	0 00	0.00	0.00	0.00	0.00	0.09
Lagenophora stipitata	0.00	0.00	0.00	0.00	0.00	0.09
Ozothamnus purpurascens	0.00	0.00	0.00	0.00	0.00	0.09
Pratia pedunculata	0.00	0.00	0.00	0.00	0.00	0.09
Cheilathes sieberi	0.00	0.00	0.00	0 00	0 00	0.09
Stylidium dilatatum	0.00	0.00	0.00	0.00	0.00	0.09
Pultenaea juniperina	0.00	0.00	0.00	0.00	0.00	0.09
Veronica sp.	0.00	0.00	0.00	0.00	0.00	0.09
Euchiton sp. A	0.00	0.00	0.00	0.00	0.00	0 18
Leptospermum lanigerum	0.00	0.00	0.00	0.00	0 00	0 18
Callistemon pallidus	0.00	0.00	0.00	0 00	0 00	0.18

Appendix 3 List of vascular plant species and genera recorded from Tasmanian dry closed-forest.

Species	Exotic (e)/ Native (n)	Endemic?	Life-form	Life-form codes	
Acacia dealbata	n		t	carn	carnivorous
Acacia melanoxylon	n		t	cl	climber
Acacia mucronata	n		s	f	fern
Acacia riceana	n	yes	s	g	grass
Acacia verniciflua	n		s	h	herb
Acacia verticillata	n		t	o	orchid
Acaeca novae-zelandiae	n		h	pa	parasite
Actites megalocarpa	n		h	s	shrub
Australopyrum pectinatum	e		g	l/se	lily/sedge
Agrostis billardierei	n		g	t	tree
Agrostis parviflora	n		g		
Allocasuarina verticillata	n		t		
Anopterus glandulosus	n	yes	t		
Aristotelia peduncularis	n	yes	s		
Asplenium bulbiferum	n		f		
Asplenium flabellifolium	n		f		
Asterotrichion discolor	n	yes	t		
Atherosperma moschatum	n		t		
Australina pusilla	n		h		
Australopyrum pectinatum	e		g		
Austrofestuca littoralis	n		g		
Banksia marginata	n		t		
Bedfordia salicina	n	yes	t		
Beyeria viscosa	n		t		
Billardiera longiflora	n		cl		
Blechnum chambersii	n		f		

Appendix 3 continued.

Species	Exotic (e)/ Native (n)	Endemic?	Life-form
Blechnum nudum	n		f
Blechnum pattersonii	n		f
Blechnum watsii	n		f
Bursaria spinosa	n		t
Callistemon pallidus	n		t
Callitris rhomboidea	n		t
Cardamine lilacina	n		h
Carex spp	?		l/se
Cassinia aculeata	n		s
Cassytha pubescens	n		par/cl
Centaurium erythraea	e		h
Cerastium glomeratum	n		h
Cheilanthes austrotenuifolia	n		f
Cheilathes sieberi	n		f
Chiloglottis sp.	n		o
Cirsium vulgare	e		h
Clematis aristata	n		cl
Coprosma hirtella	n		s
Coprosma quadrifida	n		s
Correa lawrenceana	n		s
Correa reflexa	n		s
Corybas sp	n		o
Cotoneaster glaucophyllus	e		t
Crataegus monogyna	e		t
Chrysanthemoides monilifera	e		s
Ctenopteris heterophylla	n		f
Cyathea australis	n		f
Cyathodes divaricata	n		s

Appendix 3 continued.

