

**Ecological and Biogeographical Correlates of Rarity in Two Narrow  
Endemics in Tasmania: *Spyridium microphyllum* (F. Muell. ex Reisseck)  
Druce and *Spyridium obcordatum* (Hook. f. ) W. M. Curtis**

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## ABSTRACT

*Spyridium microphyllum* (F. Muell. ex Reissek) Druce and *Spyridium obcordatum* (Hook. f) W. M. Curtis are narrow endemic shrubs which are confined to Tasmania and are rare within their present ranges. *Spyridium microphyllum* is an obligate seed regenerator, whilst *S. obcordatum* is apparently able to regenerate both by seed and by resprouting. Ecological and biogeographical explanations for rarity in the two species were investigated by analysing their biological, bioclimatic, phytosociological and phytochorological correlates.

*Spyridium microphyllum* was not significantly affected by grazing and is unlikely to be rare because of predation. *Spyridium obcordatum* is moderately to heavily grazed in summer but is able to recover biomass the following spring. Seedlings are likely to be particularly vulnerable. Seed production was not significantly affected at one site where the grazing trial was conducted, where rabbits were the main predator and the ground layer consisted of a high proportion of herbs and grasses. However, concentrations of native animals may significantly affect reproductive output where herbaceous food sources are scarce. Consequently, predation may contribute to rarity under these circumstances.

Phenological observations revealed markedly different patterns relating to flowering, fruit maturation and time to reproductive maturity, suggesting that the two species may have different evolutionary histories. *Spyridium microphyllum* flowers in mid to late summer and seed is released one year later. This may enable plants to avoid competition for pollinators in spring, as well as maximise seed storage in the soil when ant activity is highest. Although seeds are exposed to threats for most of the year after fertilisation, the same pattern is known from widespread *Spyridium* taxa and does not explain rarity in *S. microphyllum*. However, plants may be disadvantaged by this regime where there is a reduced seed bank. *Spyridium microphyllum* does not set seed for at least four years after germination and may be eliminated by a series of successive fires. *Spyridium obcordatum* flowers in early spring and produces seed within two months. In this respect, it is similar to a number of widespread taxa within the Rhamnaceae and other families. Plants become reproductively active within two years. Thus, phenological patterns do not explain rarity in this species.

Seed dormancy results from physical characteristics of the seed coat. Seed viability is high, and seed of both taxa germinate after scarification of the testa, or after stimulus by heat within similar ranges required to break dormancy in widespread congeners. In some instances, the two rare species responded to a wider range of heat stimuli than some widespread species. However, there were genecological differences in the germination behaviour of populations from different sites. In spite of these, rarity could not be explained by poor seed viability or lack of stimulus for germination.

The loss of soil stored seed may partially contribute to rarity in the two species. Seed burial trials revealed *S. microphyllum* seed is only partially retained in the soil. *Spyridium obcordatum* was less vulnerable to seed bank depletion. However,



losses are within the ranges recorded for other taxa and are replaced annually. Seed burial did not increase germinability in either of the two species. Consequently, loss of soil stored seed may be significant only if seed banks are not replenished annually because of repeated disturbance by fire or excessive predation.

An analysis of the geographic patterns of distributions of *Spyridium* taxa determined that centres of endemism and species richness within the genus are in the South West Province of Western Australia and in southern South Australia. Eastern Tasmanian *Spyridium* species comprise an outlying concentration of endemics. There are no endemic centres in eastern Australia. The majority of taxa had no topographic or edaphic preference but were mainly associated with heathland or shrubland. A comparison of the geographic and climatic distributions of *Spyridium* taxa enabled hypotheses to be constructed which might explain rarity in the genus. *Spyridium microphyllum* and *S. obcordatum* were geographically and climatically narrowly distributed. In respect of the latter, they were similar to some geographically widespread *Spyridium* taxa and it was concluded that the two species are unlikely to be entirely restricted by climate. Recent divergence, inadequate time for dispersal, drastically reduced ranges or poor competitive ability were more likely explanations.

Analysis of quadrat data using multivariate statistical methods showed that the two rare taxa are restricted by environmental conditions. Sites supporting the same species differ floristically and environmentally, and perturbations resulting from fire, soil disturbance or periodic flooding are influential events. Edaphic controls maintain environments where more competitive vegetation, especially trees and tall shrubs, are excluded. In combination, these characteristics ensure the perpetuation of shrub dominated vegetation supporting *S. microphyllum* or *S. obcordatum*. The frequency of such habitats in Tasmania and the range of habitats supporting populations, suggests that rarity in *S. microphyllum* and *S. obcordatum* cannot be attributed to confinement to a rare habitat. Thus, combinations of locally specific environmental conditions and interspecific competition, rather than a unique habitat, appears to be linked to rarity in both taxa.

A phytochorological analysis determined that the two *Spyridium* species are associated with aggregates of taxa with restricted ranges. *Spyridium microphyllum* was primarily associated with other narrow endemics or with rare non - endemics concentrated in eastern Australia. *Spyridium obcordatum* had a stronger relationship with taxa concentrated in southern and southwestern Australia, some of which are rare in Tasmania. Where soil disturbance was substantial at one site, also thought to have been a refugium for forests during the late Pleistocene, *S. obcordatum* was associated with taxa widespread in southeastern and southern Australia. The results suggested that sources of interspecific competition have a basis in the disturbance and biogeographical histories of sites.

Ultimate causes of rarity in *S. microphyllum* and *S. obcordatum* are best considered from a biogeographical viewpoint. *Spyridium microphyllum* is likely to be relictual under the present climate, having been a member of shrub dominated

vegetation formerly more widespread in Tasmania under more arid conditions than exist at present. *Spyridium obcordatum* populations are likely to have been more or less continuous as part of a Bassian flora which is now extinct, the relicts of which have been incorporated into coastal heathland or open rocky environments. Thus, the most parsimonious explanation for rarity in both species is temporal remoteness from optimal conditions. Stochastic events relating to local extinction, establishment and maintenance of populations have influenced their survival. Ecological explanations for rarity in the two species are most likely to be a consequence of their present relictual status. These relate to poor competitive ability under conditions of improved soil moisture, or in closed or undisturbed vegetation, and a lack of safe sites for regeneration. Land use practices since European occupation of Tasmania further endanger populations at present.

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## **CHAPTER 1**

### **PERCEPTIONS AND CAUSES OF RARITY AND THE NATURE OF THE PROBLEM**

#### **Introduction**

Nearly 17% of the vascular flora of Australia is rare or threatened (Briggs & Leigh 1988). However, there have been few studies that have highlighted the causes of scarcity and endangerment at the species level. With growing concern for the preservation of biodiversity, scientific interest in rarity has increased.

In the Australian island State of Tasmania there are many rare species within unique assemblages of endemic rainforest and alpine vegetation, whose taxonomic and biogeographic affinities are with ancient floras (Barlow 1980). Dry sclerophyll vegetation also harbours concentrations of rare Tasmanian endemic species. The origins of rarity in these species are largely unknown and their ecology and biogeography has received little attention. This study investigates causes of rarity in two narrowly endemic species, distributed in lowland eastern Tasmania. It investigates the putative biological, environmental, climatic and historical causes of their rarity.

#### **The ecological and biogeographical significance of rarity and endemism**

Rare species contribute to species richness and diversity and may account for a significant proportion of species rich floras. Consequently, they are an important element in studies of biodiversity and evolution. Species diversity is poorly understood, but is known to be related to a number of constraints such as isolation, speciation, habitat fragmentation and habitat diversity (Cody 1986). The ecology and biogeography of rare species are directly relevant to these studies.

Some rare species may be more vulnerable to the threat of extinction than common species by virtue of their biological or demographic attributes, such as poor reproductive effort or dispersal. Therefore, they have significance for conservation. The recent concern with species extinctions at both local and global scales has promoted renewed interest in rare taxa by scientists, nature conservation agencies and the public (Synge 1981; Davis *et al.* 1986; Briggs & Leigh 1988; Falk & Holsinger 1991; Eckersley 1994). Ecosystems continue to be threatened by land use practices which conflict with conservation values (Cody 1986) and further endanger taxa. Many contemporary ecological studies of rare species in Australia, including Tasmania, have been initiated in response to a growing pressure on plant

and animal biologists, biogeographers and ecologists to provide data necessary for management of threatened taxa. Much of this work has been directed towards conservation of taxa associated with dry sclerophyll forest and grassland, owing in part to the very poor reservation of these ecosystems, the fragmentation of originally larger tracts of vegetation and the high numbers of threatened species which they frequently contain (Kirkpatrick *et al.* 1988; Cropper 1989; Scarlett & Parsons 1989; Prober *et al.* 1990b; Wiltshire *et al.* 1992).

One other obstacle to plant conservation has been the absence of biological research and a reliance on theories and principles relating primarily to faunal ecology (Falk & Holsinger 1991). The response has largely been increased population dynamics and genetics research. Increased ecological and biogeographical input into rare species research is also needed, so that genetic heterogeneity can be more closely related to environmental relationships and variability. This is especially important in the formulation of reserve selection criteria and long term planning for conservation which, especially in consideration of global warming, should take into account evolutionary and biogeographical processes (Rebelo 1992).

Congregations of local and regional endemic taxa are known worldwide. Some are outstanding in their numbers and concentration and include the South West Province of Western Australia, the Cape Region of southern Africa and the alpine regions of central Africa, the Californian Floristic Province, the montane and Mediterranean regions of Europe, the northwest Caucasus Mountains; the Sino - Himalayan region; western Ecuador, Columbia and Panama (Kruckeberg & Rabinowitz 1985; Gentry 1986; Major 1988). The island floras of Madagascar, Hawaii, the Canary Islands, Corsica, New Caledonia and New Zealand also have a high endemic component. As a rule, local endemism is relatively low in the arctic and in deserts and highest in oceanic islands, mountain summits and the tropics (Kruckeberg & Rabinowitz 1985; Gentry 1986; Major 1988). However, it is apparent that temperate regions make a substantial contribution to the world's local and regional endemic flora.

In Australia, patterns of endemism and rare species distributions have been important in the interpretation of the past. Biogeographic and ecological analyses of endemic floras in Australia have generated hypotheses relating to former vegetation patterns, landscape evolution and climate change (Burbidge 1960; Hopper 1979; Kirkpatrick & Brown 1984a & b).

Although endemism might be expected as a feature of the Tasmanian flora, owing to its periodic separation from mainland Australia throughout the Quaternary, it is predominantly manifest at the species level. Tasmania does not possess high levels of endemism relative to the Southwest Botanical Province of Western Australia or the tropical rainforests of northeast Queensland (Burbidge 1960). There are no

families endemic to Tasmania and endemic genera comprise only seven per cent of the flora.

### *The distribution of rarity in Australia*

Degradation of Australian vegetation over the past 200 years has led to the extinction of about 100 species of vascular plants nationwide (Leigh & Briggs 1992). Approximately 17 per cent of the flora of Australia is rare or threatened (Briggs & Leigh 1988), the majority in southwestern Australia (Roe/Avon regions), the central and north coast regions of New South Wales, southeastern Queensland and the Cape York Peninsula (Leigh & Briggs 1992). High concentrations of threatened species also occur in southwestern Australia closer to the coast and in eastern Australia. Narrow or near narrow endemics comprise the majority of species. Habitat loss has been the prime cause of rarity in densely populated regions, Victoria being a good example, where rarity is concentrated in areas subject to intensive vegetation clearance (Scarlett & Parsons 1993).

In Tasmania, rare taxa occur throughout the State in grassy ecosystems (Kirkpatrick *et al.* 1988); coastal heath (Kirkpatrick 1977); wetlands (Kirkpatrick & Harwood 1983; Kirkpatrick & Glasby 1981); rainforest (Jarman *et al.* 1984); dry sclerophyll forest (Duncan & Brown 1985); alpine vegetation (Kirkpatrick 1986b); and buttongrass moors (Jarman *et al.* 1988). Narrow endemics are concentrated in seven areas hypothesised to be interglacial refugia (Kirkpatrick & Brown 1984a). These are thought to best approximate environmental conditions more widespread during the late Last Glacial.

Rare plants confined to specialised habitats such as alkaline pans (Jarman & Crowden 1978; Brown *et al.* 1982; Jarman *et al.* 1982) and ultramafic soils (Brown *et al.* 1986; Gibson *et al.* 1992) occur in western Tasmania. Rare eastern Tasmanian endemics occur on a variety of geologies within varying vegetation types. This apparent lack of geological specificity suggests that other specific environmental conditions may exist within broader plant associations, and that these favour rare species; or alternatively, populations of rare plants are maintained by stochastic environmental events within more or less static vegetation. Rare species might also be restricted by competition from other species or by historical factors.

### **Definitions and typologies of rarity and endemism**

Rarity is a state which describes the abundance of objects relative to others over time and in space (Drury 1980; Reveal 1981; Main 1982). Thus, changes in abundance and frequency can occur in the short or long term and are dependent on both the quantity and quality of habitable sites (Harper 1981). More recently,



concepts of rarity have been interpreted in terms of metapopulation theory, where species exploit habitats made locally available by stochastic population fluctuations in a static environment. Extinction has a direct relationship with population size and is the end result when exploitable habitat is no longer available or when environmental variability is catastrophic (Shaffer & Samson 1985; Strebel 1985; Hastings & Wolin 1989). Rarity may also arise if a species is unable to keep pace with habitat as it becomes available in the landscape (Thomas 1994).

Rabinowitz (1981) categorised combinations of geographic range, habitat specificity and local population size, drawing on observations that the occurrence of rare species can manifest as populations varying in size, habitat requirement and spatial distribution (Stebbins 1942; Drury 1974, 1980). Implicit in the scheme is a link with other geographic, environmental and historical phenomena which might, either singly or in combination, explain rarity. The typology consists of eight rarity categories. Species in large populations whose geographic range is also large, can occur in several habitats or in a specific habitat. Conversely, species with widespread geographic and habitat requirements might only occur in small populations. Populations of geographically restricted species may occur in four different ways. That is, they may be locally abundant within a particular habitat or in several habitats, or sparse within a particular habitat or several habitats. Rather than channelling preconceptions of rarity, the typology operates to challenge notions of uncommonness and the tendency to view rare plants as deficient in competitive advantages or ecological amplitude.

Harper (1981: p. 90) argues that the concept of rarity is largely subjective and is dependent on scale, that is on the breadth of "individual experience and on the range of narrowness of our special interests". He points out that judgements concerning rarity usually disregard the lack of concern plants have for political boundaries, so that their true geographic distribution and abundance may be ignored. In Australia, a distinction should be made between those species which are considered rare nationally and those which are designated rare for the purpose of conservation of regional flora. The latter have been termed 'pseudo rare' species, and may include species at the edge of their range rather than its centre (Rabinowitz, 1981).

Fiedler & Ahouse (1992) produced a classification of rarity which divided species into four classes, based on spatial distribution, measured in hectares, and temporal persistence (taxon age), measured as generation time in years. It then produces a classification of factorial combinations of short ( $10^0 - 10^3$  years) and long time ( $10^4 - 10^5$  years - equivalent to 500 generations) and narrow ( $<10,000 \text{ km}^2$ ) and wide ( $>500,000 \text{ km}^2$ ) ranges. The aim is to produce testable hypotheses in the context of combinations of these factors, rather than descriptive accounts. This is achieved by comparing causal hierarchies ranked as tiers and assigned to each of the four categories. The scheme is comprehensive and flexible but as yet has

limited use in Australia owing to the virtual absence of data, in particular fossil evidence, relating to age of extant taxa.

Scales of endemism range from taxa confined to microsites by virtue of highly specialised biological requirements, to continental distributions where their further spread is limited by geographic barriers to dispersal. Eighty percent of the indigenous Australian flora is endemic to the continent, with the remainder consisting mainly of taxa with distributions in Asia and the Pacific. However, most species belong to families most of which are also distributed more widely (Barlow 1981). Narrow endemics have a spatial distribution of less than 100 x 100 square kilometres (Briggs & Leigh 1988) and comprise a special form of rarity (Hodgson 1986c). This discussion will be confined to narrow endemism.

Endemics were classified according to their evolutionary standing or past distributions by European botanists in the late nineteenth and early twentieth centuries (Prentice 1976). Endemics were represented as either recently evolved (neoendemic) or relictual taxa (palaeoendemic).

Favarger & Contandriopoulos (1961 in Stebbins & Major 1965: p. 4-5) classified endemics into four categories on the basis of cytological data. Palaeoendemics are ancient taxa possibly undergoing the process toward extinction. They are high polyploid relicts which are frequently associated with rainforest, especially in the tropics, but are also known from temperate regions (Gentry 1986).

Schizoendemics have the same number of chromosomes as related taxa and are thought to have arisen simultaneously from the same ancestor. Patroendemics are the ancient diploid ancestors of more widespread polyploids. Apoendemics are derived from widespread diploid or lower polyploid parents. Vicariance is a common pattern in apoendemics. Stebbins & Major (1965) added two other elements to this classification: cryptoendemics which are either patroendemics or apoendemics but suffer from lack of systematic enquiry into the taxonomic consequences of their differing chromosome numbers and endemics which have not been sufficiently well studied to determine their true status.

### **Causes of rarity**

Postulated causes of rarity in higher plants have been regularly reviewed since early this century by Willis (1922); Griggs (1940); Stebbins (1942, 1980); Drury (1974, 1980); Harper (1981); Rabinowitz (1981); Kruckeberg & Rabinowitz (1985) and Fiedler (1986). The following discussion of the causes of rarity pertains only to higher plant taxa with unambiguous taxonomic status (Kruckeberg & Rabinowitz 1985; Fiedler 1986; Hopper & Coates 1990; Hopper 1994).

Fiedler (1986) reviewed the literature on causes of rarity since the nineteenth century and outlined the development of rarity theory until the present. She

concluded that from early beginnings concerned with the distribution of plants according to specific abiotic conditions, theorists began to consider rarity as a phenomenon primarily related to how recently a species had evolved.

Early twentieth century theories maintained that rare species were recently evolved having had little time to spread (Willis 1922), or were old, relictual taxa whose genetic resources were depauperate (Fernald 1926 in Fiedler 1986). Rare species may also have diverged spontaneously but lacked the genetic or biological stamina to persist. This view was popular in the 1930s and 1940s (Stebbins 1980) until botanists began to look at species' genetic resources. Stebbins (1942) proposed the notion of genetically depauperate taxa, incorporating the principle of competitive ability to explain the distributions of rare plants.

Responding to Stebbin's (1980: p. 82) call for a synthesised approach which took into account "...ecological factors, genetic structure of populations and past history of the evolutionary lines concerned..." Fiedler (1986) has proposed a synthetic method of evaluating factors which determine the commonness or rarity of a species. It incorporates earlier summaries which outline reasons for rarity (for example Harper 1981). The gene pool - niche interaction theory (Stebbins 1980) is thus expanded into a specific set of factors which can be used in the investigation of the causes of rarity. In brief, factors include: The age of the taxon; the genotype of the taxon; its evolutionary history; its taxonomic position; the ecology and population biology of the taxon; its reproductive biology; land use history including fire, exotic invasions and management practices; and recent human use (Fiedler 1986: p. 509). Some aspects of the scheme may work better for herbaceous taxa which are generally fast growing, reproduce generations in relatively quick succession and are easier to base glasshouse studies on than long lived, slow growing trees and shrubs. Fiedler has demonstrated that its application can produce a credible explanation for rarity in a selected taxon (Fiedler 1986, 1987).

### *Human impacts*

Piggott & Walters (1954) documented species with discontinuous distributions in open habitats in Britain and concluded that this could be explained by a combination of Glacial and Post Glacial edaphic and geomorphological processes, and by human disturbance during the Holocene. Since then the effect of humans has been given considerable attention in Britain and Europe (Ward 1981; Hodgson 1986a & b; Chapman *et al.* 1989). The history of human disturbance on ecosystems is also documented in the Mediterranean region, although difficulties exist with interpretation of the palynological data (Pons & Quézal 1985); Chile, California (Aschemann & Bahre 1977; ); southern Africa (Hall 1984; Deacon 1992); New Zealand (McGlone 1983) and Australia (Singh *et al.* 1981). The

history of ecological modification by fire, grazing or clearing is prominent in the literature, yet has received almost no attention by theorists of rarity.

It is puzzling why early North American theorists of rarity ignored the historical effects of humans on the landscape. To some extent, this may have arisen from the nature of the flora. The British flora contains relatively few endemics and explanations for rarity are best considered from the point of view of biological, geomorphological or edaphic controls, suggesting the restriction of rare species to rare habitats (Hodgson 1986a, b & c; Quinn *et al.* 1994). Human interference and the expansion of agricultural and later, industrial practices further modified plant distributions. Furthermore, the extent of environmental degradation in Europe is a constant reminder to ecologists of the devastating effects of human activities. Rarity elsewhere, such as California, South Africa and Australia is strongly linked to endemism and the ecology of rare species is considered principally from the perspective of abiotic factors. Large tracts of indigenous vegetation remained, or were preserved late in the nineteenth century as "wilderness", a concept which seldom takes into account past human occupation patterns and tends to reinforce assumptions of separateness between nature and human activity.

Notions of rarity and its investigation can be partly attributed to restrictions posed by cultural influences. The consequences of pre - European human activity on rare plant distributions has not been seriously examined in Australia, South Africa or North America, despite the fact that indigenous people are known to have used fire in conjunction with their economic activities during the Late Quaternary (Swain 1973; Clark, 1988; Singh *et al.* 1981; Deacon 1992). Reference to the consequences of Aboriginal burning is confined to fire sensitive species (for example Bowman & Harris 1993) but little attention is paid to the creation of heathland, shrubland and scrubs which frequently contain rare plants (Thomas 1992; Thomas & Hope 1994). In addition, the archaeological record in Australia is far from complete.

Habitat disturbance by people in comparatively recent times has frequently resulted in the confinement of rare tree and shrub species to remnant populations in niches such as fire - protected gullies or rocky hillsides. Rare herbaceous species are often distributed within vegetation with high economic potential, such as grassy dry sclerophyll ecosystems on fertile soils (Scarlett & Parsons 1982; Gilfedder & Kirkpatrick 1994a); whereas others occur in regions highly valued for urban, industrial or commercial development. The ranges of other taxa are reduced to remnants, with formerly widespread taxa becoming rare within a relatively short space of time. In particular, increased fire has induced rarity in a number of plant populations or further threatened rare plants (Cullen 1987; Scarlett & Parson 1993). The acquisition of rare species by collectors and horticulturalists has also contributed to rarity in some taxa (Moll & Grubb 1981).

The introduction of exotic flora and fauna has had an enormous impact in indigenous vegetation. However, there have been few studies in Australia on their effects on rare species, even though the consequences of grazing by introduced animals are relatively well understood (Williams & Ashton 1987; Auld 1990; Wilson 1990; Gilfedder & Kirkpatrick 1994b; Scarlett & Parsons 1993). Botanical invasions are documented in State floras and by some government agencies and their effects are beginning to be understood (Carr 1993; Humphries *et al.* 1994). Disturbance is a major agent which renders plant communities vulnerable to invasion, even though intermediate levels are generally considered beneficial and necessary for regeneration and the maintenance of species richness (Stuwe & Parsons 1977; Hobbs & Huenneke 1992).

#### *Environmental specificity and confinement to rare habitats*

Confinement to rare habitat may be a cause of rarity and is considered by many authors to be especially effective in promoting narrow endemism (Gentry 1986; Kruckeberg 1987; Cowling *et al.* 1992). Widely accepted interpretations of plant population sizes and distribution (for example Harper 1981) assume to some extent that although rare species come and go in time and space, they are distributed according to reasonably rigid laws of habitat partitioning, where one plant is best suited to a position within a continuously varying environment, and where it responds to, and performs best under specific conditions. Factors related to narrow or specialised physiological requirements of rare or restricted species or narrow endemics which are confined to rare habitats, such as cliffs, rocky outcrops or unusual soils or lithologies, or by a combination of factors have been documented by Bunce (1968); Denton (1979); Brooks (1987); Gehlbach & Polley (1982); Kruckeberg (1987); Prober & Austin 1990; van Wyk (1990); Coates & Kirkpatrick (1992); Cowling *et al.* (1992); Gibson *et al.* 1992; Matthews *et al.* (1993); Mayer & Soltis (1994).

However, this relationship is not always clear. Narrow endemism in Amazonia has been attributed to relictual status as a consequence of Pleistocene aridity (Colinvaux 1989 and Prance 1979 in Nelson *et al.* 1990) or alternatively, to edaphic specialisation (Gentry 1986). The argument is further confounded by the knowledge that some putative centres of endemism are artefacts of botanical collecting bias (Nelson *et al.* 1990).

#### *Reproductive performance, growth and ecophysiology*

Aspects of growth and reproduction have been investigated recently in a number of autecological studies. These have principally concentrated on aspects of basic biology and life history (Moll & Grubb 1981; Hall 1986; Hall & Parsons 1987; Auld 1990; Auld *et al.* 1991; Watson *et al.* 1994; Quinn *et al.* 1994) or

ecophysiology (Baskin & Baskin 1988; Baskauf & Eickmeier 1994). They frequently provide baseline information relating to the ecological and demographic status of species and may coincide with genetic investigations, since poor reproductive performance may indicate reduction in variation. In this case, reproductive failure is a likely consequence, rather than a cause of rarity.

Kunin & Gaston (1993) assessed the reproductive characteristics of rare plants and concluded that they tend to be autogamous and small seeded, especially in the case of narrow endemics. However, they also maintained that some characteristics may have arisen as a consequence of rarity. Some taxa are likely to have evolved adaptations to the conditions of rarity over evolutionary meaningful time, rather than differing from common species as a result of evolution.

### *Genetic fitness*

Estimation of patterns of genetic variation using enzyme electrophoresis has been used in recent investigations into the genetics of rare plant species and populations (Levin *et al.* 1979; Moran & Hopper 1983; Prober *et al.* 1990a & b; Cosner & Crawford 1994; Mayer & Soltis 1994; Prober & Brown 1994). These studies address the question of genetic diversity in rare species in relation to evolutionary history or range fragmentation and make invaluable contributions to gene pool conservation, systematics and taxonomy of rare species. Since these studies began, a number of species, both common and rare, have been identified which have low genetic diversity, especially where they are self compatible. Consequently, genetic studies alone may be inconclusive. Low genetic diversity can be inherent in a taxon or a consequence of small population size which has been limited by ecological or historical factors (Barretta & Kohl 1991; Huennecke 1991). More recently, they have combined with applied ecological studies to address the functional relationship between genetic diversity and the ecology of a taxon in relation to its competitive ability, reproductive success and potential for range expansion (Watson *et al.* 1994). They support the principle of conserving diversity and are necessary for management of populations so that increased inbreeding, or reduction in genetic variation, is avoided (Moritz *et al.* 1994).

### *Competition and co- existence*

The ability of a taxon to maintain its abundance and to be ecologically successful may rely on its ability to compete for resources, or to withstand competition from other organisms. Chapman & Rose (1982 in Chapman *et al.* 1989); Palmer *et al.* (1987); Calder *et al.* 1989 and Watson *et al.* (1994) assessed the advantages of disturbance and concluded that it increased the target species' ability to compete. Prober (1992) used greenhouse trials and reciprocal transplant trials to evaluate interspecific competition between a rare and a common eucalypt which were

mutually exclusive dominants of adjacent plant communities. She concluded that they were able to exclude each other because their competitive abilities varied according to site conditions. This suggests that habitat differentiation (Werner 1979) can explain rare species' distributions. Experimental studies of the competitive abilities of rare understorey shrubs are not apparent in the literature, probably because of difficulties related to slow growth and the identification of likely competitors among co - occurring taxa.

Some of the competition studies referred to above have shown that regeneration of rare species is critically influenced by random environmental disturbances. Co - existence or lottery models have been developed to explain how species which have similar requirements can share resources, and are purported to override interspecific competition (Shmida & Ellner 1984). These models assume that species compete for space, being "trophically equivalent" (Shmida & Ellner 1984), and that space is made available at random, thus allowing those with the most appropriate means of colonisation to succeed.

Hypothetically, co - existence between ecologically similar species can occur because plants "time-share" ecological space (Ellner 1987). A species can survive throughout many competitively unfavourable years by means of a low risk strategy, such as a soil seed bank that is replenished occasionally and is "stored" (Chesson 1986) during unfavourable periods. Under a favourable disturbance regime, a population can, in theory, always be restored. The disadvantages are that once mature adults have been removed and the soil seed bank is depleted or conditions are unfavourable for seedlings, then the species will become locally extinct. There is virtually no chance of re-invasion into the site because seed is unable to arrive from other populations and because the vacant niche is rapidly occupied by other plants. Co - existence applies to species which are active coincidentally and who experience stressful conditions periodically. For time-sharing, environmental fluctuations are needed: perturbations which are unpredictable and intermittent and which effect all taxa equally, so that species develop an "evolutionarily stable strategy" (Ellner 1987).

Time-sharing may explain rarity in some Australian taxa. Rare species have been observed to colonise areas following fire, floods or mechanical disturbance and in some cases have proliferated under artificial disturbance regimes (Gullan *et al.* 1990; Coates 1991; Pyke 1994). A spatial scale should also be considered: taxa which occupy relatively discrete patches within environmental space (locally abundant, *sensu* Rabinowitz 1981), rather than occurring in low numbers over a widespread area (constantly sparse *sensu* Rabinowitz 1981), may be favoured by disturbance if they are able to produce dense populations which are not as vulnerable to competition.

*Models of species diversity and abundance as ecological explanations for rarity*

The close relationship between the incidence of narrow endemism and high species richness is well known from tropical and temperate regions (Gentry 1986; Cody 1986; Major 1988). Cody (1986) has suggested a plausible method of determining the causes of rarity, drawing from concepts currently believed by vegetation theorists to influence the composition of plant communities. He postulated that in species rich (high alpha diversity) plant communities rarity may develop in some taxa because of resource allocation, thus leading to their occurrences at only low densities. This applies only to those communities which have putatively achieved equilibrium and are insulated from disturbance, predation and "resource superabundance" (p. 129).

Beta - diversity describes species replacements over environmental gradients and  $\beta$  - rarity is expressed in taxa confined to specific habitats such as edaphic endemics. It is correlated with spatial aspects of habitat and has little relationship with competition for resources or population dynamics.

Gamma - diversity describes changes in species within a habitat type with distance between sites. It is strongly linked to isolation and the potential for speciation within taxa as a result of stochastic and historical factors. Consequently,  $\gamma$  - taxa exhibiting are local endemics belonging to species rich genera which occupy wide ranging habitats.

The mechanisms which control diversity are poorly understood. High alpha - diversity is thought to result primarily from disturbance, niche diversity and habitat partitioning. Beta - diversity is difficult to separate from gamma diversity, especially where steep environmental gradients exist.

Recent attempts to model natural population dynamics by taking into account chaotic behaviour have been applied to animal populations, but have been slow to infiltrate the botanical sphere. According to Tilman & Wedin (1991: p. 653), there were at that time, no "ecological models to describe the conditions required for chaotic population dynamics...for perennial plants". Their work, using experimental grass populations, still appears to be the only botanical example of chaotic dynamics (Stone 1993). The application of the theory of chaotic dynamics may be of importance to the study of rarity, especially where small populations, such as those occupying refugia, are concerned (Vandermeer 1982). Chaotic population fluctuations may be significantly controlled by ecological factors, preventing or suppressing detrimental population fluctuations (May 1986; Stone 1993). Understanding these regulatory forces and the associated time delays which transpire prior to their effects being expressed could contribute to our understanding of rarity. By considering extinctions from the perspective of chaos dynamics, it may be possible to identify potentially detrimental controls operating within systems and separate these from seemingly stochastic behaviour.



### *Climate change, biogeographic and evolutionary history*

Rare species, in particular narrow endemics or taxa known to have been previously more widespread (palaeoendemics), may be restricted at present by unsuitable climatic conditions. Cycles of glaciation and deglaciation in Tasmania and New Zealand are thought to have contributed to concurrent cycles of extinctions and speciation, the contraction of some taxa into refugia and their inability to recolonise suitable habitat either because of competition or because they have had inadequate time to disperse (Kirkpatrick & Brown 1984b; McGlone 1985; Potts & Jackson 1986).

Failure to disperse may also be a consequence of neoendemism. Denton (1979) argued on the basis of cytological evidence, that taxa in the genus *Sedum* (section *Gormanina*, Crassulaceae) showed different levels of ploidy, ecological, morphological and reproductive attributes which indicated their evolutionary history and that the genus contained both relictual and recently diverged species. More recently, cladistic analyses have largely replaced her methods and in some cases have clarified evolutionary relationships (Prober *et al.* 1990a).

### **Rare species research in Tasmania**

Rare species research in Tasmania has been mainly directed towards management, because of the pressing need to recover or preserve populations and to identify threats to their survival (Kirkpatrick *et al.* 1980; Kirkpatrick *et al.* 1988; Fensham 1989; Fensham & Kirkpatrick 1989; Coates 1991; Lynch 1993). Response to fire and the importance of other forms of disturbance in maintaining species populations have been central to autecological studies (Coates 1991; Lynch 1993; Pyrke 1994). Morphometric studies of three rare eucalypts have sought to identify phenotypic variation within and between populations and to assess the adequacy of conservation of populations (Potts 1989; Wiltshire *et al.* 1992).

Another study identified predation by introduced fauna, habitat loss resulting from European settlement, invasion of populations by exotic flora and interspecific competition as causes of rarity in a non - endemic rare taxon in grassy dry sclerophyll vegetation (Gilfedder & Kirkpatrick 1993, 1994a & b).

Other more general theories attempt to explain the occurrence of Tasmanian endemics, are primarily concerned with the influence of past climate change on present distributions (Ladiges *et al.* 1983; Kirkpatrick & Brown 1984a & b; Potts & Reid 1985b). Whereas some species are thought to be occupying interglacial refugia others may have diverged only recently and are restricted because they have

had either too little time to expand from glacial refugia or have been restricted by competition.

However, rarity resulting from unfavourable environmental change can sometimes be inferred from ecological and biological data. This hypothesis has been tested using physiological correlates of an endemic species which is restricted to central eastern Tasmania but is not rare (Blake & Jordan 1993a & b; Kirkpatrick *et al.* 1991). Macro - climatic correlates can also be used to test which physical conditions constrain rare endemic species' distributions in eastern Tasmania compared to those of widespread congeners (Williams 1990).

### **Aims and rationale**

In Australia, of the roughly 190 species, subspecies and varieties of Rhamnaceae<sup>1</sup>, approximately 60 are either rare or threatened. To date, there have been few ecological or biogeographical studies of rare narrow endemics in Australia, one in the Rhamnaceae (Hall 1986; Hall & Parsons 1987) and none of any taxa in *Spyridium*.

The high level of rarity in the Rhamnaceae suggests that it is an important family in the study of rarity and narrow endemism. Genera in the family contribute significant proportions of species to floras noted for their floristic diversity and high levels of endemism in southern Africa and California. There is little or no ecological work on narrow endemic Rhamnaceae taxa apparent in the literature. Consequently, causes of rarity in the two species selected for this study may contribute to an understanding of rarity in the family elsewhere.

The two species were selected for the study because of their biogeographic and conservation significance. *Spyridium microphyllum* and *Spyridium obcordatum* are rare narrow endemic species<sup>2</sup> which occur in the dry sclerophyll forests and woodlands of lowland eastern Tasmania. They comply with Rabinowitz's (1981) criterion of locally abundant in several habitats but are restricted geographically. They are associated with concentrations of localized endemics, a high proportion of which are rare or threatened, nationally and in Tasmania. Narrow endemism is known in only one other *Spyridium* species in eastern Australia, with the majority of narrow endemics concentrated in southwestern West Australia and in southern South Australia. At the time the study was initiated, there had been no single species research in Tasmania, and very little in the rest of Australia, that addressed

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<sup>1</sup>Compiled from Briggs & Leigh 1988; Hnatiuk 1990; Harden 1990; Kirkpatrick *et al.* 1991; N. Walsh, pers. comm. B. Rye pers. comm.; K. Thiele pers. comm; W. Barker pers. comm.

<sup>2</sup>*Spyridium microphyllum* has a conservation status of 2VC-, denoting a geographic range of less than 100 km, vulnerable and adequacy of reservation unknown. It is reserved in the Douglas - Apsley National Park. The conservation status of *Spyridium obcordatum* is 2VCi, meaning narrowly endemic, vulnerable and inadequately reserved.

the ecology or biogeography of narrow endemics and the factors that might be responsible for their distribution and abundance.

The reproductive biology of rare species has been shown to influence their level of abundance and breadth of distribution. However, research has shown that the reproductive capacity of rare plants varies between species. In Australia, where biotic and abiotic disturbance to ecosystems is a major ecological determinant of species' survival, aspects of reproduction in narrow endemics which occur in disturbed vegetation are likely to be important. This thesis identifies phenological traits of the two rare species; their ability to recover from grazing; whether they are likely to form persistent seed banks; and how they differ from widespread *Spyridium* taxa in Tasmania with respect to seed germination, particularly after fire.

Confinement to a rare habitat is a widely accepted cause of rarity in some taxa. However, the habitats of narrow endemics are seldom quantified. An analysis of the floristic and abiotic components of vegetation supporting rare species will contribute to an understanding of their phytosociological and environmental correlates.

Biogeographic history may explain the present scarcity of narrow endemics, yet biogeographic studies of narrow endemics are almost entirely lacking in the literature. This study identifies the bioclimatic envelopes of rare and common *Spyridium* taxa. An analysis of the phytochorological composition of vegetation containing the two rare species is also carried out. The latter approach has not been previously used in rare plant research and may reveal patterns of species' distributions that contribute toward an understanding of rarity.

#### *Research program and thesis structure*

A preliminary reconnaissance of sites supporting populations of the target species revealed that they occupied diverse environments. These appeared to have little in common, either topographically, edaphically or floristically. They formed substantial populations which were reproductively active and producing seed. However, seedlings were absent or rare and plants appeared to experience variable levels of grazing. Consequently, an ecological and biogeographical research program was decided on, focussing on aspects of the reproductive ecology of the two species, the climatic and environmental correlates of populations and their phytosociological and phytochorological characteristics.

Chapter 2 discusses the general distribution and characteristics of the Rhamnaceae and previous research, and describes the physical features of the study area. In chapter 3, levels of predation, seed production, seed viability, stimuli for germination, and the ability to store seed in the soil are examined, to test the hypothesis that aspects of the reproductive performance of *S. microphyllum* and *S. obcordatum* may explain rarity in the two species. In

chapter 4 the geographic patterns of distribution of *Spyridium* taxa are compared with their climatic distributions. It explores the notion that rarity in *Spyridium microphyllum* and *S. obcordatum* is determined by climate. Chapter 5 determines the phytosociological relationships of vegetation containing *S. microphyllum* and *S. obcordatum* compared to vegetation where they are absent and tests the hypothesis that they are rare because of confinement to rare habitat. In Chapter 6, the phytochorological composition of vegetation containing *S. microphyllum* and *S. obcordatum* is analysed and compared to vegetation where they are absent. This aims to determine biogeographic patterns of species distributions and how they might relate to the current rare status of the two species. Chapter 7 draws together the evidence for ecological and biogeographical causes of rarity in *S. microphyllum* and *S. obcordatum*.

Botanical nomenclature follows Kirkpatrick *et al.* (1991) for dicotyledoneae, pteridophyta and gymnospermae, except for Asteraceae, Aspleniaceae, *Callistemon*, *Rhytidosperma*, *Cyrtostylis* and *Cerastium*, which follow Ross (1993). Monocotyledoneae follow Morris & Curtis (1994). Nomenclature for taxa occurring outside Tasmania follows individual State floras, unless recent taxonomic changes have occurred. In these cases, the appropriate authority will be included in the text. Nomenclature for Rhamnaceae genera follows Brummitt (1992).

## CHAPTER 2

### PROJECT BACKGROUND: THE DISTRIBUTION OF THE RHAMNACEAE, PREVIOUS RESEARCH AND PHYSICAL CHARACTERISTICS OF THE STUDY AREAS

#### The Rhamnaceae

##### *Diagnostic characteristics*

The Rhamnaceae (Buckthorns) are a cosmopolitan group of small trees and shrubs consisting of approximately 900 species (Conn 1983) and 52<sup>1</sup> genera world wide (Brummitt 1992). Climbers are uncommon in the family but the few that do exist testify to their close relationship with the Vitaceae or grape family (Chadefaud & Emberger 1960). Herbaceous species are confined to the genus *Crumenaria* (Chadefaud & Emberger 1960). The Rhamnaceae have simple, alternate but sometimes opposite leaves, with serrate or entire margins and frequently spinous branches. Stipules are often deciduous (Chadefaud & Emberger 1960; Engler 1964; Conn 1983). Flowers are small, regular, usually monoecious but sometimes dioecious and occur in tightly clustered inflorescences, loose cymes, racemes, panicles or singly (Conn 1983). There are 4 or 5 petals with an equal number of stamens positioned opposite, although in some taxa, such as *Pomaderris apetala*, petals are absent (Chadefaud & Emberger 1960; Curtis & Morris 1975). Petals may be hooded, enclosing the anthers within them (for example *Cryptandra*). The ovary is usually inferior or semi - inferior and less frequently superior (Chadefaud & Emberger 1960; Engler 1964; Conn 1983). Fruits may be a drupe or a capsule which releases seeds by septicidal or explosive dehiscence. The genus *Spyridium* consists of prostrate, medium or tall shrubs with tomentose branches and sessile flowers arranged in tightly clustered heads or loose corymbose cymes. One to three specialised bracts (floral leaves) subtending the flower head may be similar to the branch leaves or appear as conspicuous whitish structures. Leaves are alternate with scarious stipules. Petals are hooded, enclosing the stamens and the calyx lobes are usually persistent (Curtis & Morris 1975; Harden 1990). *Spyridium* has an inferior ovary and produces a capsule which separates septicidally into three pyrenes.

*Spyridium microphyllum* is a small shrub. It has very small, convex leaves, which are glabrous, soft and thick. The veins are indented on the upper leaf

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<sup>1</sup>Including *Stenanthemum*, not included by Brummitt (1992) but recognised as a result of more recent taxonomic research (B. Rye, Western Australian Herbarium, pers. comm.). One new genus, *Granitites*, may soon be erected (K. Thiele, Australian National Herbarium, pers. comm.).





Plate 2.1a. *Spyridium microphyllum*, occurring as a much branched, open shrub, typical in open habitat.



Plate 2.1b. *S. microphyllum*, flowering branches.

surface and the lower leaf surface is tomentose. Flowers are tightly clustered in heads at the ends of branchlets, and are surrounded by whitish bracts (Curtis & Morris 1975). *Spyridium microphyllum* occurs as a much branched, compact shrub in open situations, or as straggling individuals in shadier sites (Plates 2.1a & b).