Species	Exotic (e)/ Native (n)	Endemic?	Life-form
Cyathodes glauca	n		s
Cystopteris tasmanica	n		f
Danthonia spp	?		g
Deyeuxia spp	?		g
Derwentia derwentiana	n		h
Dianella revoluta	n		l/se
Dianella tasmanica	n		l/se
Dichondra repens	n		h
Dicksonia antarctica	n		f
Diplazium australe	n		f
Dockrillia striolata	n		o
Dodonaea viscosa	n		t
Drymophila cyanocarpa	n		l/se
Echinopogon ovatus	n		g
Ehrharta stipoides	n		g
Epacris impressa	n		s
Epilobium spp	?		h
Eucalyptus delegatensis	n		t
Eucalyptus globulus ssp globulus	n		t
Eucalyptus obliqua	n		t
Euchiton collinus	n		h
Euchiton sp A	n		h
Euchiton sp. B	n		h
Exocarpos cupressiformis	n		t
Gahnia grandis	n	-	l/se
Galium australe	n		h
Gaultheria hispida	n		s
Genista monspessulana	e		s

Appendix 3 continued.

Species	Exotic (e)/ Native (n)	Endemic?	Life-form
Geranıum spp.	n		h
Goodenıa lanata	n		h
Goodenia ovata	n		s
Goodia lotifolia	n		s
Grammitıs billardierei	n		f
Hydorocotyle callıcarpa	n		h
Hydrocotyle hırta	n		h
Hedera helix	e		cl
Hıstıopterıs ıncısa	n		f
Huperzia varıa	n		f
Hymenophyllum australe	n		f
Hymenophyllum cupressiforme	n		f
Hymenophyllum flabellatum	n		f
Hymenophyllum rarum	n		f
Hypochoeris radıcata	e		h
Ilex aquıfolıum	e		t
Isolepıs spp.	n		l/se
Juncus spp.	?		l/se
Lagenophora stipıtata	n		h
Lepidosperma laterale	n		l/se
Lepıdosperma gunnıı	n		l/se
Leptospermum lanıgerum	n		t
Leptospormum scoparıum	n		t
Leycesterıa formosa	e		s
Leucopogon lanceolatus	n		s
Lomandra longifolia	n		l/se
Lomatıa tınctorıa	n	yes	s
Luzula spp	?		l/se

Appendix 3 continued.

Species	Exotic (e)/ Native (n)	Endemic?	Life-form
Melaleuca ericifolia	n		t
Microsorum pustulatum	n		f
Monotoca glauca	n		t
Myosotis australe	n		h
Muehlenbeckia gunnii	n		cl
Nematolepis sqaumea	n		t
Notelaea ligustrina	n		t
Nothofagus cunninghamii	n		t
Olearia argophylla	n		t
Olearia lirata	n		s
Olearia phlogopappa	n		s
Olearia stellulata	n		s
Olearia viscosa	n		s
Oxalis perennans	n		h
Ozothamnus purpurascens	n		s
Ozothamnus thyrsoideus	n		s
Parsonsia brownii	n		cl
Passiflora mollissima	e		cl
Pelargonium australe	n		h
Pellaea falcate	n		f
Phyllanthus gunnii	n		h
Picris angustifolia	n		h
Pimelea drupacea	n		s
Pittosporum bicolor	n		t
Plantago varia	e		h
Poa labillardierei	n		g
Poa rodwayi	n		g
Poa tenera	n		g

Appendix 3 continued.

Species	Exotic (e)/ Native (n)	Endemic?	Life-form
Polyphlebium venosum	n		f
Polystichum proliferum	n		f
Pomaderris apetala	n		t
Pratia pedunculata	n		h
Prostanthera lasianthos	n		t
Pteridium esculentum	n		f
Pteris comans	n		f
Pteris tremula	n		f
Pterostylis sp	n		o
Pultenaea juniperina	n		s
Rubus fruticosus sp. agg	e		cl
Rumohra adiantiformis	n		f
Sambucus gaudichaudiana	n		s
Sarcochilus australis	n		o
Selliera radicans	n		h
Senecio linearifolius	n		h
Senecio minimus	n		h
Senecio quadridentatus	n		h
Solanum laciniatum	n		s
Sonchus oleraceus	e		h
Spinifex sericeus	n		g
Stellaria media	e		h
Stellaria flaccida	n		h
Stellaria pungens	n		h
Sticherus tener	n		f
Stylidium despectum	n		h
Tasmannia lanceolata	n		t
Taraxicum officinale	e		h
Tmesipteris obliqua	n		f
Urtica incisa	n		h
Veronica sp	?		h

Appendix 3 continued.