*Spyridium obcordatum* is a delicate, prostrate shrub with brittle, wiry branches. It has obcordate, bright green leaves which have a glossy surface and are silky beneath. The white flowers are loosely clustered in small heads surrounded by brown bracts and subtended by an inconspicuous floral bract (Curtis & Morris 1975). Plants form large mats or scramble over rocks and embankments (Plates 2.2a & b). However, no plants were seen during the study which approached Hooker's description of "...large patches, 4-6 feet in diameter..." (Hooker 1860: p. 71).

### *Geographic distribution*

Rhamnaceae macrofossils from the genera *Rhamnus*, *Ziziphus*, *Paliuris* and *Ceanothus* are known from Upper Cretaceous, early Tertiary and Late Miocene sediments from Europe and North America (De Saporta 1888 in Pons 1981; Chadeaud & Emberger 1960), although some identifications have more recently been questioned by Pons & Quézal (1985). Ancestors of *Ziziphus* in Europe are thought to have originated from more or less xeromorphic southern Asian taxa (De Saporta 1888 in Pons 1981), with ancient pantropical disjunctions of ancestral types dating as far back as the Lower Cretaceous (Quézal 1985). *Paliuris* and *Rhamnus* belong to mesothermic flora identified from the Upper Oligocene and Oligocene - Miocene boundary (Anglada *et al.* 1978 in Pons & Quézal 1985), thought to be a precursor to present day Mediterranean flora (Pons & Quézal 1985). Vegetation in this group was refugial during glacials and did not become widespread until the Holocene, in conjunction with increased human disturbance (Pons & Quézal 1985).

The present day distribution of the family is worldwide, in temperate Europe and Africa including southern Africa and Madagascar, southeast Asia and the Himalayas, North and South America and the West Indies, the Pacific, New Guinea, New Zealand and Australia (Engler 1964). *Rhamnus* (Africa, Europe, Asia, Pacific North America) contains the largest number of species (about 155), followed by *Phyllica* (southern Africa, Madagascar, St Helena, Tristan da Cunha, Mascarene Island; approximately 150 species) and *Ziziphus* (Africa, west and southeast Asia including the Himalayas, tropical and subtropical Australia; approximately 100 species). Taxa from the principal genera, in addition to others, are well represented in regions frequently referred to as experiencing a mediterranean - type climate and prone to frequent fires. These include *Phyllica* in South African fynbos (Cowling & Holmes 1992; Kilian & Cowling 1992; van Wilgen & Forsyth 1993); *Ceanothus* in North American chaparral (Hanes 1981; Keeley 1987; Rice 1993); *Trevoa*, *Colletia*, *Retanilla* and *Talguenea* in Chilean matorral (Rundel 1981) and *Paliuris*, *Rhamnus* and *Ziziphus* in sclerophyllous European shrublands (Quézal 1981). The endemic





Plate 2.2a. *Spyridium obcordatum* (centre), growing at the edge of a rocky embankment.



Plate 2.2b. *S. obcordatum*, flowering branches



Australian genera *Spyridium*, *Stenanthemum*, *Siegfriedia*, *Blackallia*, *Trymalium* and *Cryptandra* frequently occur mainly within semi - arid climatic zones.

The family consists of 5 tribes, all of which have representatives in the 17 indigenous Australian genera (Engler 1964; Hnatiuk 1990; Brummitt 1992). Ventilagineae is represented by three endemic species of *Ventilago*, a genus of climbing shrubs or trees found in Australia in all States and the Northern Territory, except Victoria and Tasmania, in the inland tropics, semi - arid and arid areas (Harden 1990). Gouanieae consists of 2 rare endemic *Gouania* species confined to northeast Queensland (Briggs & Leigh 1988; Conn 1983). Zizipheae is represented by *Rhamnella* (1 species) and the widespread genus *Ziziphus*, comprising 2 indigenous and 1 introduced species which are distributed across northern Australia in coastal monsoon vine thickets, as well as drier deciduous vine thickets and semi - evergreen vine forest (Brock 1988; Conn 1983; Hnatiuk 1990; Adam 1992). *Ziziphus oenoplia* frequently occurs on steep rocky slopes and rock outcrops (Brock 1988; Adam 1992).

In Australia, Colletieae contains 2 species, both in the genus *Discaria*. Both species are rare and endemic to eastern Australia (Briggs & Leigh 1988) although the genus has what is frequently referred to as a "Gondwanan" distribution (Hall & Parsons 1987), having representatives in New Zealand and South America.

The Australian Rhamneae include *Alphitonia*, *Colubrina*, *Emmenosperma*, *Schistocarpha*, *Sageretia*, *Pomaderris*, *Cryptandra*, *Blackallia*, *Siegfriedia*, *Trymalium* and *Spyridium* (Engler 1964). *Alphitonia* consists of 6 species, including 4 endemics and occurs across the north of the continent in tropical rainforest forest, woodland and vine thickets (Gillison 1987; Brock 1988; Harden 1990; Adam 1992; Wheeler 1992) and as far east as New South Wales in open eucalypt forest and dry, littoral subtropical and temperate rainforest (Floyd 1980; Harden 1990). *Alphitonia whitei* occurs in mature rainforest whereas *A. excelsa* is known from both coastal rainforest as well as from dry scrubs further inland with other rainforest taxa (Gillison 1987).

*Emmenosperma* consists of two endemic species indigenous to temperate and subtropical rainforests (Floyd 1980) or tropical savannah, woodland and vine thickets (Brock 1988). *Colubrina* is an almost pantropical genus, confined in Australia to one species in North Queensland (Conn 1983). *Rhamnella* and *Schistocarpha* is also confined to North Queensland (Hnatiuk 1990). The latter is poorly known in Australia (Briggs & Leigh 1988) but the genus extends as far as the Himalayas (Sareen *et al.* 1974).

*Pomaderris* consists of approximately 60 taxa and is found in all States but not in the Northern Territory, as well as in New Zealand. It attains its greatest diversity in eastern New South Wales and eastern Victoria along the Great Dividing Range. *Cryptandra* is a large genus endemic to Australia and until recently was thought to contain about 40 species. However, recent taxonomic work has shown that in fact these comprise taxa also belonging to

*Stenanthemum* and two species which are now included under *Spyridium* (K. Thiele, pers. comm.). Nevertheless, the group still has a very wide distribution in all States but not the Northern Territory, predominantly in heathlands and shrublands. These include heaths in semi - arid southern Australia and in subtropical southeastern Queensland. *Trymalium* and *Spyridium*, which contain about 13 and 40 species respectively (Hnatiuk 1990; K. Thiele, B. Rye pers. comm.), are confined to southern Australia in shrublands, woodland and open forest. *Blackallia* is endemic to the South West and Southwestern Interzone Provinces in Western Australia in semi - arid and arid vegetation, and *Siegfriedia* to southwest Western Australia (Pate & Beard 1984).

The Rhamnaceae in Tasmania comprises *Discaria*, *Pomaderris*, *Cryptandra*, *Stenanthemum* and *Spyridium*, having a total of 26 species, subspecies and varieties (Kirkpatrick *et al.* 1991). Regional endemism occurs only in *Cryptandra*, *Stenanthemum* and *Spyridium*.

*Discaria pubescens* is now found only on the Central Plateau. From a former distribution which included the Fingal and Derwent Valleys and Midlands, the east coast and southeast, its range has been considerably reduced. This decline is undoubtedly due to agricultural clearing.

There are no Tasmanian endemic species in the genus *Pomaderris*, although most (*P. aspera*, *P. elachophylla*, *P. intermedia*, *P. oraria* ssp. *oraria*, *P. paniculosa* ssp. *parvifolium*, *P. phyllifolia* var. *phyllifolia*, *P. racemosa* and the coastal taxon *P. aff. apetalata*) are restricted geographically or if widely dispersed, consist of rare, localized populations. There are three common species. *Pomaderris apetalata* is probably the best known Tasmanian Rhamnaceae. This species is a component of a number of vegetation types, including the margins of dry sclerophyll forest, coastal and riparian scrub, but is most frequent in gaps arising after environmental perturbations in wet forests or in gullies. *P. elliptica* and *P. pilifera* occur over most of the island, but predominantly in the east in dry sclerophyll vegetation.

*Cryptandra* consists of three species plus one undescribed species. *Cryptandra alpina* is endemic to areas above 600 metres on the Central Plateau in alpine heath, while *C. exilis*, which is easily confused morphologically with the former species, is endemic to the East Coast and also occurs in heathland. Its known distribution consists of a series of disjunct populations from the Tasman Peninsula to St Helens in the northeast. *Cryptandra amara* is relatively widespread in eastern mainland Australia but forms localized populations in grassy vegetation in central and eastern Tasmania. *Cryptandra* sp. *nova* is endemic to Schouten Island off the East Coast. Except for *C. alpina*, all are considered rare or threatened (Kirkpatrick *et al.* 1991).

Tasmanian species of *Spyridium* are a diverse group. There are eight species including five endemics. Non endemic taxa are *S. parvifolium*, *S. vexilliferum* and *S. eriocephalum*. *Spyridium parvifolium* consists of two varieties, *S. parvifolium* var. *parvifolium* and the less common *S. parvifolium* var. *molle*, although the latter is a doubtful taxon. *S. parvifolium* is common in Victoria

and South Australia in open forest and woodland, but less common in southeastern New South Wales. *S. vexilliferum* is rare (*sensu* Kirkpatrick *et al.* 1991) in Tasmania with a mostly coastal distribution in the northwest and east, with one inland population on infertile lateritic sands in the northern Midlands. It is common in coastal Victoria and South Australia. *Spyridium eriocephalum* has the most remarkable distribution of all *Spyridium* species which occur in Tasmania. It is only known at present from the Risdon Hills near Hobart, although Hooker (1860), Bentham (1863), Rodway (1903) and Curtis & Morris (1975) all record the species from the South Esk near Launceston, where it has been confused with *S. ulicinum*. Rodway and Curtis also cite its distribution as including the east, north and northwest. There are no specimens in the Tasmanian Herbarium and it is likely that these records are *S. vexilliferum*. Elsewhere, the nearest population is near Bacchus Marsh west of Melbourne, and in South Gippsland near Mt Howitt. However, it is common in mallee<sup>2</sup> shrubland in the Murray Basin. All three non endemic taxa are at the edge of their range in Tasmania.

All endemic taxa are confined to eastern Tasmania, except for *S. gunnii* which is a medium shrub in riparian rainforest, as well as eucalypt woodland or shrubland on ultramafics in the west of the State. *Spyridium obovatum* is a medium to tall shrub and consists of two varieties, *S. obovatum* var. *obovatum* and *S. obovatum* var. *velutinum*. Both are found in the central East Coast region and southeast, with *S. obovatum* var. *obovatum* extending further south to the Tasman Peninsula. *Spyridium ulicinum* is a medium shrub confined to cooler areas in the southeast and the lower reaches of the Central Plateau, with one record from Ben Lomond in the north east.

#### *Rarity in the Australian Rhamnaceae*

Rhamnaceae have been identified in all States as rare at the national level, but not in the Northern Territory (Briggs & Leigh, 1988). Western Australia (approximately 30% of the Western Australian Rhamnaceae) has the highest percentage, followed by New South Wales (25%), Tasmania (23%), Queensland (21%), South Australia (18%) and Victoria (18%). In addition to the national classification (Briggs & Leigh 1988), Victoria has adopted a scale of rarity at the State level and on this basis has identified 21 species (38%) of the family in Victoria which are rare or threatened (Gullan *et al.* 1990).

*Pomaderris*, *Cryptandra* and *Spyridium* are the most diverse genera and contain the highest numbers of rare or threatened species respectively on a national level. However, the distribution of the three genera are quite distinct. Whereas *Pomaderris* is concentrated in southeastern Australia, *Spyridium* is most diverse in southwestern Western Australia and southern South Australia. *Cryptandra* and *Stenanthemum* are more widespread, with centres of diversity

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<sup>2</sup>The term mallee describes multi stemmed eucalypt species, generally less than 8 metres high and dominant in semi - arid shrublands in Australia.

in southwest Western Australia and southeast Queensland, including about 40 rare or threatened taxa. *Spyridium* contains approximately 12 rare or threatened species (Briggs & Leigh 1988; B. Rye & K. Thiele pers. comm), and at present *Cryptandra* and *Spyridium* account for most of the rare Rhamnaceae across southern mainland Australia and Tasmania. *Trymalium* contains five rare or threatened species. *Siegfriedia* is a rare monospecific genus endemic to sandplain heath in Southwest Western Australia (Pate & Beard 1984). Rarity in southeastern Australian Rhamnaceae can be attributed primarily to *Pomaderris*. In sub - tropical and tropical Queensland, a mixture of tropical genera (*Gouania*, *Sageretia*) and otherwise autochthonous temperate genera (*Cryptandra*, *Pomaderris*, *Discaria*, *Trymalium*) account for most rare Rhamnaceae, although rarity is highest in the latter group.

Six Tasmanian Rhamnaceae are rare or threatened nationally, including three *Spyridium*. On a State-wide basis, there are a total of 13 species which are rare or threatened, including six *Spyridium* species. *Spyridium microphyllum* and *S. obcordatum* have two of the most restricted distributions within the Tasmanian Rhamnaceae. *Stenanthemum pimeleoides* is equally restricted.

#### *Research relating to the Rhamnaceae in Australia and overseas*

The Rhamnaceae have received little attention in the literature from ecologists, relative to the global distribution of the family. Californian, South African, European and Chilean ecologists have provided the majority of ecological research, specifically in relation to the fire and reproductive ecology of mediterranean - type taxa (Keeley & Zedler 1978; Keeley 1987, 1991; 1992a; Kilian & Cowling 1992; van Wilgen & Forsyth 1993). There have also been broader studies or overviews of the phytosociological, physiognomical, biogeographical and ecological relationships of vegetation containing Rhamnaceae (for example Kirkpatrick & Hutchinson 1980; Boucher & Moll 1981; Quézal 1981; Rundel 1981; Arroyo & Maranón 1990; Batianoff *et al.* 1991).

A number of cytological, morphological, chemotaxonomic, reproductive and descriptive studies have been undertaken (Sareen *et al* 1974; Harvey & Braggins 1985; van Wyk & Schrine 1986; Boyd *et al.* 1990; Viswanathan 1990; Zygadlo & Guzman 1991; Medan & Hilger 1992; Tourn *et al.* 1992; Zietsman & Botha; 1992).

The genus *Discaria* has attracted the most widespread interest from both taxonomists and plant biologists. Tortosa (1983) has undertaken a major taxonomic revision of the genus. Other work of interest includes morphological and anatomical studies (Medan 1986) and investigations of reproductive biology or biochemistry (Tschesche *et al.* 1980; Medan 1985, 1991; Medan & Hilger 1992). The New Zealand species, *D. toumatou* has received much attention, probably because of its occurrence on agricultural lands. Studies include reproductive biology, distribution, taxonomy, ecophysiology and aspects of management (Scott 1986). *Discaria* has been an

object of curiosity to Australian botanists for many years (Willis 1942b, 1955; Lunt 1987). However, aspects of the ecology and biology of *D. pubescens* and *D. nitida* have only been recently investigated (Hall 1986; Hall & Parsons 1987; Coates 1991).

In Australia, work on the Rhamnaceae to date has been largely confined to taxonomic studies, (Willis 1942a; Walsh 1988, 1989, 1990a & b; Barker & Rye 1993), with work in progress (B. Rye in prep; K. Thiele in prep). The Australian literature provides little information on other Rhamnaceae genera, and is mainly restricted to broad scale observations of species' distributions (Floyd 1980, 1990) or are mentioned where they are a component of major ecosystems (Adam 1992). A limited amount of information has resulted from attempts to rehabilitate land after disturbance by mining in northern and western Australia, where nitrogen-fixing pioneer species such as *Alphitonia excelsa*, *Trymalium ledifolium* and *Spyridium spathulatum* (formerly *Trymalium spathulatum* F. Muell.), have been used by mining companies to stabilise disturbed land (Fox *et al.* 1987). Nitrogen-fixing root nodules are known to occur in several genera of Rhamnaceae (D. Medan, University of Buenos Aires, pers. comm.) or can be induced by inoculation (Hall & Parsons 1987). This phenomenon is significant in view of the ability of many Rhamnaceae (including rare species) in Australia and elsewhere, to establish in areas after disturbance, or to behave as post-fire colonisers (Keeley 1987; Gullan *et al.* 1990). A particularly interesting occurrence is that of *T. ledifolium* which colonises *Phytophthora* affected sites in Western Australia jarrah forests (Fox *et al.* 1987). Rhamnaceae in Tasmania are also known to be resistant to the fungus (F. Podger, CSIRO, pers. comm.).

## **Previous ecological and biogeographical research in Tasmania**

### *Historical perceptions of endemic flora in lowland eastern Tasmania*

The vegetation of the drier parts of Tasmania is seldom referred to in the literature, or given only brief mention (for example Barlow 1981). One of the earliest observers to consider the flora biogeographically was J. D. Hooker. Hooker assessed, correctly, that the autochthonous element of Tasmania's flora was similar to that of Victoria but was mostly interested in the relationships between the western Tasmanian flora and that of lands of similar latitude (Hooker 1860). Drawing on the work of two of his contemporaries, Darwin and Wallace, as well as his own observations, he realised that the present day distribution of taxa could only be accounted for by climate change and geological upheaval. Hooker estimated an endemic component of about 25% (280 out of a total of the 1093 species known in Tasmania at the time). In two three month sojourns with the Tasmanian collector and naturalist Ronald Gunn, Hooker travelled around the Hobart area (Hooker 1860; Burns & Skemp 1961; Buchanan 1988). The localized, shrubby endemics of the central east were mostly unknown to Gunn, he never having ventured to this region, although the

area to the south and the central north coast were familiar to him (Buchanan 1988).

In 1836, Charles Darwin was mostly interested in the view from Mt Wellington and the fate of indigenous Tasmanians at the hands of the combined forces of the occupying British army and colonists (Darwin 1961). He makes virtually no comment on the vegetation or its relationships with taxa elsewhere, despite his extensive travels around the South American seaboard. Other early eminent visitors including Jacques - Julien Houtou de Labillardière in 1793 and Robert Brown in 1804, concentrated on collecting. In the prevailing late eighteenth and nineteenth century climate of scientific discovery and its emphasis on empirical research, their interests lay chiefly in accumulating as many specimens as possible, including those taxa which may have had agricultural or economic potential; a matter for prime consideration in an age of international exploration and colonisation (Stafleu 1966).

Brown appears to have had only limited interest in the origins and affinities of Tasmanian vegetation. However, after a voyage plagued by nautical nightmares, the loss of a large number of specimens and being marooned in Port Jackson and then in Van Diemens Land, during which time he ascended Mount Wellington 10 times only to find nothing new (Stearn 1962), it is hardly surprising that Brown is now criticised as less than enthusiastic (Mabberly 1985; Thomas 1992). All botanists collected extensively, with Labillardière collecting *Pomaderris apetala*, and Brown making the earliest collection of a rare member of the Rhamnaceae, *Discaria pubescens*, from New Norfolk in the Derwent Valley.

#### *Current botanical research*

Whereas botanical research in cool temperate rainforest in Tasmania has been more or less ongoing since the late 1960s (for example Jackson 1968; Mount 1979; Bowman & Jackson 1981; Brown & Podger 1982; Jarman *et al.* 1984; Read 1985; Cullen 1987; Read & Hill 1988; Kantvilas & Minchin 1988; Shapcott, 1993), research into dry sclerophyll ecosystems is relatively recent. The first serious attention to be given to the dry country endemic flora was by Kirkpatrick *et al.* (1980) who conservatively estimated 59 endemic taxa from the Central East Coast, approximately 11% of the total endemic flora in the State. This figure is more likely to be in the order of 65-70 taxa following more recent taxonomic changes and surveys (for example Orchard 1981; Duncan & Brown 1985; Crowden 1986; Williams 1989; Williams & Duncan 1991; Morris 1991a & b; Barker 1991). State wide surveys identified "centres of endemism" containing groups of taxa whose north - south and east - west geographic distribution was less than 100 km (Kirkpatrick & Brown 1984a; Kirkpatrick 1994). Seven centres were recognised, including four at altitudes below 600 m in the dry eastern half of the State. *Spyridium microphyllum* and *S. obcordatum* occur in central eastern and central northern centres respectively. A centre is recognised on the basis of 10 by 10 kilometre grid squares whose

local endemic component is in excess of two species per square, with squares clustering to form groups.

From the late 1970s to the present, most botanical inquiry in lowland eastern Tasmania concentrated on describing and documenting vegetation types. Some of this work was aimed at management of State Reserves, some aimed to identify sites of significance or to relate vegetation patterns to macro - environmental factors (Brown & Bayly - Stark 1979a & b; Kirkpatrick 1977, 1981, 1986a & b; Kirkpatrick & Wells 1987; Kirkpatrick *et al.* 1988; Brown & Duncan 1989; Fensham 1989; Fensham & Kirkpatrick 1989; Askey - Doran 1993); or was undertaken because of a growing pressure on natural areas by industry, in particular forestry (Brown & Buckney 1983; Duncan 1983; Williams 1989; Coates 1993; Askey - Doran & Fry 1994). Few of these studies address the biogeographical relationships of Tasmanian dry sclerophyll vegetation.

## The study areas

### *Spyridium microphyllum*

#### *Geographic location*

Past and present herbarium and survey records indicate that *Spyridium microphyllum* is naturally confined to the central east coast of Tasmania between 41° 45' and 42° 37' south and 147° 53' 148° 15' east, at altitudes between 20 m and 640 m (Fig. 2.1). Populations are concentrated on the Swan, St Pauls and Apsley Rivers and in the Douglas - Apsley National Park, northwest of Bicheno. It has also been recorded from Hardings Falls on the upper Swan River. A single plant was observed at Bald Hill in the Eastern Tiers west of Swansea, and one disjunct population occurs at the Thumbs near Orford. Most populations have been recorded in the last 10 years, except on the St Pauls River, where the first collections were made by Rodway in 1897. Searches located all known populations other than at Hardings Falls and along the Apsley River where there had been a recent fire, suggesting that this population may not have re-established.