Species	Exotic (e)/ Native (n)	Endemic?	Life-form
Viola hederacea	n		h
Wahlenbergia quadrifida	n		h
Wahlenbergia sp	n		h
Zieria arborescens	n		t

Appendix 3 continued.

Species	Exotic (e)/ Native (n)	Endemic?	Life-form

Appendix 4. Significant results of species segregation within dry closed-forest stands. S is a segregation index, while the statistic Z tests the hypothesis that a nearest neighbour count is a chance event. The p-value associated with Z is derived from z tables. T1 and T2 are an abbreviation of transect 1 and transect 2, and are used to differentiate stands where 2 transects were investigated.

From	To	Observed Count	Expected Count	S	Z	p-value (normal)	sig. level
Bangor							
Coprosma quadrifida	*Coprosma quadrifida*	7	2 129032258	0 812306	2.96058	0.003	sig <0.01
Notelaea ligustrina	*Notelaea ligustrina*	2	0 032258065	N/A	8 65422	<0.001	sig <0.01
Olearia argophylla	*Olearia argophylla*	2	0 096774194	1 778151	4 885305	<0.001	sig <0.01
Pittosporum bicolor	*Pittosporum bicolor*	1	0.096774194	1 176091	2.31845	0 02	sig <0.05
Bedgood Hill							
Bedfordia salicina	*Coprosma quadrifida*	1	0.156862745	1.070038	2 229073	0 026	sig <0.05
Coprosma quadrifida	*Bedfordia salicina*	1	0 156862745	0 912045	2 208677	0 027	sig <0 05
Olearia argophylla	*Olearia argophylla*	1	0.117647059	1 088136	1 969414	0 049	sig <0 05
Pittosporum bicolor	*Ziena arborescens*	3	0 470588235	1 352183	3 982633	<0.001	sig <0 01
Ziena arborescens	*Beyeria viscosa*	0	2.705882353	N/A	-2 21065	0 027	sig <0 05
Ziena arborescens	*Pittosporum bicolor*	3	0 470588235	1 070038	3 94389	<0.001	sig <0 01
Block & Stable Creek							
Bedfordia salicina	*Pomaderris apetala*	1	0 1	1 278754	2 930516	0 003	sig <0.01
Notelaea ligustrina	*Beyeria viscosa*	1	4 275	-0 85962	-2.11263	0 035	sig <0.05
Notelaea ligustrina	*Notelaea ligustrina*	7	1 8	1 146128	3.496302	<0 001	sig <0 01
Pomaderris apetala	*Bedfordia salcina*	1	0 1	1 278754	2 930516	0.003	sig <0.05
Cloudy Bay							
Cassinia/Ozothamnus	*Bedfordia salicina*	1	4 909090909	-0 88169	-2 27206	0 023	sig <0 05
Cassinia/Ozothamnus	*Cassinia/Ozothamnus*	8	2	1	3.824488	<0 001	sig <0 01
Cassinia/Ozothamnus	*Pomaderris apetala*	0	3 090909091	N/A	-2 05707	0 04	sig <0 05
Coningham CA							
Acacia melanoxylon	*Acacia melanoxylon*	2	0.214285714	1 130334	3 060359	0 002	sig <0 01
Asterotrichion discolor	*Asterotrichion discolor*	2	0 085714286	1 659599	5 125316	<0 001	sig <0.01
Bedfordia salicina	*Bedfordia salicina*	4	0.3	1.473892	5 39177	<0 001	sig <0.01
Bedfordia salicina	*Prostanthera lasianthos*	1	0 1	1 060698	2 890448	0 004	sig <0 01
Beyeria viscosa	*Beyeria viscosa*	28	15.44285714	0 478774	3.379505	0.001	sig <0 01
Beyeria viscosa	*Coprosma quadrifida*	2	6.714285714	-0 57403	-2 06191	0 039	sig <0 05
Prostanthera lasianthos	*Prostanthera lasianthos*	2	0.014285714	N/A	12 86929	<0 001	sig <0 01
Dalco Creek							
Acacia melanoxylon	*Olearia argophylla*	1	0 075949367	1.403692	3 419543	0 001	sig <0 01
Acacia riceana	*Prostanthera lasianthos*	2	0.506329114	0 631218	2 139339	0 032	sig <0.05
Olearia argophylla	*Acacia melanoxylon*	1	0 075949367	1 193125	3 380335	0 001	sig <0 01
Pittosporum bicolor	*Pittosporum bicolor*	2	0.189873418	1 184691	3.304201	0.001	sig <0 01
Pomaderris apetala	*Coprosma quadrifida*	3	0 462025316	0 827923	3.847525	<0 001	sig <0 01
Daley's							
Coprosma quadrifida	*Olearia argophylla*	4	1 111111111	N/A	3 198729	0 001	sig <0 01
Olearia argophylla	*Coprosma quadrifida*	4	1 111111111	1 146128	3 095977	0 002	sig <0 01
Olearia argophylla	*Olearia argophylla*	0	1 111111111	N/A	3.444204	0 001	sig <0.01
Forester River							
Pomaderris apetala	*Pomaderris apetala*	8	3.818181818	0 524648	2.059143	0.039	sig <0 05