The Swan River, Thumbs and Douglas Apsley populations are robust and consist of reproductively mature plants approximately one metre high. The number of plants exceeds 1,000 at all three sites. At the Swan River, colonies are distributed along the river banks for approximately 20 km. At the Douglas - Apsley they occur over an area of approximately 0.3 km. The Thumbs populations are smaller, consisting of three stands approximately 30 metres in diameter. At the St Pauls River, *S. microphyllum* populations have been encroached upon by heavy infestation of gorse (*Ulex europaeus*) and sweet

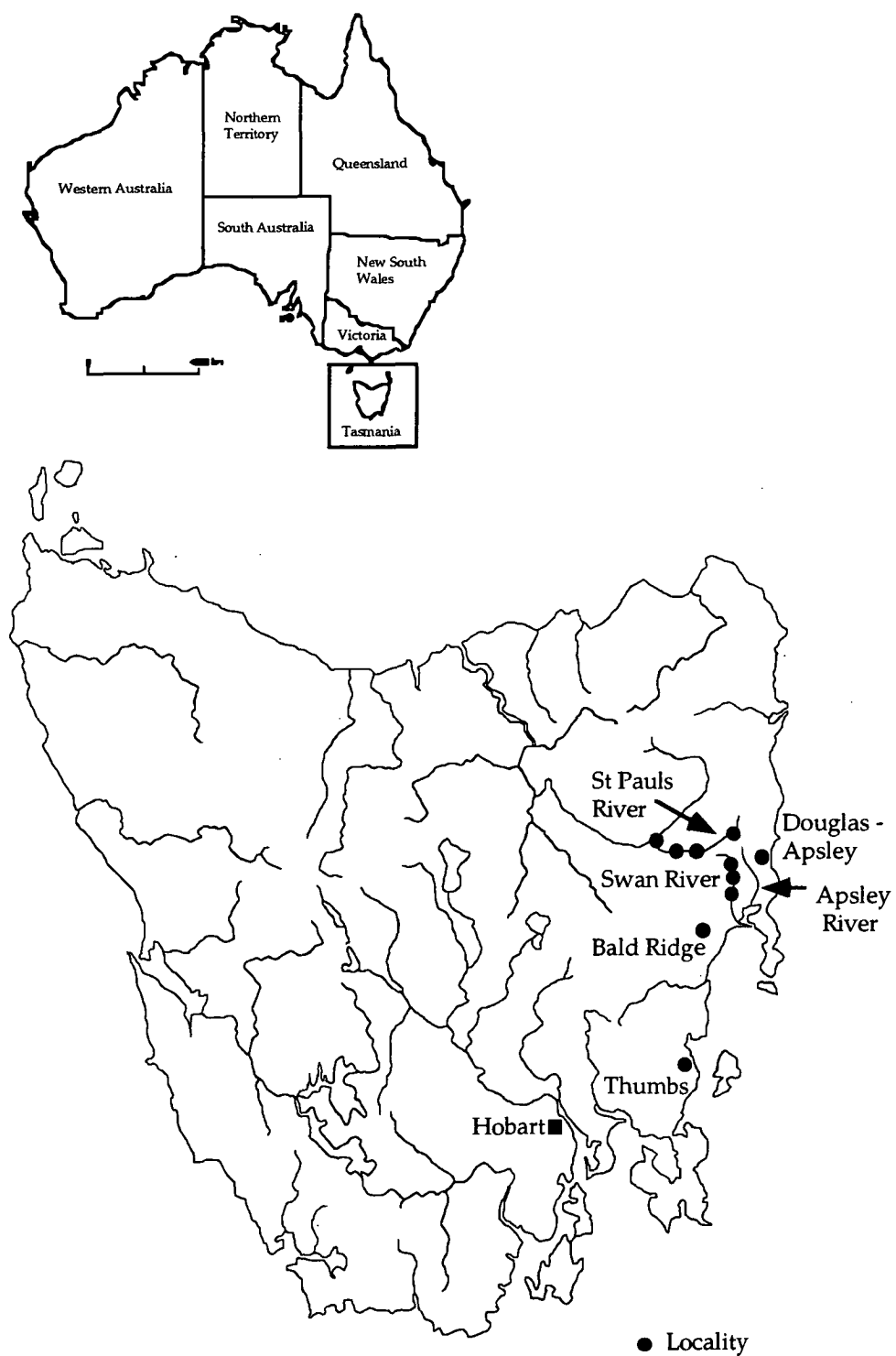


Figure 2.1. The distribution of *Spyridium microphyllum* and locations of the study areas.



briar (*Rosa rubiginosa*), and the general loss of indigenous vegetation resulting from land clearance has forced extant populations to occupy a narrow strip close to the river's edge.

### *Geology and landforms*

The geology of the region includes Jurassic dolerite, Triassic sandstone, Devonian granite, Cambrian mudstone, Tertiary basalt, Quaternary and Tertiary deposits. *Spyridium microphyllum* occurs on dolerite at all sites, except along the St Pauls River, where it is confined to clay alluvium on the boundary of granite and basalt, or on Cambrian mudstone (Mathinna beds). Deeper soils are dark brown loam or clay loam developed over bedrock or on exposed slopes consist of duplex soil having a stony clay loam surface over a yellowish brown clay (Davies 1988).

Landforms of the central east coast can be broadly categorised as coastal plains, the Eastern Tiers escarpment and dissected plateau terrain. *Spyridium microphyllum* populations are associated with ridges or hill crests, and with exposed dolerite rock plates. Alternatively, plants occur within, or close to the riparian zone where they are associated with steep, rocky or eroded slopes, blocks of dolerite bedrock or eroded river banks.

### *Climate*

*Spyridium microphyllum* populations experience a mild subhumid to humid climate with a mean annual precipitation of 714 mm distributed more or less evenly throughout the year but with a subdued spring maximum. Mean annual temperature is 11.7°C (Table 2.1). Estimates are derived using BIOCLIM (Busby 1986b) and are discussed in detail in chapter 4.

### *Vegetation*

The central east coast supports a diverse flora including approximately 65 - 70 endemics. Almost half of these are confined to, or concentrated within the region. A wide range of vegetation types has been recognised, which include relict rainforest and closed forest (Duncan 1983; Neyland 1991); coastal heath (Kirkpatrick 1977); dry sclerophyll vegetation (Kirkpatrick 1981; Duncan & Brown 1985); riparian associations (Duncan 1983); scrub, wet heath and sedgeland (Kirkpatrick *et al.* 1980).

Rare and threatened taxa are frequently concentrated within riparian vegetation, on isolated, rocky ridges which are often protected from frequent fires, or in gaps within forest where canopy cover is either minor or absent, owing to disturbance or rocky soils (Kirkpatrick *et al.* 1980; Kirkpatrick 1981; Askey - Doran 1993). Localized communities which contain rare or restricted species

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
<b>Minimum temperature (°C)</b>	10.5	11.2	9.5	7.7	5.3	3.2	2.8	3.6	4.8	5.8	7.6	9.1
<b>sd</b>	1.0	1.0	1.0	1.0	1.0	0.9	0.9	0.9	1.0	1.0	1.0	1.0
<b>Maximum temperature (°C)</b>	22.0	22.3	20.2	17.5	14.1	11.7	11.3	12.1	14.0	16.0	17.8	19.7
<b>sd</b>	1.0	0.9	1.0	1.1	1.1	1.1	1.2	1.2	1.1	1.0	1.0	1.0
<b>Precipitation (mm)</b>	47.0	55.0	58.0	65.0	64.0	66.0	59.0	59.0	50.0	62.0	60.0	69.0
<b>sd</b>	6.7	12.2	10.5	14.5	13.1	12.2	13.0	16.0	8.8	10.7	15.0	13.3

Table 2.1. Mean monthly temperature and precipitation estimates at *S. microphyllum* sites (n = 17) derived from BIOCLIM.

are often dominated by shrubs, with eucalypts either absent or present only in low density.

*Spyridium microphyllum* populations occur in dry sclerophyll forest, shrubland or scrub. Dominant forest taxa are *Eucalyptus pulchella*, *E. amygdalina*, *E. viminalis* and occasionally *Callitris rhomboidea*. Scrub and shrubland consists of small trees or tall shrubs, and Tasmanian endemics. Typically, these are *Acacia mucronata*, *Melaleuca pustulata*, *Leptospermum grandiflorum*, *Spyridium obovatum*, *Grevillea australis* and *Epacris tasmanica*.

### ***Spyridium obcordatum***

#### *Geographic location*

*Spyridium obcordatum* is restricted to a small area in northern Tasmania between 41° 04' and 41° 13' south and 146° 31' and 146° 46' east at altitudes between 40 and 100 metres (Fig. 2.2). Four known populations occur in State Forest at Dans Hill, near the town of Beaconsfield, on private property at Greens Beach and in the Asbestos Range National Park in the West Tamar area; and to the west on Crown Land near Hawley Beach. The earliest collection was made by Ronald Gunn in 1843 from the Asbestos Hills, probably in the Dans Hill area. Other collections cite Yorktown. This population has not been found and may also refer to the Dans Hill population. A population recorded from West Head near Greens Beach in the mid nineteenth century was not relocated. Searches of the area reconfirmed herbarium records for the Greens Beach and Asbestos Range populations. However the Hawley population was not known until 1991, when it was discovered by field naturalists. Extensive searches in the West Tamar area failed to locate any previously unknown populations. There are no records for the Bass Strait islands (P. Cullen, pers. comm.).

The Dans Hill, Greens Beach and Asbestos Range populations consist of colonies comprising in excess of 1,000 plants. At Dans Hill, there are four colonies known from the general area. However, the Greens Beach population is threatened with local extinction by a housing development. The Hawley population is small (approximately 100 plants), consisting mainly of large individuals.

#### *Geology and landforms*

The geology of the region is extremely diverse (Burrett and Martin 1989). *Spyridium obcordatum* has no geological preference within its range but is restricted to specific rock types at individual sites. It is most prolific at Dans Hill on ultramafic soils derived from rocks of Cambrian age containing high levels of ferromagnesium minerals and comprising layered serpentine pyroxenite

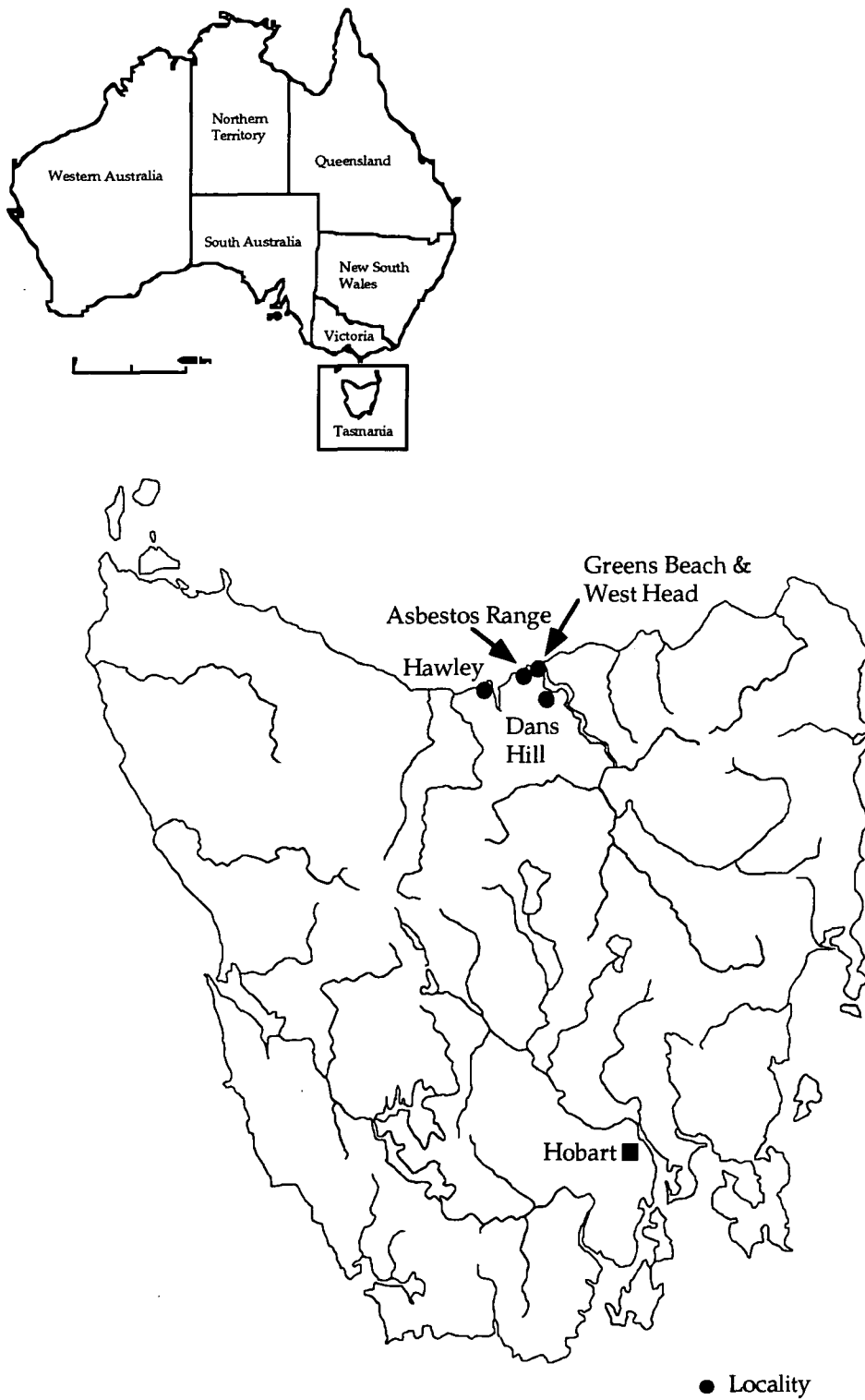


Figure 2.2. The distribution of *Spyridium obcordatum* and locations of the study areas.

as the principal rock type (Burrett and Martin 1989). It is absent from other geologies in the immediate vicinity including Cambrian sedimentary rocks, Tertiary ironstone and Tertiary and Quaternary sands and gravels. At Greens Beach and at Hawley it is found on Jurassic dolerite crests which outcrop from Tertiary sands. At Asbestos Range National Park, *S. obcordatum* forms a localized community on Precambrian schists.

Topographically, the central north coast consists of rugged steep and rocky hills or coastal headlands, gently undulating foothills and forested coastal plains. *Spyridium obcordatum* is associated with low hills which are open and rocky, or coastal headlands.

### *Climate*

*Spyridium obcordatum* populations experience a temperate, humid climate, with a mean annual precipitation of 850 mm and a mean annual temperature of 12.4°C (Table 2.2). Estimates are derived using BIOCLIM (Busby 1986b) and are discussed in detail in chapter 4.

### *Vegetation*

Although far less diverse than its counterpart to the east, the Central North Coast has received some attention from ecologists, mainly in relation to the ultramafic flora in the West Tamar area (Brown *et al.* 1986; Gibson *et al.* 1992; Ong 1992) or because of its association with taxa which are rare or restricted in Tasmania (Askey - Doran & Fry 1994). Local endemics consist of only four species, *Spyridium obcordatum*, *Epacris virgata*<sup>3</sup>, *Pimelea filiformis* and *Tetratheca gunnii* with the latter restricted to ultramafic soils (Gibson *et al.* 1992). In contrast to ultramafic floras elsewhere (Kruckeberg 1986, 1987), endemism is very low on ultramafic soils in Tasmania.

The vegetation of the region is principally dry sclerophyll forest, dominated by *Eucalyptus amygdalina* and *E. obliqua*. *Allocasuarina verticillata* woodland and extensive heathlands occur close to the coast (Kirkpatrick 1977; Askey - Doran & Fry 1994). Wet sclerophyll forest dominated by *E. delegatensis* or *E. regnans* is less common in the region being confined to upland areas, gullies or limestone soils. Relict rainforest occurs in fire protected gullies in the Asbestos Ranges (Neyland 1991).

*S. obcordatum* is found in open eucalypt forest, *Allocasuarina* woodland and coastal heathland.

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<sup>3</sup>The taxonomy and distribution of *Epacris virgata* is disputed. Recent work by Crowden & Menadue (1990) proposed a disjunct distribution between the north and south of the State. However, it has long been considered narrowly endemic to the small area where it co - occurs with *S. obcordatum* and *T. gunnii* and is treated as such here, following Brown *et al.* (1983).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
<b>Minimum temperature (<math>^{\circ}\text{C}</math>)</b>	11.4	12.2	10.2	8.5	6.0	4.0	3.5	4.2	5.5	6.6	8.3	9.9
<b>sd</b>	0.3	0.3	0.3	0.3	0.4	0.4	0.4	0.3	0.3	0.3	0.3	0.3
<b>Maximum temperature (<math>^{\circ}\text{C}</math>)</b>	22.5	23.1	21.0	18.2	15.0	12.7	12.2	13.0	14.4	16.8	18.4	20.2
<b>sd</b>	0.2	0.1	0.4	0.2	0.2	0.2	0.2	0.2	0.2	0.1	0.1	0.1
<b>Precipitation (mm)</b>	39.0	49.0	45.0	67.0	87.0	95.0	110.0	97.0	74.0	74.0	58.0	56.0
<b>sd</b>	3.0	4.0	3.0	5.5	8.0	9.1	12.3	12.1	8.9	6.7	4.2	4.5

Table 2.2. Mean monthly temperature and precipitation estimates at *S. obcordatum* sites (n = 8) derived from BIOCLIM.

## CHAPTER 3

### BIOLOGICAL ASPECTS OF RARITY IN *SPYRIDIMUM MICROPHYLLUM* AND *SPYRIDIMUM OBCORDATUM*

#### Introduction

Predation, poor seed production or viability, the absence of appropriate stimuli for germination, or the loss of soil stored seed may explain rarity in some taxa. In this chapter, reproductive traits of *S. microphyllum* and *S. obcordatum* are examined.

Species may be rare because they are excluded from otherwise habitable sites by predators and pathogens (Drury 1980; Harper 1981). Predation may occur above ground, affecting photosynthetic and reproductive structures, or below ground, thus reducing the regenerative capacity of the population. In Australia, predation from grazing animals has been documented as influencing regeneration of populations of both rare and common species (Chesterfield & Parsons 1985; Cullen 1987; Williams & Ashton 1987; Auld 1990; Scarlett & Parsons 1993). Introduced animals such as rabbits, sheep and cattle have been profoundly effective since their introduction in the mid nineteenth century, in reducing plant biomass and altering patterns of diversity and abundance in indigenous plant and animal populations (Auld 1990; Wilson 1990).

Seed set, seed dispersal and seedling recruitment are vital life history stages. The timing and occurrence of these stages may interact with other factors to prevent the establishment of a species on a particular site. For example, rare species are known which have either failed to set seed or produce only low numbers of seed as a result of predation or the absence of pollinators (Calder *et al.* 1989; Auld 1990; Lynch 1993; Auld *et al.* 1991). This chapter tests the hypothesis that populations of the two narrow endemics are restricted by their biological characteristics.

Since a large proportion of hard - seeded taxa in the Australian flora rely on the breaking of seed coat imposed dormancy before germination can take place, fire provides an important stimulus for germination (Gill 1975; Floyd 1976; Purdie 1977; Gill & Groves 1981; Auld & O'Connell 1991). Rhamnaceae seed are known to respond to heat in Australia (Floyd 1976; Fox *et al.* 1987; Warcup 1980); South Africa (Kilian & Cowling 1992), and North America (Keeley 1987; 1991). There have been few studies in Australia which have investigated the germination requirements of narrow endemics. Studies which have been undertaken have found that seeds vary in response to stimuli (Auld *et al.* 1991; Lynch 1993). However, these were not compared to widespread congeners. Other studies have investigated the effect of cold smoke (De Lange & Boucher 1990; Dixon *et al.*

1994), and the effects of water - soluble products of charred vegetation (Keeley 1987) in promoting germination of dormant seeds having a hard testa, with variable results. In this chapter, the results of germination trials comparing narrow endemics with other *Spyridium* taxa are reported.

The capacity to form persistent seed banks is a characteristic of shrubs in environments prone to intermittent perturbations, and the relationship between disturbance and regeneration in the maintenance of species and ecosystems is widely recognised (Grubb 1977; Keeley 1987, 1991; Grime 1989; Keddy *et al.* 1989; Chambers *et al.* 1990). *Spyridium* has a hard seed coat and small seeds that suggest an ability to store seed in the soil, if seeds were dormant on release (Grime 1989). This suggests that *S. microphyllum* and *S. obcordatum* could be rare because they are unable to regenerate in the absence of disturbance.

### **Aims**

1. To test the hypothesis that *Spyridium microphyllum* and *S. obcordatum* are rare because of predation.
2. To identify life history stages which may be crucial to the reproductive success of *S. microphyllum* and *S. obcordatum*.
3. To test the hypothesis that *Spyridium microphyllum* and *S. obcordatum* are rare because of a narrow germination response relative to other Rhamnaceae taxa.
4. To determine whether *S. microphyllum* and *S. obcordatum* are likely to form persistent seed banks.

### **Methods**

#### ***Predation***

Vertebrate animals were excluded from plots by the erection of fences constructed from 125 mm bird wire and star pickets. At two sites, twenty-five plants within plots were tagged and assigned a number, as were twenty-five plants outside plots. The size of plots depended on the distribution of the 25 individual plants. Plants were of similar stature. Animal scats from each site were collected and identified to gain an idea of the species likely to be inhabiting sites.



Each plant was assessed monthly for grazing damage and assigned a score that represented the percentage of biomass of an individual that was damaged by grazing. This gave an estimate only of whether or not plants were affected by grazing. It was not designed to calculate the amount of plant material lost from a population. The classes were: 1 = <5%; 2 = 5-24%; 3 = 25-49%; 4 = 50-74%; 5 = 75-100%. Areas surrounding tagged plants within and outside plots were observed for seedling establishment. It was not possible to identify the time of the year when plants were most vulnerable, because the data collected were cumulative and the purpose of trials was to assess whether plants were grazed over a 12 month period.

The Mann-Whitney U test was used to compare monthly scores for protected and unprotected plants, within each grazing class.

### *Phenology*

#### *Spyridium microphyllum* and *S. obcordatum*

Observations were made at the St Pauls River and at Blacks Creek (*S. microphyllum*) and at two locations in the Dans Hill area (*S. obcordatum*).

Fifty plants were observed monthly at two sites for each species. Twenty-five were in fenced plots and 25 were unprotected (see above). The aim was to identify peak times for specific life history events and to gain an idea of the period of time over which such events occurred. By these means, the development of life history stages was recorded for the population as a whole, rather than for a few selected individuals.

The timing of bud development and flowering, seed set, pyrene dispersal and leaf production were observed. Floral leaf production, which was conspicuous in *S. microphyllum* was also recorded for this species. Each plant, both within and outside plots, was examined and the presence of one or more of these stages noted. In addition, two branchlets on each plant were tagged and their lengths measured monthly to identify time of maximum shoot elongation. Observations were carried out from August, 1989 to September, 1990.

The results were collated by plotting the percentage of plants in the population exhibiting one or more life history stages, then devising a calendar showing a life history sequence. Comparisons of life history events between protected and unprotected populations were made using the Mann Whitney U test.

### *Phenology of other Tasmanian Rhamnaceae*

Observations of the timing of flowering and fruit production were made of other Rhamnaceae taxa for comparison with the two rare species. These consisted of site visits and inspection of herbarium material. Taxa observed were *S. eriocephalum*, *S. gunnii*, *S. obovatum* var. *obovatum*, *S. obovatum* var. *velutinum*, *S. parvifolium*, *S. ulicinum*, *S. vexilliferum*, *Stenanthemum pimeleoides*, *Cryptandra alpina*, *C. amara*, *C. exilis*, *Discaria pubescens*, *Pomaderris apetala*, *P. aff. apetala* (coastal form), *P. aspera*, *P. elachophylla*, *P. elliptica*, *P. intermedia*, *P. oraria* ssp. *oraria*, *P. paniculosa* ssp. *paralia*, *P. phyllicifolia*, *P. pilifera* and *P. racemosa*.

Measurements of shoot elongation were made for three other rare Rhamnaceae species. These were *Discaria pubescens*, *Stenanthemum pimeleoides* and *Pomaderris elachophylla*.

### *Time to flowering*

*Spyridium microphyllum* and *S. obcordatum* seeds were immersed in boiling water for 10 seconds (see below) and transplanted to pots. They were placed initially in a greenhouse at the Department of Plant Science in Hobart, and subsequently a shade house, where they were subject to ambient light and temperature conditions. Plants were observed regularly and development of buds and flowers observed.

### *Germination*

#### *Seed Collection*

Seed was collected from populations of all *Spyridium* taxa which occur in Tasmania. These were *S. microphyllum*, *S. obcordatum*, *S. gunnii*, *S. ulicinum*, *S. obovatum* var. *obovatum*, *S. obovatum* var. *velutinum*, *S. parvifolium*, *S. vexilliferum* and *S. eriocephalum* (Table 3.1). There were too few *S. eriocephalum* plants in Tasmania to collect sufficient seed, so seed from the nearest Victorian population was used (Table 3.1). Voucher specimens are held by the author.

Some other Rhamnaceae were included for comparison in the heat trials. Taxa used for comparison were *Discaria pubescens*, *Stenanthemum pimeleoides*,

Taxon	Location	Latitude (S)	Longitude (E)	Altitude (m)	Conservation status	Regeneration
<i>S. microphyllum</i>	Douglas - Apsley	41° 05"	148° 14"	200	Vv	OS
<i>S. microphyllum</i>	Thumbs	42° 36"	147° 53"	200	Vv	OS
<i>S. microphyllum</i>	Swan River	41° 54"	148° 05"	30	Vv	OS
<i>S. obcordatum</i>	Dans Hill	41° 11"	146° 46"	55	Vv	S/R?
<i>S. obcordatum</i>	Hawley	41° 09"	146° 31"	65	Vv	S/R?
<i>S. gunnii</i>	McIvor Hill	41° 53"	145 16	260	Rr2	OS?
<i>S. ulicinum</i>	Neika	42° 56"	147° 14"	500		OS?
<i>S. obovatum</i> var. <i>obovatum</i>	Swan River	41° 54"	148° 05"	30		OS
<i>S. obovatum</i> var. <i>velutinum</i>	Orford	42° 34"	147° 51"	60		OS
<i>S. parvifolium</i>	Rubicon River	41° 15"	146° 34"	40		OS
<i>S. vexilliferum</i>	Epping Forest	41° 46"	147° 20"	200	r2	OS
<i>S. eriocephalum</i>	Long Forest	37° 39"	144° 30"	180		OS
<i>Discaria pubescens</i>	Hermitage	42° 12"	146° 51"	600	ue	S/R
<i>Stenanthemum pimeleoides</i>	Epping Forest	41° 46"	147° 20"	200	Rr1	S/R
<i>Cryptandra exilis</i>	Bicheno	41° 48"	148° 16"	20	Rr2	OS?
<i>C. amara</i>	Cranbrook	42 03	148 03	20	eu	OS?
<i>Pomaderris elliptica</i>	Dans Hill	41° 11"	146° 46"	55		OS
<i>P. pilifera</i>	Risdon	42° 50"	147° 19"	20		OS
<i>P. phyllicifolia</i>	Black Bridge	42° 33"	147° 49"	60	ur2	OS
<i>P. racemosa</i>	Lake Sorrel	42° 09"	147° 10"	840	r2	OS
<i>P. apetala</i>	Sandy Bay	42° 54"	147° 19"	40		OS
<i>P. aff. apetala</i> (coastal form)	Hawley	41° 09"	146° 31"	65	Rr1	OS
<i>P. aspera</i>	Bicheno	41° 50"	148° 16"	20		OS
<i>P. elachophylla</i>	Butlers Gorge	42 16	146 16	680	uv	OS

Table 3.1. Locations, geographic co-ordinates, altitudes, conservation status and mode of regeneration for taxa used in germination trials. Conservation codes follow Kirkpatrick *et al.* (1991), other than *Stenanthemum pimeleoides* and *Pomaderris aff. apetala* (coastal form), which are updated from this publication. No conservation status indicates that the taxon is widespread.

Key (lower case applies to Tasmania only): **E** = taxa that are likely to become extinct if present land use changes and patterns and other causal factors of decline continue. **V** = taxa that are likely to become extinct over a longer period of time than those classified E. **R** = taxa that have limited distributions nationally following Briggs & Leigh (1988), where "1" denotes a distribution in Tasmania that does not exceed 100 km x 100 km and "2" denotes taxa that occur in 20 or less 10 km x 10 km National Mapping grid squares in Tasmania. **U** = taxa not known from any secure reserve (World Heritage Area and reserves requiring the approval of both houses of parliament for revocation).

Regeneration: **OS** = obligate seeder; **S/R** = regeneration by seed or resprouting; **?** = unknown.

*Cryptandra exilis*, *C. amara*, *Pomaderris elliptica*, *P. pilifera*, *P. phyllicifolia*, *P. racemosa*, *P. apetala*, *P. aff. apetala* (coastal form), *P. aspera* and *P. elachophylla* (Table 3.1). Seeds were collected at the same site as for the two narrow endemics where possible.

Calico bags were tied to fruiting branches as close as possible to estimated time of seed fall. Seed was also hand picked from plants. Old flower heads and capsules were discarded after collection and seeds stored in paper envelopes. For each species, seeds used in treatments were collected from the same locations at the same time.

### *Laboratory methods*

The seed coat surface was sterilised prior to incubation by soaking seeds in 70% alcohol for 60 seconds and in 5% solution of sodium hypochlorite for 10 minutes, with water rinses in between. Germination pads, consisting of two layers of filter paper, were sprayed with a 5% solution of "Thiram" fungicide and seeds were sprayed after sowing.

Two or four replicates each of twenty-five seeds were used for treatments. The limited number of seed available in some cases and the amount of space and time available precluded higher numbers of replicates. Seeds were soaked in tap water for one hour, then placed on germination pads in 90 mm petri dishes. Petri dishes were placed in controlled temperature cabinets and watered with an atomiser filled with tap water, and scored daily. Incubation of all *Spyridium* seeds was at 20°C and at 12°C; non - *Spyridium* taxa were incubated at 20°C only. Again time and space constraints precluded all trials being incubated at both temperatures. The higher temperature was chosen because it approximates the mean monthly maximum at the time of seed release in most populations. A number of successful germination trials have been conducted in Tasmania, including seeds of rare taxa at this temperature (Harris & Gilfedder 1991; Battaglia 1993; Lynch 1993; Gilfedder & Kirkpatrick 1994). The cooler temperature was chosen as an approximation of mean annual temperature at *Spyridium* sites. Seeds were kept in the dark and exposed to light when scored daily.

Trials were halted after 100% germination was obtained; when 80% germination was obtained then no further germination after 10 days; after 50 days, when there had been some germination but none for a 10 day period; or after 100 days when no or little germination had occurred. Germination was scored at the appearance of the radicle.

### *Seed viability*

Percentage viability was determined by a combination of methods. Prior to treatments, seeds were gently squeezed and any empty, wrinkled, discoloured, shrunk or poorly developed seeds were discarded. Tetrazolium tests for viability (Lakon 1949) were trialled for *S. microphyllum* and *S. obcordatum*. However, although these were successful, screening such small seeds was time consuming, especially when the total number of seeds used for the experiments was considered. Consequently, squashes of ungerminated seeds were carried out at the close of each trial and the number of apparently unviable, and apparently viable but ungerminated, seeds recorded. The overall viability of seeds of each taxon was assessed by averaging the numbers of non - viable seeds in all trials for each taxon and adjusting the final germination percentages accordingly.

### *Seed dormancy*

Preliminary germination trials were established less than two weeks after seed was collected, to establish whether seeds were likely to be dormant on release. Trials aimed to establish whether dormancy was physical or physiological. Seeds used in trials were less than 6 weeks old.

### *Non-Heat Treatments*

All seeds were subjected to a number of trials designed to maximise germination. These were:

1. No treatment prior to incubation at 12<sup>0</sup>C and at 20<sup>0</sup>C.
2. Stratification at 5<sup>0</sup>C for 60 days prior to incubation at 12<sup>0</sup>C and at 20<sup>0</sup>C.

*S. microphyllum* and *S. obcordatum* were subjected to additional trials. These were:

3. Scarified then incubated at 20<sup>0</sup>C. Scarification was achieved by gently rubbing seeds between fine grade sand paper but proved to be an unreliable method with such small seeds, which were prone to destruction. Consequently, this treatment was not used for all taxa.
4. Untreated and incubated in total darkness for 30 days at 20<sup>0</sup>C, then placed in germinating cabinets at 20<sup>0</sup>C.

## *Soil Seed Treatments*

Observations were made on *S. microphyllum* and *S. obcordatum* seed left to germinate in soil collected from two field sites to determine whether seed germinated more readily under more natural conditions, and whether soil - stored seed was likely to germinate.

### 1. Sown seed

Two plastic trays (34 cm x 29 cm x 5 cm), each containing fifty seeds and filled with soil (collected to a depth of 5 cm) were placed in a greenhouse. The position of each seed was marked to preclude any confusion between germinants and seed which was present in the soil.

### 2. Soil stored seed

Six trays of soil were collected close to adult plants known to have recently dispersed seed. Soil was excavated to a depth of approximately 5 cm, based on the assumption that this was likely to represent a reasonable sample of the seed bank. Stones, twigs and other matter were removed by sieving soil through 1 cm and 0.5 cm wire mesh sieves respectively. Soil was then spread out on trays lined with porous fabric and watered regularly by an automatic spray jet system in the greenhouse.

Trays were sprayed regularly with a solution of "Benlate" fungicide. Temperatures ranged between -4°C and 37°C, but were most frequently 20°C-5°C at night and 20°C-25°C during daylight hours. Trays experienced a 16 hour photoperiod supplied by two 40W Growlux fluorescent tubes and the trial ran for 200 days.

## *Heat Treatments*

1. Seeds were submerged in boiling water for 10 seconds prior to incubation at 12°C and at 20°C.

2. Seeds were wrapped in aluminium foil, measuring approximately 3 cm x 5 cm. Care was taken to keep these "packets" as uniform as possible. Packets were connected to a thermocouple and placed in a pre-heated oven. Treatments were one, five and ten minutes at temperatures of 40°C, 60°C, 80°C, 100°C and 120°C. A duplicate set of *Discaria pubescens* seeds were cold stratified at 5°C for 60 days after heating.

After heating, packages were opened and left to cool to room temperature, sterilised, soaked in tap water for one hour and incubated.

### *Seed bank longevity*

Four replicates of 25 seeds of each species were placed in 5 cm x 5 cm nylon mesh bags having apertures of 0.5 mm x 0.5 mm. Twelve bags were buried at depths of 1 cm, 5 cm and 10 cm, within an area of 1m<sup>2</sup>. After 12 and 24 months, 4 bags at each depth were excavated and returned to the laboratory. Excess dirt was removed with a small brush; seeds were removed from bags, examined and counted. The number of seeds recovered was scored, as were the number of germinated seeds, the number ungerminated and intact, the number damaged and number absent.

Where there were sufficient numbers retained, seeds from each treatment were divided in half. One group was incubated at 20°C and the other group immersed in boiling water for 10 seconds and incubated at 20°C.

*Spyridium microphyllum* seeds were buried at the Swan River site and *S. obcordatum* seeds at Dans Hill.

### *Statistical analyses*

Percentage germination data were adjusted for viability and tested for normality, then arcsine transformed. Comparisons between total germination at the two incubation temperatures were carried out using Student's t test. The effect of incubation temperature for each taxon was compared using a one way analysis of variance (ANOVA).

The germination response of the two narrow endemics were compared with all other taxa, for all treatments, by a one way ANOVA followed by Tukey HSD simultaneous pairwise mean comparisons. Three arbitrary categories were defined on the basis of percentage germination of *S. microphyllum* or *S. obcordatum* relative to other taxa. Categories were greater success, lesser success and equivalent. A taxon was deemed to have had greater germination success than a comparative taxon if it returned significantly higher germination after one or more heat treatments, assuming that this indicates receptivity to a wider range of stimuli. Lesser germination success was defined as significantly lower percentage germination after one or more treatments. When no two species showed no significant difference between percentage germination in any treatment, the two were considered equivalent.

The statistical software package SYSTAT 5.03 was used for all analyses.

## Results

### *Predation*

#### *Spyridium microphyllum*

Identification of scats collected from the study sites indicated that populations were potentially subject to grazing pressure from sheep, rabbits and native animals such as wallabies and possums. During the previous year at the Blacks Creek site, sheep stocking rates had been relatively heavy (M. Woolnough, Farmer, pers. comm.).

Mann-Whitney tests used to compare the numbers of plants inside plots with those outside plots for each grazing category showed that grazing pressure did not significantly effect the population during the experimental period. Trends in the data suggest that unprotected plants may take longer to recover from any previous damage. However, the majority of plants both inside and outside plots had scores showing that less than 5% of the plant was damaged by grazing (Table 3.2a). The results confirm field observations, that noticeably grazed plants are rare in most cases. Heavy grazing damage by cattle was observed on the St Pauls River, where the combination of high stocking rates and little feed close to a water source had resulted in severe damage to the *S. microphyllum* population present, the only intact plants being those which were protected by gorse (*Ulex europaeus*).

There were no seedlings recorded within or outside plots. Consequently, the effect of grazing pressure on seedlings is unknown.

#### *Spyridium obcordatum*

Scats identified indicated that rabbits, wallabies, possums and wombats are the major source of grazing pressure at the study site.

Plants which were protected by fences were significantly less grazed throughout the trial than those with no protection (Table 3.2b). Mann-Whitney tests used to compare observations of the numbers of plants in each grazing category within and outside plots, showed there were significantly more protected plants which had sustained less than 5% damage ( $W = 179$ ,  $P < 0.001$ ). There were more unprotected plants with higher grazing scores than protected ones. For categories 2 (5 - 24%), 3 (25 - 49%) and 5 (75 - 100%), more plants outside plots were



Grazing class	1		2		3		4		5	
	(0 - 5%)		(5 - 25%)		(25 - 50%)		(50 - 75%)		(75 - 100%)	
	P	U	P	U	P	U	P	U	P	U
<b>Month</b>										
September	25	23	0	2	0	0	0	0	0	0
October	15	19	7	3	1	0	2	2	0	1
November	15	19	7	3	1	0	2	2	0	1
December	13	16	9	6	3	0	0	2	0	1
January	17	19	7	2	1	2	0	1	0	1
February	19	19	5	3	1	1	0	1	0	1
March	19	21	5	1	1	1	0	1	0	1
April	22	21	5	1	0	2	0	0	0	1
May	23	19	2	4	0	1	0	0	0	1
June	25	20	0	4	0	4	0	0	0	1
July	25	20	0	3	0	0	0	0	0	2

Table 3.2a. Monthly numbers of protected (P) and unprotected (U) *S. microphyllum* plants for each grazing class, where each class represents the total estimated damage to each plant. Each figure in columns represents the number of plants grazed out of a total of 25 each month.

Grazing class	1		2		3		4		5	
	(0 - 5%)		(5 - 25%)		(25 - 50%)		(50 - 75%)		(75 - 100%)	
	P	U	P	U	P	U	P	U	P	U
<b>Month</b>										
September	4	2	13	10	5	11	3	2	0	0
October	9	4	10	8	4	11	2	2	0	0
November	14	1	7	12	4	9	0	3	0	0
December	20	5	5	17	0	2	0	0	0	1
January	18	4	7	13	0	7	0	0	0	1
February	25	9	0	13	0	2	0	0	0	1
March	24	9	0	12	0	3	0	0	0	1
April	21	5	4	15	0	3	0	0	0	2
May	23	5	2	1	0	5	0	2	0	2
June	25	4	0	11	0	7	0	0	0	3
July	25	4	0	9	0	9	0	1	0	2

Table 3.2b. Monthly numbers of protected (P) and unprotected (U) *S. obcordatum* plants for each grazing class, where each class represents the total estimated damage to each plant. Each figure in columns represents the number of plants grazed out of a total of 25 each month.

damaged than inside plots ( $W = 76.5$ ,  $P < 0.001$ ;  $W = 78.5$ ,  $P < 0.002$ ;  $W = 86$ ,  $P < 0.01$ ). These results confirmed field observations which suggested that plants were moderately to heavily grazed except where protected by other plants such as *Lomandra longifolia* tussocks. Plants had been fenced off prior to the main growth season and recovery was rapid.

No seedlings were found at the study site and they were rare elsewhere, but the results suggest that it is likely that seedlings are grazed.

## *Phenology*

### *Spyridium microphyllum*

Ten to fourteen buds surrounded by brown bracts are formed in tightly clustered heads which terminate the main and lateral branchlets. Three tomentose floral leaves encompass the flower heads. The formation of buds begins during late September or early October in some plants, with bud production peaking in December and January in the majority of individuals, with the onset of warmer weather. Bud burst in a small number of flowers begins in late November, with most of the population flowering in February (Table 3.3). Buds in the centre of the flower head open first. Minor flowering continues in some plants until as late as April. Flowering was prolific at the study sites, both within and outside the plots. Of the total number observed, 90% of plants flowered.

After flowering, seed develops over winter and is not released until twelve months later in the following summer. Developing fruits were observed initially in April and the majority of plants begin noticeable fruit production in August and September. Seed development is at a maximum during October and November, with fruit maturing in January in most of the population. Most plants released pyrenes containing seed in late January to February. Some early seed fall may commence in November or December and extend through to April. Therefore, seed is produced from flowers fertilised during the previous season and is released after the flowering period in the following season, leaving a 12 month lag between flowering and seed fall (Table 3.3).

The gynoecium is semi - inferior, 3-carpelar and syncarpous with basal placentation. Following fertilisation and ovule maturation, a 3-chambered capsule is produced which separates into three pyrenes by septicidal dehiscence combined with a breaking away from the central column of tissue. Capsules are enclosed in the receptacle. Pyrenes are derived from the fruit's endocarp and each contains one diaspore consisting of a seed and aril. The seed may be released as a fruitlet or

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Shoot elongation	P	P	P	P					P*	P*	P*	P
New leaves	P	P	P	P	P	P	P	P	P	P	P	P
Floral leaves	P*	P*	P	P	P	P	P				P	P
Old flower heads	P	P	P	P	P	P	P	P*	*P	P	P	P
Pyrene release	P*	P*	P	P								P
Mature fruit	P*	P										P
Developing fruit				P	P	P	P	P	P	P*	P*	P
Flowers	P*	P*	P									P
Buds	P*	P	P							P	P	P*

Table 3.3. Phenological calendar for *S. microphyllum*. P = life history stage present. Asterisks represent peak periods.