Appendix 4 continued

From	To	Observed Count	Expected Count	S	Z	p-value (normal)	sig level
Harding's Falls							
Notelaea ligustrina	*Beyeria viscosa*	0	1 807692308	N/A	-2.11181	0 035	sig <0 05
Notelaea ligustrina	*Notelaea ligustrina*	2	0 076923077	1 880814	5 700701	<0 01	sig <0.01
Olearia argophylla	*Acacia melanoxylon*	2	0 333333333	0 839421	2 928706	0 003	sig <0.01
Pittosporum bicolor	*Olearia argophylla*	1	0.166666667	N/A	2 236068	0 025	sig <0.05
Hellfire Bluff T1							
Notelaea ligustrina	*Pittosporum bicolor*	1	0 125	1.060698	2.537136	0 011	sig <0.05
Pittosporum bicolor	*Notelaea ligustrina*	1	0.125	N/A	2 645751	0.008	sig <0.01
Knight's Creek							
Bedfordia salicina	*Bedfordia salicina*	7	2 869565217	0.648803	2 247841	0 025	sig <0.05
Bedfordia salicina	*Eucalyptus delegatensis*	0	3.913043478	N/A	-2 2624	0 024	sig <0.05
Eucalyptus delegatensis	*Bedfordia salicina*	0	3.913043478	N/A	-2.14969	0.032	sig <0.05
Eucalyptus delegatensis	*Eucalyptus delegatensis*	12	4.565217391	0.961082	3 382473	0.001	sig <0.01
Pittosporum bicolor	*Pittosporum bicolor*	2	0.130434783	1.643453	4.156113	<0 001	sig <0.01
Loila Tier T1							
Acacia dealbata	*Olearia argophylla*	1	0.153846154	1.079181	2 250802	0 024	sig <0.05
Bedfordia salicina	*Bedfordia salicina*	2	0.230769231	1 380211	2 945599	0 003	sig <0 01
Olearia argophylla	*Acacia dealbata*	1	0.153846154	1.079181	2 250802	0 024	sig <0.05
Loila Tier T2							
Beyeria viscosa	*Bedfordia salicina*	2	0.5	0.778151	2 231066	0.026	sig <0 05
Mount Direction HS T2							
Olearia argophylla	*Pomaderris apetala*	2	0 631578947	N/A	2 054524	0 04	sig <0 05
Mount Henry							
Bedfordia salicina	*Bedfordia salicina*	2	0 27027027	1.066947	2 675782	0 007	sig <0.01
Beyeria viscosa	*Beyeria viscosa*	22	10.21621622	0.805006	3 877866	<0 001	sig <0 01
Beyeria viscosa	*Pomaderris apetala*	1	12.10810811	-1.31326	-3 8953	<0 001	sig <0 01
Notelaea ligustrina	*Olearia argophylla*	1	0 081081081	N/A	3 366502	0 001	sig <0 01
Olearia argophylla	*Notelaea ligustrina*	1	0 081081081	1 164353	3.249145	0 001	sig <0.01
Pomaderris apetala	*Pomaderris apetala*	24	13 40540541	0 619228	3.224016	0.001	sig <0 01
Pomaderris apetala	*Beyeria viscosa*	1	12 10810811	-1.27576	-3 74739	<0 001	sig <0 01
Notley Gorge							
Olearia.argophylla	*Beyeria viscosa*	3	0.681818182	0.977724	2.951921	0.003	sig <0 01
Pittosporum bicolor	*Olearia argophylla*	3	0.909090909	1 0086	2.43825	0.015	sig <0 05
Pomaderris apetala	*Pomaderris apetala*	6	2.545454545	0.808114	2 164029	0.03	sig <0 05
Quoin Cliffs T2							
Pomaderris apetala	*Pomaderris apetala*	2	0 3	1.255273	2.429317	0 015	sig <0 05
Pomaderris apetala	*Olearia argophylla*	0	2 1	N/A	-2.39208	0 017	sig <0 05
Spinning Gum CA							
Pomaderris apetala	*Asterotrichion discolor*	6	2 4	0.740363	2.150831	0 031	sig <0 05
St Mary's Pass							
Acacia dealbata	*Olearia argophylla*	1	0.18556701	0 99024	1 984245	0 0477	sig <0 05
Olearia argophylla	*Acacia dealbata*	2	0 18556701	1.132626	4.253097	<0 0001	sig <0.01