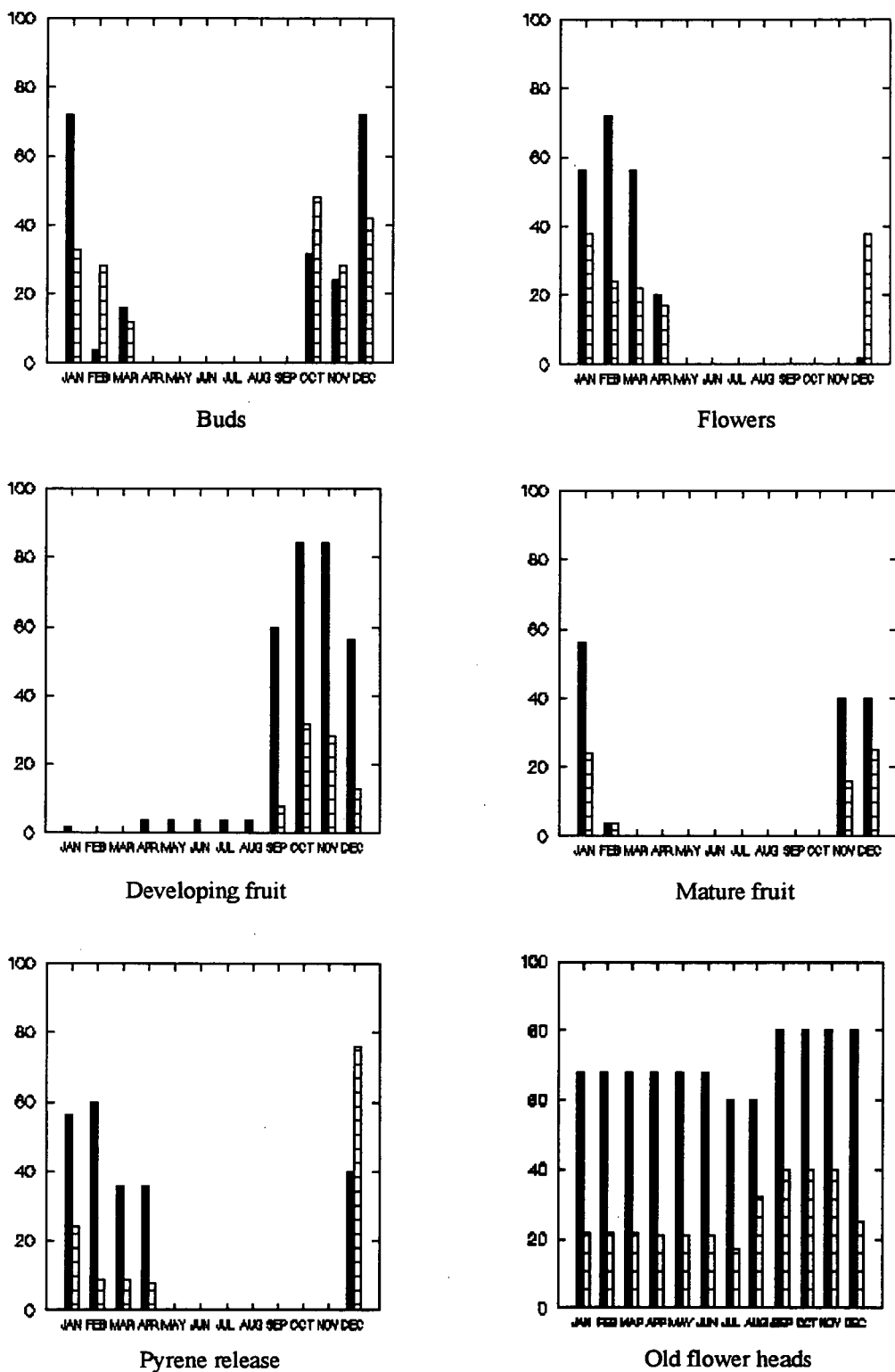
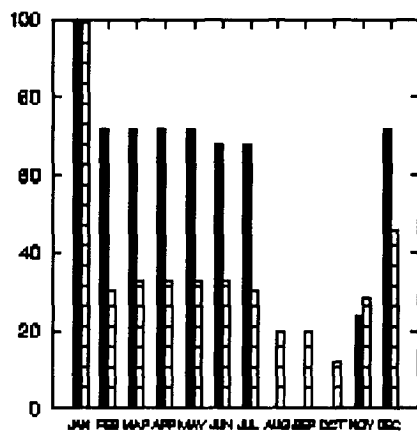
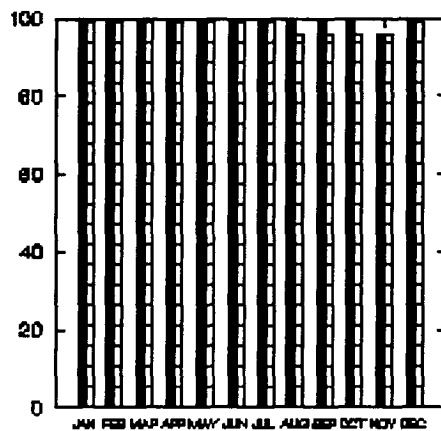


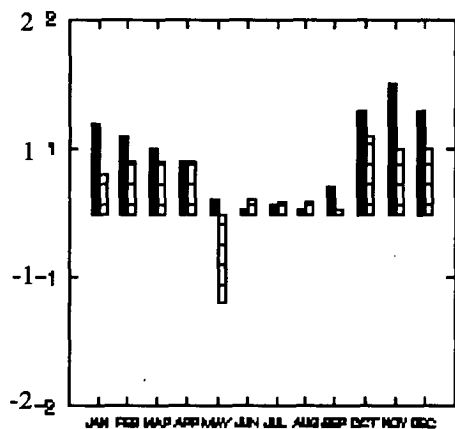
Figure 3.1. Comparison of life history stages between 25 *S. microphyllum* plants in plots (solid bars) and 25 unprotected plants (shaded bars). Bars represent percentage of plants in which an event was recorded.



Floral leaves



New leaves



Shoot elongation

Figure 3.1 continued. Comparison of life history stages between 25 *S. microphyllum* plants in plots (solid bars) and 25 unprotected plants (shaded bars). Bars represent percentage of plants in which an event was recorded, except for shoot elongation, where they represent centimetres of growth. Negative growth was recorded where shoots were grazed or damaged.

expelled independently. Empty pyrenes as well as those containing seed were observed on plants as well as at their base. Entire seed-bearing heads may also fall intact from parent plants. Following release from the parent plant, pyrenes or seed fail to disperse far from the parent plant. Longitudinal dehiscence of the fruitlet wall along the suture where it was formerly attached to the central column begins at its point of original attachment and indicates that seed is at least physically free to germinate, providing that environmental conditions are appropriate and that the entry of water to within the seed is not obstructed by the aril. *S. microphyllum* seeds have a honey coloured testa which is hard, shiny and coriaceous. Seeds are approximately 1.5 x 1.0 mm in dimension, with a rounded back and a flattened, shallowly keeled face. Of the total plants observed, 80% produced mature seed.

Old flower heads remain on bushes. It is possible, therefore, to detect whether plants flowered during the previous season. Old flower heads were present during the twelve month cycle, but were observed on more bushes during August to December. These are eventually blown off by wind after seed release (Table 3.3).

Floral leaves remain on plants for most of the year, but are at a peak in January surrounding new flower heads. On old, fruit-bearing heads, they appear to fade prior to the onset of peak fruit development (Table 3.3).

*S. microphyllum* produces new leaves throughout the year. The main period of shoot elongation is during Spring, from late September to the end of November. New flower heads are formed on new growth, as old heads occupy growth from the previous season. Growth continues until April, after which time it is negligible (Table 3.3).

Plants in plots tended to have higher scores for life history events compared to unprotected plots, suggesting they may be subject to some grazing pressure (Fig. 3.1). However, most were not statistically significant. Exceptions were numbers of plants showing old flower head retention ( $W = 17.8$ ,  $P < 0.001$ ,  $df = 2$ ), and number of plants with developing fruit ( $W = 6.33$ ,  $P < 0.05$ ,  $df = 2$ ). The latter category was not supported by numbers of individuals with mature fruit or with fruit being dispersed. There may be some food value in spent flower heads for birds or other vertebrates. The overall results supported the results of the grazing trials that mature individuals of *S. microphyllum* are not significantly affected by grazing.

### *Spyridium obcordatum*

Reproductive activity in *S. obcordatum* takes place over a short period of time, relative to *Spyridium microphyllum*, during September to January (Table 3.4).

Four to six buds are formed in tightly clustered heads and are surrounded by brown bracts. Curtis & Morris (1975) ascribe a single floral leaf to each flower head, which is green, unlike the tomentose floral leaves in *Spyridium microphyllum*. Flower heads occur in groups of 2 to 5. Buds are conspicuous from March and continue to swell until bud burst and consequently flowering, is initiated in mid-September (Table 3.4). Buds in the centre of the flower head are the first to open, and bud burst is completed by mid October. The peak flowering time is during early October and is completed by the end of the month. Flowering was prolific at the study site, both within and outside plots. One hundred percent of the plants observed produced flowers.

Fruit development commences immediately in early November and the majority of plants in the population have fruit developing by mid-November. Fruit matures over December and is released over a short period in late December and early January. Spent flower heads remain for a few months but have detached from plants by July (Table 3.4). It is not possible, to detect whether plants flowered during the previous season.

Fruit structure and composition in *S. obcordatum* is similar to *Spyridium microphyllum*. The developing fruiting body is a capsule derived from the 3-carpelar, semi - inferior gynoecium which is syncarpous with basal placentation. It eventually separates into three pyrenes by septicial dehiscence, combined with a breaking away from the central column of tissue. The capsule develops while enclosed in the receptacle (Curtis & Morris, 1975). Each fruitlet contains a seed plus aril which attaches the seed at its hilum to the fruitlet. Pyrenes are derived from the endocarp. Seed fall occurs when pyrenes or seed are released, but these fail to disperse far from the parent plant. The fruitlet partly dehisces longitudinally along the suture where it was formerly attached to the central column, so that seed is at least physically free to germinate under suitable environmental conditions. Seeds are hard, light chestnut brown in colour with a rounded back and a shallowly keeled face. The testa is shiny and coriaceous, with a prominent aril. On average, seeds are 1.5 x 1.0 mm in dimension. All plants observed produced seed.

Maximum shoot elongation occurs from mid-November to late February, with growth peaking from November to December. Leaves are produced throughout the year (Table 3.4).

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
<b>New leaves</b>	P	P	P	P	P	P	P	P	P	P	P	P
<b>Shoot elongation</b>	P	P									P*	P*
<b>Old flower heads</b>	P	P	P	P	P	P	P					
<b>Pyrene release</b>	P											P
<b>Mature fruit</b>	P											P*
<b>Developing fruit</b>											P*	
<b>Flowers</b>									P	P*	P	
<b>Buds</b>			P	P	P	P	P	P	P	P		

Table 3.4. Phenological calendar for *S. obcordatum*. P = life history stage present. Asterisks represent peak periods.



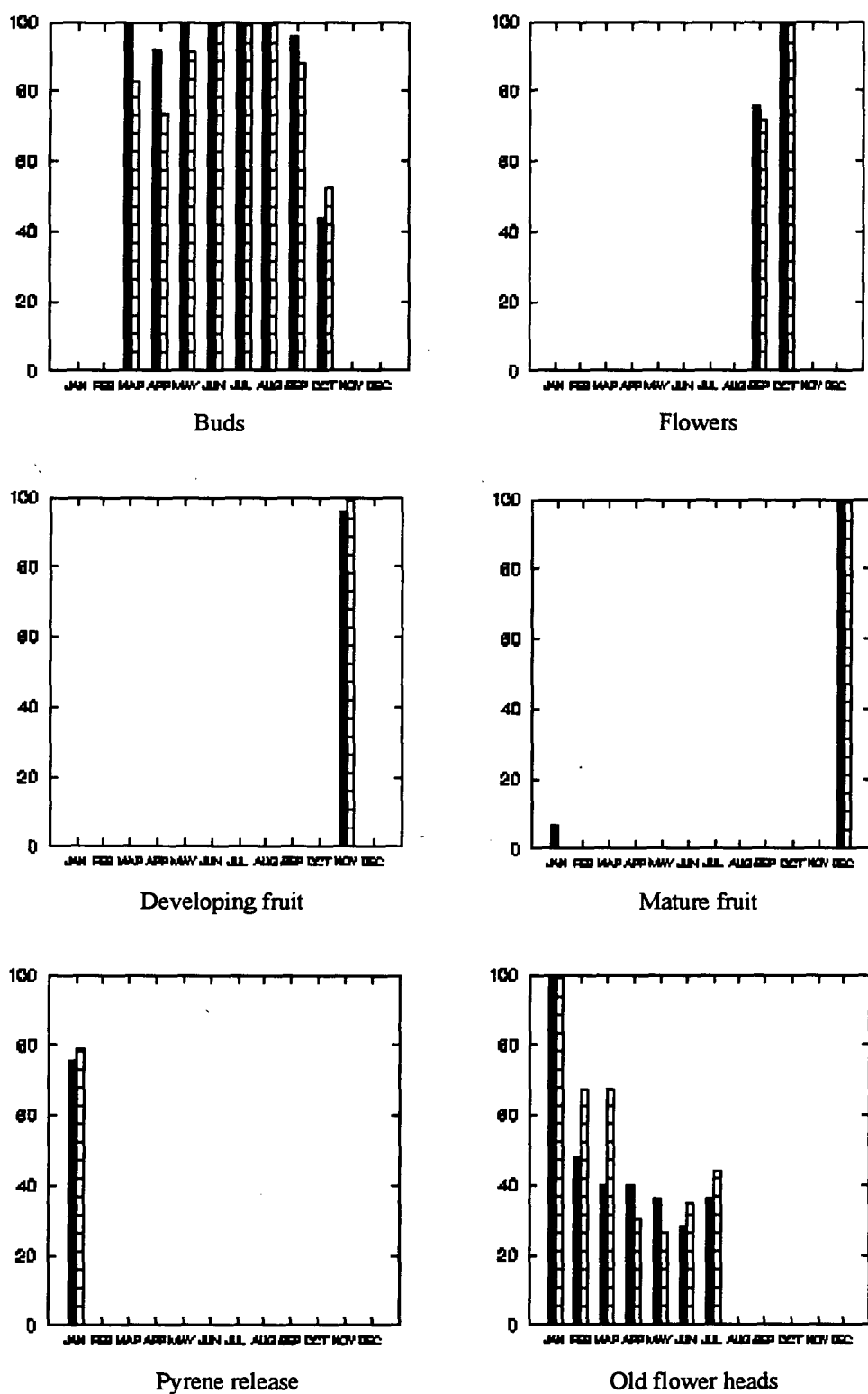
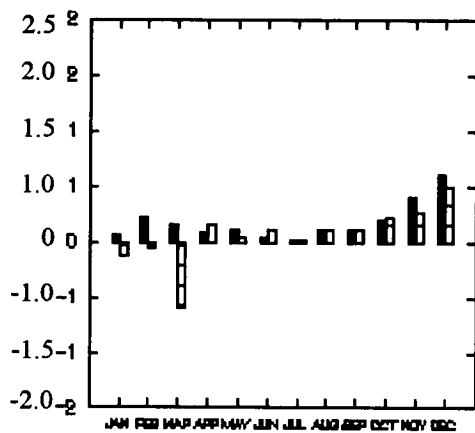
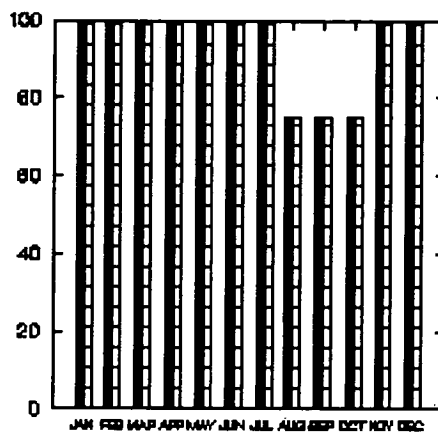


Figure 3.2. Comparison of life history stages between 25 *S. obcordatum* plants in plots (solid bars) and 25 unprotected plants (shaded bars). Bars represent percentage of plants in which an event was recorded.



Shoot elongation



New leaves

Figure 3.2 continued. Comparison of life history stages between 25 *S. obcordatum* plants in plots (solid bars) and 25 unprotected plants (shaded bars). Bars represent percentage of plants in which an event was recorded, except for shoot elongation, where they represent centimetres. Negative growth was recorded where shoots were grazed or otherwise damaged.

There was no significant difference between grazed and ungrazed plants for numbers of plants scored for life history events, suggesting that *S. obcordatum* populations suffer from grazing damage at times of the year when the plant is not producing reproductive material (Fig. 3.2). Negative shoot growth recorded during January, February and March suggests that plants are most vulnerable at this time and that during spring and early summer, vigorous vegetative growth and development of flowers and fruit outweighs the affects of grazing.

### *Comparative phenological observations*

Both patterns of fruit development and dispersal were repeated in other taxa (Table 3.5). Immediate fruit development and dispersal was apparent in *S. obovatum* var. *obovatum*, *S. obovatum* var. *velutinum*, *S. parvifolium*, *S. ulicinum*, *Cryptandra amara*, *Discaria pubescens* and in all *Pomaderris* taxa. Flowering in these taxa occurred between mid - spring and early summer. *Spyridium* taxa with immediate fruit development and dispersal all have inflorescences arranged in loose cymose panicles.

Delayed fruit development and dispersal was observed in *S. eriocephalum*, *S. gunnii*, *S. vexilliferum*, *C. alpina*, *C. exilis* and *Stenanthemum pimeleoides*. These taxa flowered between early to late summer. All taxa had inflorescences arranged in dense clusters. An exception was *S. gunnii*, which was intermediate between the two inflorescence types.

Shoot elongation in *S. pimeleoides* was similar to that of *S. microphyllum* and *S. obcordatum*, with maximum extension between September and December. Summer growth (November to January) was observed in *Discaria pubescens* and *Pomaderris elachophylla*, which were situated in cool climates, with low spring temperatures possibly delaying vegetative growth.

### *Time to flowering*

*Spyridium obcordatum* seedlings appeared to be comparatively more vigorous and faster growing than those of *S. microphyllum*. Buds formed after 12 months and flowering took place within 18 months. *Spyridium microphyllum* plants failed to flower after three years and growth was apparently slower, although this was not measured.

Taxon	Flowers	Mature fruit	Pyrene dispersal	Shoot elongation
<i>S. microphyllum</i>	Jan - Feb	Jan - Feb	Delayed	Sep - Nov
<i>S. obcordatum</i>	Oct	Dec - Jan	Immediate	Nov - Dec
<i>S. obovatum</i> var. <i>obovatum</i>	Oct	Dec - Jan	Immediate	*
<i>S. obovatum</i> var. <i>velutinum</i>	Oct	Dec - Jan	Immediate	*
<i>S. eriocephalum</i>	Dec - Jan	Dec	Delayed	*
<i>S. parvifolium</i>	Oct	Dec - Jan	Immediate	*
<i>S. ulicinum</i>	Oct	Jan	Immediate	*
<i>S. gunnii</i>	Jan - Feb	Feb - Mar	Delayed	*
<i>S. vexilliferum</i>	Nov - Dec	Dec - Jan	Delayed	*
<i>Discaria pubescens</i>	Nov - Dec	Feb - Mar	Immediate	Nov - Jan
<i>Cryptandra alpina</i>	Feb - Mar	Dec - Feb	Delayed	*
<i>C. amara</i>	Oct - Nov	Dec - Jan	Immediate	*
<i>C. exilis</i>	Jan	Dec	Delayed	*
<i>Stenanthemum pimeleoides</i>	Dec	Jan - Feb	Delayed	*
<i>P. apetala</i>	Nov	Jan	Immediate	*
<i>P. aff. apetala</i> (coastal form)	Nov	Jan	Immediate	*
<i>P. aspera</i>	Nov	Jan	Immediate	*
<i>P. elachophylla</i>	Nov - Dec	Jan - Feb	Immediate	Dec - Jan
<i>P. elliptica</i>	Oct - Nov	Jan	Immediate	*
<i>P. intermedia</i>	Nov	Jan	Immediate	*
<i>P. oraria</i> ssp. <i>oraria</i>	Nov - Dec	Jan - Feb	Immediate	*
<i>P. paniculosa</i> ssp. <i>paniculosa</i>	Nov - Dec	Jan - Feb	Immediate	*
<i>P. phyllicifolia</i>	Oct - Nov	Jan	Immediate	*
<i>P. pilifera</i>	Oct - Nov	Jan	Immediate	*
<i>P. racemosa</i>	Nov - Dec	Jan - Feb	Immediate	*

Table 3.5. Summary of timing flowering, production of mature fruit and pyrene dispersal in Tasmanian Rhamnaceae, and timing of shoot elongation in three additional rare Rhamnaceae species. Timing of pyrene dispersal is categorised as either delayed, where fruit development extends over 12 months until the year following flowering, or immediate, where pyrene dispersal occurs within 2 months of flowering. Asterisks denote missing data.

### ***Germination***

Few *S. microphyllum* capsules appeared to contain three seeds that had fully developed. A count of 25 capsules revealed that 6 contained 3 fully developed seeds, 6 contained 2 fully developed seeds and 14 contained only 1 fully developed seed.

Ninety per cent of *S. obcordatum* capsules contained three seeds having a healthy appearance. The remainder contained two healthy seeds.

### ***Seed viability***

All taxa had a significant proportion of seeds which were viable. Average viability was 80% - 96%, with *S. microphyllum* and *S. obcordatum* 80% - 88% and 80% - 84% respectively (Tables 3.6 & 3.7). *Spyridium gunnii* was an exception and had a relatively low level of seed viability of 64% (Table 3.7). *Spyridium obovatum* var. *obovatum* and *S. obovatum* var. *velutinum* were also relatively low at 72% and 76% respectively (Table 3.7). There was a small difference between seeds from different sites. *Pomaderris pilifera* and *Discaria pubescens* had the highest proportions of viable seed (Table 3.7).

### ***Dormancy***

Incubation of fresh seeds of *S. microphyllum* and *S. obcordatum* resulted in very low levels of germination, suggesting that seeds are dormant prior to or very soon after release (Table 3.6). The highest level of germination of fresh seeds was at the Swan River site (8%), and was even lower at other sites (0% - 2%).

### ***Non heat treatments***

Few trials resulted in germination in excess of ten per cent, regardless of incubation temperature (Tables 3.6 & 3.7). *Discaria pubescens* and *Pomaderris apetala* were above average, at 16% at 20°C (Table 3.7). Fourteen per cent of *S. microphyllum* seeds from the Swan River also germinated at 20°C. However, germination levels

Treatment	Viability (%)	FRESH	C/12	C/20	D/20	5/12	5/20	SCAR	Sown	Soil stored
<b>Taxon</b>										
<i>S. microphyllum</i> (Thumbs.)	88 ± 2	2 ± 2	0	4 ± 4	4 ± 2	1 ± 1	0	100	*	*
<i>S. microphyllum</i> (Swan River)	80 ± 4	8 ± 2	0	14 ± 6	2 ± 2	0	5 ± 0	98 ± 2	4 ± 2	19
<i>S. microphyllum</i> (Douglas Apsley)	84 ± 2	0	0	0	0	0	0	98 ± 2	*	*
<i>S. obcordatum</i> (Dans Hill)	80 ± 3	1 ± 1	7 ± 7	4 ±	2 ± 2	0	0	90 ± 5	14 ± 11	10
<i>S. obcordatum</i> (Hawley)	84 ± 4	0	0	0	3 ± 3	0	0	90 ± 4	*	*

Table 3.6. Percentage germination ( $\pm$  SE) for non heat treatments for *S. microphyllum* and *S. obcordatum* (columns 1-9), and number of seeds germinated in soil collected from sites (column 10).

Key: **FRESH** = seeds less than 2 weeks old; **C/12** = no treatment, incubated at 12<sup>0</sup>C; **C/20** = no treatment, incubated at 20<sup>0</sup>C; **D/20** = seeds incubated at 20<sup>0</sup>C after a 30 day period of total darkness at room temperature; **5/12** = cold stratified at 5<sup>0</sup>C for 60 days, then at 20<sup>0</sup>C; **5/20** = cold stratified at 5<sup>0</sup>C for 60 days, then at 20<sup>0</sup>C; **SCAR** = scarified; **sown** = seeds sown in soil and incubated in greenhouse; **soil stored** = seeds present in soil collected from field sites. The last two treatments were incubated on average at 2<sup>0</sup>C - 5<sup>0</sup>C and at 20<sup>0</sup>C - 25<sup>0</sup>C with a 16 hour photoperiod. Asterisks represent missing data.

Treatment	Viability (%)	C/12	C/20	5/12	5/20
<b>Taxon</b>					
<i>S. obovatum</i> var. <i>obovatum</i>	72 ± 3	0	2 ± 3	0	0
<i>S. obovatum</i> var. <i>velutinum</i>	76 ± 3	10 ± 0	3 ± 3	0	0
<i>S. eriocephalum</i>	80 ± 3	5 ± 0	0	0	3 ± 3
<i>S. parvifolium</i>	80 ± 3	12 ± 2	0	0	0
<i>S. ulicinum</i>	84 ± 3	0	5 ± 0	0	12 ± 2
<i>S. gunnii</i>	64 ± 6	0	3 ± 3	0	0
<i>S. vexilliferum</i>	92 ± 2	4 ± 4	0	0	2 ± 2
<i>Discaria pubescens</i>	96 ± 1	*	16 ± 5	*	100
<i>Cryptandra exilis</i>	80 ± 2	*	10 ± 5	*	7 ± 2
<i>C. amara</i>	NR	*	0	*	0
<i>Stenanthemum pimeleoides</i>	84 ± 1	*	10 ± 5	*	0
<i>Pomaderris elliptica</i>	72 ± 1	*	3 ± 3	*	0
<i>P. pilifera</i>	96 ± 3	*	0	*	0
<i>P. phyllicifolia</i>	NR	*	0	*	0
<i>P. racemosa</i>	NR	*	0	*	0
<i>P. apetala</i>	88 ± 2	*	16 ± 5	*	7 ± 2
<i>P. aff. apetala</i> (coastal form)	92 ± 2	*	0	*	0
<i>P. aspera</i>	92 ± 1	*	0	*	13 ± 9
<i>P. elachophylla</i>	76 ± 2	*	0	*	0

Table 3.7. Percentage germination ( ± SE) for non heat treatments for *Spyridium*, *Discaria*, *Stenanthemum* and *Pomaderris* taxa.

Key: C/12 = no treatment, then incubated at 12<sup>0</sup>C; C/20 = no treatment, then incubated at 20<sup>0</sup>C; 5/12 = cold stratified at 5<sup>0</sup>C, then incubated at 12<sup>0</sup>C; 5/20 = cold stratified at 5<sup>0</sup>C, then incubated at 20<sup>0</sup>C. NR = no result obtained. Asterisks represent missing data.

of *S. microphyllum* seeds from the other two sites, as well as *S. obcordatum* seeds from both sites were half this number. Incubation following a dark period had no significant effect on germination (Table 3.6).

Germination after scarification of *S. microphyllum* and *S. obcordatum* seeds was very high (90% and 98% - 100% respectively) indicating physical dormancy imposed by the seed coat is responsible for low germination levels in untreated seed (Table 3.6).

Cold stratification resulted in low germination in seeds of all taxa except *Discaria pubescens*, which resulted in 100% success after incubation at 20°C for up to ten days (Tables 3.6 & 3.7). Most seeds germinated within 5 days. The few seeds which germinated in other taxa generally did so at 5°C, with subsequent incubation at 12°C or 20°C ineffective.

### *Soil seed treatments*

#### *Sown seed*

Four per cent of *S. microphyllum* seeds germinated in soil collected from near the Swan River and placed in the greenhouse. These appeared toward the middle of the experiment after 80 days (Table 3.6).

Similarly in the greenhouse, results for *S. obcordatum* seeds were poor, consisting of a single seed (1%) germinating in soil collected from Dans Hill (Table 3.6).

#### *Soil Stored Seed*

Nineteen soil - stored *S. microphyllum* seed germinated in soil collected from beneath adult plants (Table 3.6). These were very slow to appear, with identifiable true leaves not present until after 150 days. Other species present in trays were predominantly from the Juncaceae or Cyperaceae families, with the most frequent being *Juncus bufonius*, *Cyperus tenellus*, *Centrolepis strigosa* and *Isolepis* sp. Grasses were also prominent, most of which were still unidentifiable at the close of the experiment, but which included *Aira caryophyllea* and *Briza minor*. Dicotyledons were mostly *Hypericum japonicum* and occasionally *Hypochaeris radicata*.



Ten seeds germinated in soil collected from near adult plants at Dans Hill and identifiable true leaves were apparent between 60 and 70 days (Table 3.6). Associated species which also germinated were predominantly grasses such as *Aira caryophyllea* and *Danthonia* sp. Other species were *Gnaphalium* sp., *Astroloma humifusum*, *Gonocarpus tetragyna* and *Wahlenbergia gracilentia*.

### **Heat treatments**

#### ***Spyridium* taxa**

All *Spyridium* taxa responded to both boiling and at least some dry heat treatments prior to incubation at 12°C. However, boiling tended to result in higher germination in some taxa which showed poor dry heat responses (Table 3.8).

At 20°C, the results were more variable, with generally lower germination in most taxa overall (Table 3.9). Boiling also tended to produce better results prior to incubation at this temperature, except in *S. ulicinum* and *S. gunnii*, in which no germination was observed after boiling.

Statistical comparisons between total germination at either incubation temperature were variable. There was no significant difference at either incubation treatment for *Spyridium microphyllum* although at the Douglas - Apsley site, overall germination tended to be higher at 12°C. Incubation temperature was insignificant on germination for *Spyridium obcordatum* at Dans Hill but produced significantly higher germination at Hawley at 12°C ( $T = 2.15$ ;  $P < 0.05$ ). *Spyridium parvifolium* and *S. eriocephalum* had very poor responses when seed was incubated at 20°C, but achieved significantly higher percentages at 12°C.

*Spyridium obovatum* ( $T = -2.9$ ,  $P < 0.01$ ), *S. obovatum* var. *velutinum* ( $T = -2.5$ ,  $P < 0.05$ ) and *S. ulicinum* ( $T = -2.8$ ,  $P < 0.05$ ) all achieved higher germination at 12°C. However, *S. gunnii* ( $T = 4.03$ ,  $P < 0.0001$ ) achieved significantly higher germination at 20°C. *Spyridium vexilliferum* seed performed equally at both incubation temperatures but tended to be higher at 12°C.

Treatment	Boiled	40/1	40/5	40/10	60/1	60/5	60/10	80/1	80/5	80/10	100/1	100/5	100/1 0	120/1	120/5	120/1 0
<b>Taxon</b>																
<i>S. microphyllum</i> (Thumbs)	84 ± 4	0	26 ± 6	33 ± 3	79 ± 15	76 ± 21	97 ± 4	100	93 ± 8	93 ± 7	91 ± 2	46 ± 8	57 ± 4	0	0	0
<i>S. microphyllum</i> (Swan River)	59 ± 9	7 ± 7	3 ± 3	43 ± 28	43 ± 8	35 ± 7	37 ± 16	54 ± 18	47 ± 11	58 ± 6	36 ± 1	23 ± 2	14 ± 0	3 ± 3	0	0
<i>S. microphyllum</i> (Douglas Apsley)	93 ± 2	0	0	2 ± 2	52 ± 13	62 ± 9	64 ± 8	72 ± 5	82 ± 4	69 ± 4	68 ± 25	55 ± 14	6 ± 6	0	0	0
<i>S. obcordatum</i> (Dans Hill)	95 ± 0	9 ± 4	9 ± 2	7 ± 2	6 ± 0	20 ± 5	58 ± 8	78 ± 28	86 ± 1	60 ± 3	77 ± 3	82 ± 18	77 ± 6	42 ± 2	19 ± 14	0
<i>S. obcordatum</i> (Hawley)	77 ± 2	0	12 ± 2	4 ± 4	45 ± 3	11 ± 2	33 ± 3	37 ± 1	69 ± 15	19 ± 1	32 ± 9	13 ± 2	28 ± 4	5 ± 0	4 ± 4	5 ± 0
<i>S. obovatum</i> var. <i>obovatum</i>	100	0	46 ± 13	96 ± 5	86 ± 15	83 ± 6	92 ± 2	98 ± 2	97 ± 3	90 ± 4	88 ± 13	95 ± 5	80 ± 3	0	0	0
<i>S. obovatum</i> var. <i>velutinum</i>	84 ± 3	26 ± 12	46 ± 11	87 ± 9	81 ± 14	86 ± 5	74 ± 7	91 ± 2	94 ± 1	93 ± 7	88 ± 3	88 ± 1	79 ± 12	27 ± 12	14 ± 1	4 ± 2
<i>S. eriocephalum</i>	89 ± 1	8 ± 3	16 ± 4	34 ± 1	64 ± 4	72 ± 2	61 ± 4	95 ± 0	100	98 ± 3	36 ± 3	89 ± 8	76 ± 1	47 ± 15	14 ± 5	0
<i>S. parvifolium</i>	83 ± 3	7 ± 2	4 ± 2	45 ± 10	18 ± 4	95 ± 1	87 ± 4	95 ± 5	94 ± 3	95 ± 1	69 ± 6	78 ± 5	39 ± 7	32 ± 3	0	0
<i>S. ulicinum</i>	53 ± 3	0	18 ± 1	17 ± 8	39 ± 1	40 ± 11	31 ± 2	33 ± 8	56 ± 1	36 ± 7	38 ± 2	13 ± 2	26 ± 1	0	5 ± 5	0
<i>S. gunnii</i>	54 ± 4	0	3 ± 3	9 ± 3	3 ± 3	0	0	0	4 ± 4	0	0	0	0	0	0	0
<i>S. vexilliferum</i>	100	0	6 ± 2	47 ± 8	38 ± 3	47 ± 5	21 ± 5	86 ± 5	92 ± 9	79 ± 4	89 ± 3	73 ± 2	88 ± 12	2 ± 2	0	0

Table 3.8. Percentage germination ( $\pm$  SE) after wet heat treatment, and dry heat treatments of 15 factorially combined temperatures and times, for *Spyridium*. Treated seeds were incubated at 12<sup>0</sup>C.

Key: **boiled** = immersed in boiling water for 10 seconds; 40/1 - 120/10 = seeds heated at 40<sup>0</sup>C, 60<sup>0</sup>C, 80<sup>0</sup>C, 100<sup>0</sup>C & 120<sup>0</sup>C for 1, 5 and 10 minutes.

Treatment	Boiled	40/1	40/5	40/10	60/1	60/5	60/10	80/1	80/5	80/10	100/1	100/5	100/1 0	120/1	120/5	120/10
<b>Taxon</b>																
<i>S. microphyllum</i> (Thumbs)	100	9 ± 0	16 ± 2	64 ± 0	84 ± 2	93 ± 7	96 ± 5	96 ± 5	100	94 ± 3	71 ± 3	62 ± 3	46 ± 5	12 ± 3	37 ± 5	0
<i>S. microphyllum</i> (Swan River)	70 ± 0	0	0	5 ± 0	60 ± 5	48 ± 13	61 ± 1	35 ± 5	38 ± 3	43 ± 3	30 ± 15	45 ± 5	30 ± 10	45 ± 10	38 ± 8	40 ± 5
<i>S. microphyllum</i> (Douglas Apsley)	94 ± 6	8 ± 3	3 ± 3	7 ± 7	24 ± 5	36 ± 3	31 ± 7	57 ± 5	64 ± 7	93 ± 7	84 ± 3	12 ± 7	5 ± 5	8 ± 3	3 ± 3	0
<i>S. obcordatum</i> (Dans Hill)	98 ± 3	7 ± 2	13 ± 3	34 ± 9	42 ± 2	52 ± 2	57 ± 2	77 ± 2	87 ± 2	87 ± 2	85 ± 0	91 ± 8	89 ± 4	74 ± 6	49 ± 1	0
<i>S. obcordatum</i> (Hawley)	86 ± 15	0	0	0	0	8 ± 3	3 ± 3	12 ± 2	5 ± 5	26 ± 7	65 ± 3	17 ± 3	10 ± 5	10 ± 5	10 ± 5	0
<i>S. obovatum</i> var. <i>obovatum</i>	58 ± 14	3 ± 3	0	3 ± 3	56 ± 0	36 ± 3	62 ± 6	39 ± 22	78 ± 11	64 ± 14	61 ± 11	34 ± 6	67 ± 6	36 ± 14	14 ± 3	3 ± 3
<i>S. obovatum</i> var. <i>velutinum</i>	92 ± 8	25 ± 3	9 ± 3	59 ± 3	53 ± 14	33 ± 6	64 ± 3	28 ± 6	11 ± 0	31 ± 9	59 ± 3	75 ± 8	53 ± 20	64 ± 3	78 ± 6	64 ± 3
<i>S. eriocephalum</i>	1 ± 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. parvifolium</i>	13 ± 3	0	0	0	3 ± 3	3 ± 3	0	3 ± 3	3 ± 3	3 ± 3	3 ± 3	0	3 ± 3	0	0	0
<i>S. ulicinum</i>	0	0	0	0	15 ± 5	0	17 ± 3	38 ± 5	27 ± 3	22 ± 3	29 ± 5	26 ± 7	19 ± 0	10 ± 0	10 ± 0	3 ± 3
<i>S. gunnii</i>	0	10 ± 3	0	6 ± 0	32 ± 7	7 ± 7	19 ± 6	38 ± 0	10 ± 4	19 ± 0	25 ± 0	0	0	0	0	0
<i>S. vexilliferum</i>	8 ± 8	0	0	2 ± 2	20 ± 3	7 ± 3	37 ± 2	43 ± 0	44 ± 5	52 ± 9	44 ± 9	85 ± 7	63 ± 11	24 ± 7	16 ± 7	7 ± 3

Table 3.9. Percentage germination ( $\pm$  SE) after wet heat treatment, and dry heat treatments of 15 factorially combined temperatures and times, for *Spyridium* taxa. Treated seeds were incubated at 20°C.

Key: **boiled** = immersed in boiling water for 10 seconds; **40/1 - 120/10** = seeds heated at 40°C, 60°C, 80°C, 100°C & 120°C for 1, 5 and 10 minutes.

### *Comparative taxa*

*Cryptandra amara*, *Pomaderris phyllicifolia* and *P. racemosa* failed to respond to either wet or dry heat treatments. Incubation at 20°C is likely to have been inappropriate for these taxa. However, most taxa, particularly *Pomaderris* spp., returned high percentages at 20°C. Poor germination was observed in *Discaria pubescens* but this was improved after seeds were cold stratified following heat treatments and prior to incubation (Table 3.10).

### *Comparison of germination niches by temperature range*

#### *Incubation at 12°C*

Fifty per cent or higher germination in *Spyridium microphyllum* from the Thumbs and Douglas - Apsley was achieved over a similar range of treatments to *S. obovatum* var. *obovatum*; *S. obovatum* var. *velutinum* and *S. eriocephalum* (40°C/10 minutes - 100°C/10 minutes). *Spyridium microphyllum* (Swan River) and *S. obcordatum* (Dans Hill) were within this range but had lesser germination success, as did *S. parvifolium* and *S. vexilliferum*. *Spyridium obcordatum* (Hawley) and *S. ulicinum* achieved the same level of germination after a single treatment (80°C/10 minutes). *Spyridium gunnii* produced little or no germination (Table 3.8).

#### *Incubation at 20°C*

The range of temperature and time combinations required to produce above 50% germination is similar for *S. microphyllum* (Thumbs) and *S. obovatum* var. *obovatum*. These are 40°C/10 minutes or 60°C/12 minute to 100°C/10 minutes. *Spyridium obcordatum* (Dans Hill) and *Pomaderris* taxa other than *P. racemosa* and *P. phyllicifolia*, responded to a similar range of treatments, between 60°C/1 minute and 120°C/1 minute (Tables 3.9 & 3.10).

The Swan River and Douglas - Apsley populations of *S. microphyllum* and the Hawley population of *S. obcordatum* were within this range but were restricted to 60°C and 80°C respectively (Table 3.9).

Treatment	Boiled	40/1	40/5	40/10	60/1	60/5	60/10	80/1	80/5	80/10	100/1	100/5	100/10	120/1	120/5	120/10
<b>Taxon</b>																
<i>Discaria pubescens</i>	0	6 ± 2	0	11 ± 3	13 ± 9	4 ± 4	4 ± 4	0	0	13 ± 5	9 ± 5	0	0	0	0	0
<i>D. pubescens</i> (+ cold stratification)	*	67 ± 0	96 ± 4	98 ± 2	82 ± 7	100	100	94 ± 6	100	0	52 ± 2	0	0	0	0	0
<i>Cryptandra exilis</i>	75 ± 5	0	0	0	5 ± 0	22 ± 3	14 ± 0	29 ± 10	29 ± 19	24 ± 5	29 ± 5	67 ± 5	53 ± 15	50 ± 2	13 ± 3	0
<i>C. amara</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Stenanthemum pimeleoides</i>	100	12 ± 7	8 ± 3	10 ± 0	12 ± 2	17 ± 3	5 ± 5	12 ± 2	17 ± 3	15 ± 10	31 ± 2	26 ± 7	64 ± 7	77 ± 10	41 ± 8	34 ± 10
<i>Pomaderris elliptica</i>	100	6 ±	6 ± 6	9 ± 3	50 ± 6	50 ± 6	58 ± 14	84 ± 6	95 ± 6	100	70 ± 3	50 ± 17	50 ± 0	48 ± 9	3 ± 3	0
<i>P. pilifera</i>	100	0	0	0	25 ± 17	32 ± 11	69 ± 6	92 ± 9	80 ± 17	92 ± 0	100	96 ± 0	90 ± 11	70 ± 1	46 ± 4	6 ± 2
<i>P. phyllicifolia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. racemosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. apetala</i>	100	10 ± 5	39 ± 3	16 ± 2	98 ± 3	100	83 ± 18	89 ± 12	77 ± 9	100	82 ± 14	96 ± 5	78 ± 14	0	0	3 ± 3
<i>P. aff. apetala</i> (coastal form)	100	0	2 ± 2	2 ± 2	72 ± 2	68 ± 3	55 ± 2	91 ± 0	87 ± 13	84 ± 16	83 ± 9	96 ± 5	96 ± 5	15 ± 15	5 ± 5	2 ± 2
<i>P. aspera</i>	100	15 ± 2	7 ± 3	13 ± 0	19 ± 11	74 ± 4	61 ± 9	83 ± 13	85 ± 15	70 ± 27	68 ± 7	79 ± 5	85 ± 15	42 ± 29	24 ± 2	5 ± 5
<i>P. elachophylla</i>	100	3 ± 3	3 ± 3	3 ± 3	34 ± 13	11 ± 6	35 ± 19	90 ± 6	29 ± 3	74 ± 16	92 ± 8	90 ± 11	100	74 ± 27	0	0

Table 3.10. Percentage germination (± SE) after wet heat treatment, and dry heat treatments of 15 factorially combined temperatures and times, for *Discaria*, *Cryptandra*, *Stenanthemum* and *Pomaderris* taxa. Treated seeds were incubated at 20°C.