Appendix 4 continued.

From	To	Observed Count	Expected Count	S	Z	p-value (normal)	sig. level
South Brown Mountain							
Bedfordia salicina	*Bedfordia salicina*	2	0.058823529	N/A	6.507688	<0.0001	sig <0 01
Notelaea ligustrina	*Pittosporum bicolor*	1	0.176470588	0 90309	2.030445	0 042	sig <0 05
Pittosporum bicolor	*Notelaea ligustrina*	1	0 176470588	1 01424	2.057374	0.04	sig <0.05
Three Thumbs T1							
Beyeria viscosa	*Beyeria viscosa*	5	1 909090909	0.823909	2 149975	0 032	sig <0.05
Three Thumbs T2							
Atherosperma moschatum	*Coprosma quadrifida*	1	0.15	N/A	2 380476	0 017	sig <0.05
Bedfordia salicina	*Pomaderris apetala*	1	0 1	1.278754	2.912121	0.004	sig <0.01
Olearia argophylla	*Notelaea ligustrina*	3	0 75	0.929419	2.761848	0.006	sig <0.01
Pomaderris apetala	*Bedfordia salicina*	1	0 1	N/A	3	0 003	sig <0.01
Tiger Gully							
Bedfordia salicina	*Bedfordia salicina*	10	2 75	1 225779	4 110785	<0.0001	sig <0 01
Beyeria viscosa	*Notelaea ligustrina*	1	0 0625	1 371068	3.779606	<0.0001	sig <0.01
Notelaea ligustrina	*Beyeria viscosa*	1	0 0625	N/A	3 872983	<0 0001	sig <0 01
Olearia argophylla	*Ziera arborescens*	6	2.979166667	0 509306	1 982881	0.047	sig <0 05
Pomaderris apetala	*Pomaderris apetala*	1	0.125	1 060698	2.02878	0.042	sig <0.05
Tinderbox							
Pomaderris apetala	*Pomaderris apetala*	6	1.65	1 06	3.134693	0.0017	sig <0 01
Pomaderris apetala	*Olearia argophylla*	0	2 82	N/A	-1.96388	0.0496	sig <0 05
Trevallyn SRA							
Notelaea ligustrina	*Pittosporum bicolor*	2	0.514285714	0 985277	2 26012	0.024	sig <0 05
Pittosporum bicolor	*Notelaea ligustrina*	2	0 514285714	0 726999	2.138785	0.032	sig <0.05
Truganini Reserve							
Acacia melanoxylon	*Bedfordia salicina*	1	0 140625	N/A	2 332881	0.0198	sig <0 05
Acacia melanoxylon	*Pittosporum bicolor*	0	0.078125	N/A	-0 28228	0.03752	sig <0 05
Acacia melanoxylon	*Pomaderris apetala*	3	0 734375	1.12517	2 923845	0 0035	sig <0 01
Asterotrichion discolor	*Pomaderris apetala*	0	3 48828125	N/A	-2 05793	0 0444	sig <0 05
Bedfordia salicina	*Bedfordia salicina*	3	0.28125	1.190332	4 132521	<0 0001	sig <0 01
Bedfordia salicina	*Acacia melanoxylon*	1	0 140625	0 896251	2 309803	0.0209	sig <0 05
Bedfordia salicina	*Beyeria viscosa*	0	3.26953125	N/A	-2.25422	0 0244	sig <0 05
Beyeria viscosa	*Beyeria viscosa*	63	33 421875	0.573275	5 430135	<0.0001	sig <0.01
Beyeria viscosa	*Coprosma quadrifida*	9	20.34375	-0 41719	-2.76698	0 0057	sig <0 01
Coprosma quadrifida	*Coprosma quadrifida*	22	12 03125	0.373777	2 670538	0 0075	sig <0 01
Coprosma quadrifida	*Beyeria viscosa*	13	20.34375	-0 27582	-1 97045	0 0488	sig <0 05
Olearia argophylla	*Olearia argophylla*	8	1 8046875	0 805811	3 857266	0 0001	sig <0.01
Pittosporum bicolor	*Pittosporum bicolor*	2	0 078125	1 623249	5.481906	<0.0001	sig <0 01
Pomaderris apetala	*Pomaderris apetala*	16	8 4453125	0 37222	2 346038	0 01928	sig <0 05
Pomaderris apetala	*Acacia melanoxylon*	3	0 734375	0.633009	2.664838	0.00782	sig <0 01
Pomaderris apetala	*Beyeria viscosa*	10	17 07421875	-0 3245	-2 08344	0.0375	sig <0 05
Pomaderris apetala	*Ziera arborescens*	3	0 3671875	0 937472	4 364062	<0 0001	sig <0 01
Ziera arborescens	*Pittosporum bicolor*	1	0.0390625	1.700704	4.910171	<0 0001	sig <0.01

Appendix 4 continued.

From	To	Observed Count	Expected Count	S	Z	p-value (normal)	sig. level
Cunny Creek							
Beyeria viscosa	*Coprosma quadrifida*	1	0 081081081	1.255273	3 26913	0.001	sig <0 01
Beyeria viscosa	*Olearia argophylla*	1	0.162162162	0 942008	2.136474	0.033	sig <0 05
Beyeria viscosa	*Pomaderris apetala*	1	2 594594595	-1.10721	-2 4367	0 015	sig <0 05
Coprosma quadrifida	*Beyeria viscosa*	1	0.081081081	N/A	3.366502	0.0008	sig <0 01
Coprosma quadrifida	*Pomaderris apetala*	0	0 864864865	N/A	-2 52982	0 0114	sig <0 05
Olearia argophylla	*Beyeria viscosa*	2	0.162162162	N/A	4 756639	<0 0001	sig <0 01
Olearia argophylla	*Pomaderris apetala*	0	1.72972973	N/A	-3 39474	0.001	sig <0.01