Key: **boiled** = immersed in boiling water for 10 seconds; 40/1 - 120/10 = seeds heated at 40°C, 60°C, 80°C, 100°C & 120°C for 1, 5 and 10 minutes.

*Discaria pubescens* responded to wide range of treatments. However, these were in a cooler temperature range, between 40°C and 100°C/1 minute, although not at 80°C/10 minutes. *Stenanthemum pimeleoides* and *C. exilis* had lesser germination success but at higher temperatures, at 100°C to 120°C (Table 3.10). *Spyridium obovatum* var. *velutinum* had the greatest germination success, between 40°C and 120°C (Table 3.10).

Less than 50% germination was recorded for *Spyridium eriocephalum*, *S. parvifolium*, *S. gunnii*, *S. ulicinum* and *C. amara* (Table 3.10).

### **Comparison of germination niches by treatment**

#### *Incubation at 12°C*

The Thumbs population had significantly higher germination after one or more heat treatments than all other taxa except *S. obovatum* var. *obovatum* and *S. obovatum* var. *velutinum*, which had greater germination success than the Thumbs population. It was variable by comparison to *S. eriocephalum* (Table 3.11).

Germination in *Spyridium microphyllum* (Swan River) was equivalent to *S. microphyllum* (Douglas - Apsley), *S. obcordatum* (Hawley), *S. ulicinum* and *S. gunnii* at 12°C. However germination was significantly lower than all other taxa after one or more heat treatments.

*Spyridium microphyllum* (Douglas - Apsley) was variable in its response compared to other *Spyridium* taxa. It had comparable responses after all treatments to *S. microphyllum* (Swan River), *S. parvifolium* and *S. ulicinum* and varied in its response compared to *S. vexilliferum*. It had greater germination success than *S. gunnii* and *S. obcordatum* (Hawley) and lesser success than *S. microphyllum* (Thumbs), *S. obovatum*, *S. obovatum* var. *velutinum* and *S. eriocephalum* (Table 3.11).

*Spyridium obcordatum* (Dans Hill) had greater germination success than the Hawley population of *S. obcordatum* and than *S. microphyllum* (Swan River and Douglas - Apsley), as well as *S. gunnii* and *S. ulicinum*. However, it had lesser germination success than *S. microphyllum* (Thumbs), *S. obovatum*, *S. obovatum* var. *velutinum*, *S. eriocephalum* and *S. parvifolium*. It was comparable to *S. vexilliferum* in all treatments (Table 3.11).

*Spyridium obcordatum* (Hawley) showed significantly less germination success after one or more heat treatments than all taxa except *S. gunnii*, which had lesser success, and *S. microphyllum* (Swan River), with which there was no significant difference (Table 3.11).

Results of all pairwise comparisons are included in Appendix A.1 - A.5.

#### *Incubation at 20°C*

Significantly higher germination in one or more dry heat treatment categories varied between taxa. There was also a different breadth of germination response within the same species, but from different sites.

*Spyridium microphyllum* (Thumbs) proved to be a robust population. It had greater germination success than all other *Spyridium* taxa, other than *S. microphyllum* (Swan), which had higher germination at 120°C, and *S. obcordatum* (Dans Hill), which had higher germination at 100°C/5 & 10 minutes and at 120°C/1 minute (Table 3.12).

*Spyridium microphyllum* (Swan River) had greater germination success than *S. eriocephalum*, *S. parvifolium*, *S. ulicinum* and *S. gunnii* but had significantly lower germination after one or more treatments than *S. obovatum* var. *velutinum* or *S. obcordatum* (both sites). It had a similar response to *S. obovatum* var. *obovatum*. It had lower germination than *S. vexilliferum* at 100°C/5 minutes but significantly better germination at 60°C treatment for 1 and five minutes. When compared to other *S. microphyllum* populations, it was generally more narrow than the Thumbs population but higher at very low or very high temperatures than the Douglas - Apsley population (Table 3.12).

*Spyridium microphyllum* (Douglas - Apsley) also varied in the breadth of its germination response compared to other taxa. It had greater germination success than *S. obcordatum* (Hawley), *S. eriocephalum*, *S. parvifolium*, *S. ulicinum* and *S. gunnii*. It had generally much lesser germination success than the Thumbs population and *S. obcordatum* (Dans Hill). It also had lesser germination success than *S. obovatum* but varied compared to *S. microphyllum* (Swan River), *S. vexilliferum*, and *S. obovatum* var. *velutinum* (Table 3.12).

*S. obcordatum* (Dans Hill) had the greatest germination success of either of the two narrow endemics from any site. There was significantly higher germination

Narrow endemic	Lower overall	Higher overall	Equal to
<i>S. microphyllum</i> (Thumbs)	SGU(9) SOBH(4) SOBDH(2) SMISW(2) SVV(2) SMIDA(1) *SEE(1) SPA(1) SUL(1)	SOO(2) *SEE(2) SOV(1)	
<i>S. microphyllum</i> (Swan River)		SOO(4) SEE(3) SVV(3) SOBDH(2) SMITH(2) SOV(2) SPA(1)	SOBH SMIDA SUL SGU
<i>S. microphyllum</i> (Douglas - Apsley)	SGU(6) SOBH(2) *SVV(1)	SOO(3) SOV(2) SEE(2) *SVV(2) SMITH(1)	SPA SUL SMISW
<i>S. obcordatum</i> (Dans Hill)	SGU(4) SOBH(3) SMISW(2) SUL(2) SMIDA(1)	SOV(3) SOO(3) SEE(3) SMITH(2) SPA(1)	SVV
<i>S. obcordatum</i> (Hawley)	SGU (2)	SOO (10) SEE (9) SOV (8) SVV (7) SPA (5) SMITH (4) SOBDH (3) SMIDA (2) SUL (1)	SMISW

Table 3.11. Incubated at 12<sup>0</sup>C. Comparison of number of dry heat treatments that resulted in significantly greater or lesser percentage germination success compared to narrow endemic populations. Asterisks denote membership of more than one category.

Key: **Lower overall** = taxa in this column resulted in significantly lower germination after one or more dry heat treatments (exact numbers are in brackets). **Higher overall** = taxa in this column resulted in significantly higher germination after one or more dry heat treatments (exact numbers are in brackets). **Equal to** = no significant difference between treatments.

**SOBDH** = *S. obcordatum* (Dans Hill); **SOBH** = *S. obcordatum* (Hawley); **SMISW** = *S. microphyllum* (Swan River); **SMITH** = *S. microphyllum* (Thumbs); **SMIDA** = *S. microphyllum* (Douglas - Apsley); **SOO** = *S. obovatum* var. *obovatum*; **SOV** = *S. obovatum* var. *velutinum*; **SEE** = *S. eriocephalum*; **SPA** = *S. parvifolium*; **SUL** = *S. ulicinum*; **SGU** = *S. gunnii*; **SVV** = *S. vexilliferum*.



Narrow endemic	Lower overall	Higher overall	Equal to
<i>S. microphyllum</i> (Thumbs)	SEE (12) SPA (12) SUL (11) SGU (11) *SOBH (10) SMIDA (9) SVV (8) *SMISW (7) SOV (4) SOO (3)	*SOBDH (3) *SMISW (2)	
<i>S. microphyllum</i> (Swan River)	SEE (12) SPA (10) SGU (6) SUL (5) *SMIDA (3) *SMITH (2)*SVV (2)	*SMITH (7) SOBDH (6) *SMIDA (2) SOV (1) SOBH (1) *SVV (1)	SOO
<i>S. microphyllum</i> (Douglas - Apsley)	SPA (7) SEE (7) SOBH (5) SUL (4) SGU (3) *SVV (2) *SOV (2)*SMISW (2)	SMITH (9) *SOV (6) SOBDH (4) SMISW (3) *SVV (2) SOO (1)	
<i>S. obcordatum</i> (Dans Hill)	SEE (12) SPA (12) SUL (12) SGU 912) SOBDH (11) SVV (8) SMISW (6) SMIDA (4) SOV (4) *SMITH (3) SOO (1)	*SMITH (4)	
<i>S. obcordatum</i> (Hawley)	SEE (3) SPA (3) *SMISW (1) *SUL (1) *SGU (1)	SOBDH (11) SMITH (10) SOV (8) *SMISW (6) SMIDA (5) SVV (5) SOO (4) *SUL (2) *SGU (1)	

Table 3.12. Incubated at 20<sup>0</sup>C. Comparison of number of dry heat treatments that resulted in significantly significantly greater or lesser percentage germination success compared to narrow endemic populations. Asterisks indicate membership of two categories.

Key: **Lower overall** = taxa in this column resulted in significantly lower germination after one or more dry heat treatments (exact numbers are in brackets). **Higher overall** = taxa in this column resulted in significantly higher germination after one or more dry heat treatments (exact numbers are in brackets). **Equal to** = no significant difference between treatments.

**SOBDH** = *S. obcordatum* (Dans Hill); **SOBH** = *S. obcordatum* (Hawley); **SMISW** = *S. microphyllum* (Swan River); **SMITH** = *S. microphyllum* (Thumbs); **SMIDA** = *S. microphyllum* (Douglas - Apsley); **SOO** = *S. obovatum* var. *obovatum*; **SOV** = *S. obovatum* var. *velutinum*; **SEE** = *S. eriocephalum*; **SPA** = *S. parvifolium*; **SUL** = *S. ulicinum*; **SGU** = *S. gunnii*; **SVV** = *S. vexilliferum*.

than in all other taxa, except for *S. microphyllum* (Thumbs), which varied according to treatment (Table 3.12).

*Spyridium obcordatum* (Hawley) had greater germination success than *S. eriocephalum* or *S. parvifolium*. It had lesser success compared to most other taxa. However this varied according to treatment. All other populations of narrow endemics, except *S. microphyllum* (Swan River), had substantially greater germination success, as did the two east coast endemics *S. obovatum* var. *obovatum* and *S. obovatum* var. *velutinum*, and the widespread taxon *S. vexilliferum*. *Spyridium ulicinum* and *S. gunnii* had higher germination at 80°C but lower at 100°C (Table 3.12).

Results of all pairwise comparisons are included in Appendix A.6 - A.10.

### *Seed bank longevity*

There was no significant difference between any combination of seed burial depth and period of burial for either *S. microphyllum* or *S. obcordatum*. However, the number of seed recovered differed substantially between the two species (Table 3.13).

*Spyridium microphyllum* suffered a substantial loss of seed from bags. Decay was the major source of seed loss. Fifty - five per cent of seeds from bags dug up after 12 months were recorded as having disintegrated. However, after replicates were dug up at 24 months, only 52% of seeds were recorded as having disintegrated. Predation (missing seed) was less significant, but increased over time, with buried populations sustaining a 10% and then 20% loss after 12 and 24 months respectively. The proportion of germinated seeds was insignificant compared to total loss (Table 3.14).

There was also little difference between the amount of *Spyridium obcordatum* seed lost at 12 months (32%) compared to 24 months (20%). There was little evidence that any seeds had germinated and the main source of loss was decay. Predation was of little significance at 12 months (3% lost), but increased at 24 months (20% lost), as might be expected for seeds vulnerable to organisms over a longer period of time (Table 3.14).

Buried seeds of either species which received no pre - treatment had a poor germination response after incubation at 20°C. Fewer than 10% germinated for any combination of burial depth and time. *Spyridium microphyllum* seeds which were buried close to the soil surface tended to have a higher response. However, numbers were still very low (Table 3.15).

Treatment	12R1	12R5	12R10	24R1	24R5	24R10
<b>Taxon</b>						
<i>S. microphyllum</i> (Swan River)	44	43	44	37	43	36
<i>S. obcordatum</i> (Dans Hill)	87	73	81	86	80	72

Table 3.13. Percentage of recovered, apparently viable seed of *S. microphyllum* and *S. obcordatum* after burial at nine factorially combined time and soil depth combinations. Key: **12R1** = seeds buried for 12 months at 1 cm; **12R5** = seeds buried for 12 months at 5 cm; **12R10** = seeds buried for 12 months at 10 cm; **24R1** = seeds buried for 24 months at 1 cm; **24R5** = seeds buried for 24 months at 5 cm; **24R10** = seeds buried for 24 months at 10 cm.

Seed fate	Decayed		Germinated		Missing (predated)	
	12m	24m	12m	24m	12m	24m
<b>Taxon</b>						
<i>S. microphyllum</i> (Swan River)	55	52	0	0.3	10	20
<i>S. obcordatum</i> (Dans Hill)	32	20	0.3	0.3	3	20

Table 3.14. Seed fate (% loss) for *S. microphyllum* and *S. obcordatum* seed after burial for 12 and 24 months. Results from different burial depths are combined.

Treatment	12B1	12B5	12B10	24B1	24B5	24B10
<b>Taxon</b>						
<i>S. microphyllum</i> (Swan River)	6 ± 4	4 ± 4	2 ± 2	10 ± 10	0	5 ± 5
<i>S. obcordatum</i> (Dans Hill)	3 ± 3	3 ± 3	0	0	0	0

Table 3.15. Percentage germination ( ± SE) for seed of *S. microphyllum* and *S. obcordatum* after burial at nine factorially combined time and soil depth combinations. Key: **12B1** = buried for 12 months at 1 cm; **12B5** = buried for 12 months at 5 cm; **12B10** = buried for 12 months at 10 cm; **24B1** = buried for 24 months at 1 cm; **24B5** = buried for 24 months at 5 cm; **24B10** = buried for 24 months at 10 cm. All seeds were incubated at 20°C.

Treatment	12B1H	12B5H	12B10H	24B1H	24B5H	24B10H
<b>Taxon</b>						
<i>S. microphyllum</i> (Swan River)	IS	IS	IS	IS	IS	IS
<i>S. obcordatum</i> (Dans Hill)	100	94 ± 6	91 ± 0	98 ± 3	90 ± 11	81 ± 13

Table 3.16. Percentage germination ( ± SE) for seed of *S. obcordatum* after burial at nine factorially combined time and soil depth combinations followed by immersion in boiling water for 10 seconds. Key (all seeds immersed in boiling water for 10 seconds, prior to incubation at 20°C): **12B1H** = buried for 12 months at 1 cm; **12B5H** = buried for 12 months at 5 cm; **12B10H** = buried for 12 months at 10 cm; **24B1H** = buried for 24 months at 1 cm; **24B5H** = buried for 24 months at 5 cm; **24B10H** = buried for 24 months at 10 cm.

There were insufficient *S. microphyllum* seeds retained for heat treatments following burial. However, substantial germination (81% - 100%) was achieved in *S. obcordatum* after seeds were immersed in boiling water for 10 seconds, prior to incubation at 20°C (Table 3.16).

## Discussion

Predation by herbivores is unlikely to influence the abundance or distribution of *S. microphyllum* populations. In spite of exposure to sheep, which can closely graze plants (Wilson 1990), the experimental unprotected population was not significantly affected by herbivore pressure. Grazing pressure on seedlings is unknown, but their close proximity to ground level suggests additional vulnerability to smaller animals such as rabbits and native mammals. However, some unprotected plants were quite low in stature (< 0.5 m) and the effects of grazing were also inconsequential in these individuals.

*Spyridium obcordatum* was affected by grazing. Its prostrate habit renders plants particularly vulnerable to a range of animals and seedlings are likely to be particularly exposed. Negative shoot growth was recorded in summer, after spring growth ensures a build up of biomass. Heavy grazing pressure during low rainfall periods has been observed elsewhere (Wilson 1990). Additional pressure at this time may also be from young animals born in spring.

Reproductive function was not adversely affected in *S. obcordatum*. However, this was not substantiated by field observations at one other site. At Asbestos Range, *S. obcordatum* plants were so heavily grazed that it was impossible to collect enough seeds for germination trials. This suggests that although there were not high numbers of rabbits at this site, pressure from native animals is likely to be significant and the long term viability of populations may be threatened by high native animal numbers. The vegetation at this site consists of heathland, and *S. obcordatum* is one of the few soft leaved and probably one of the most palatable plants, grasses being rare. At Dans Hill there is a much higher grass component in the ground layer, which may be preferentially grazed at different times of the year.

The life histories of the two species were markedly different. Mid to late summer flowering combined with delayed fruit development was observed in *S. microphyllum* and may partially explain rarity in this species. Delayed fruit production means that the genetic and regenerative resources of the population is at risk for most of the year, until seed is shed and can be incorporated into the soil seed bank. Developing seed is particularly vulnerable to destruction by fire, as *S. microphyllum* seed is unprotected by woody fruiting structures.

Flowering is asynchronous with much of the co - existing flora at the site, the majority of which flowers in spring. This timing was coincident with a peak in floral leaf production, suggesting an association between pollinators and flowering time. The corollary is avoidance of competition for pollinators with the majority of other taxa being pollinated earlier.

Phenology does not explain rarity in *Spyridium obcordatum*, which produces fruit soon after flowering in spring. It has a similar pattern of flowering, fruit development and vegetative growth to a number of other Tasmanian Rhamnaceae, including rare and widespread *Spyridium* taxa, *Cryptandra amara*, *Discaria pubescens* and *Pomaderris* spp. Buds are produced soon after seed dispersal so that plants are theoretically vulnerable to the loss of reproductive material through fire. However, *Spyridium obcordatum* can probably resprout, although no recent evidence of this was observed, and reaches reproductive maturity within two years.

Both patterns of fruit maturation were observed in other Tasmanian Rhamnaceae taxa and are known in Rhamnaceae elsewhere in Australia. Neither is necessarily linked to rarity. *Spyridium* species which are distributed in Tasmania and have the same phenological attributes as *Spyridium microphyllum* are *S. gunnii* (endemic), *S. eriocephalum* var. *eriocephalum* (mainly widespread in semi - arid southeastern Australia, but with disjunct populations in sub - humid regions) and *S. vexilliferum* (widespread in southern Australia but mainly confined to coastal areas). Delayed fruit maturation also occurs in the Tasmanian endemics *Stenanthemum pimeleoides*, *Cryptandra alpina* and *C. exilis* and is common in *Stenanthemum* distributed elsewhere in Australia. Immediate fruit development and maturation exists in *Spyridium obcordatum* (endemic), *S. obovatum* (endemic), *S. parvifolium* (widespread in southeastern Australia), *S. ulicinum* (endemic), *Cryptandra amara* (eastern Australia) and all species of *Pomaderris*. The timing of life history events in other members of *Spyridium* is unknown at present.

Once seed of either species is shed, it is likely to be incorporated rapidly into the soil seed bank by ants (Berg 1975), as seed of both species are typical of many southern Australian Rhamnaceae in their possession of a fleshy aril. Where seed development is delayed until after the warmest period, seed coincides with maximal ant activity (Hughes & Westoby 1990).

Both narrow endemics produce viable seed, and are unlikely to be rare because of an inability to reproduce. Seed viability was comparable to other related taxa. Seed production was not measured. It was obvious while collecting seed that all taxa produce high quantities, although this appears to fluctuate between years.

All Rhamnaceae seeds used for germination trials were dormant on release. However, there were three species where no germination was recorded after any form of pre - treatment, although this may be related to incubation temperature. The seed coat was the obstacle to germination in all other taxa, other than *Discaria pubescens* which required cold stratification. Germinability was not improved by different incubation temperatures or by germination medium. However, there was some germination of soil stored seed under greenhouse conditions, suggesting that soil disturbance may influence the regenerative capacity of populations. The results are difficult to interpret because pre - trial numbers of soil stored seed were unknown, as were the age of seeds. However, the results showed that soil stored seed is germinable after 24 months but germination may occur at a low level in the absence of heat stimulus.

Cold stratification was not effective in breaking dormancy, although a few seeds were able to germinate at 5°C.

The effect of heat on germination indicates that the Rhamnaceae taxa used for trials are most likely to regenerate after fire. There is no data available for Eastern Tasmania regarding soil temperatures during fires and collection of this type of data was beyond the scope of the study. Fires are a feature of the region, particularly during summer in dry sclerophyll forest, as is the case in similar vegetation throughout much of eastern Australia (Gill 1975). Burning by Aboriginal people occurred prior to European occupation although the frequency and intensity of these burns is poorly understood (Thomas 1992). Natural ignition is extremely rare. However, deliberately or accidentally lit fires occur with regularity. It is conceivable that germination is stimulated after exposure to the heat of the sun, in particular in shallow soils or rocky ground. However, no published data exists to quantify this possibility. Data pertaining to evaporation and soil moisture is similarly unavailable.

There was a marked difference between the germination of different populations, with the disjunct Thumbs population having higher levels of germination than the other two *S. microphyllum* populations. A similar phenomenon was observed between the two *S. obcordatum* populations, with the Dans Hill population having higher germination over a wider range of treatments than the Hawley population. The results indicate possible genecological differences between populations. However, these may not necessarily relate to population size in both cases. The Hawley population is the smaller of the two and did exhibit a narrower response to heat treatments. However, the Thumbs population is the smallest and most remote *S. microphyllum* population, although numbers are still substantial. Levels of

genetic diversity within and between populations of rare or restricted taxa are variable (Levin *et al.* 1979; Moran & Hopper 1983; Prober *et al.* 1990b; Hopper & Coates 1990) and result from selection pressures in combination with local environmental heterogeneity (Loveless & Hamrick 1984). Fire frequencies at the Thumbs are likely to be far more frequent than at the other two sites, where populations are relatively protected from frequent fires. At Hawley, the *S. obcordatum* population is also relatively fire protected by exposed rock plates, compared to Dans Hill, where fires may have been frequent in the past in open forest. In order to test these conclusions, further sampling over a number of seasons is necessary.

Consideration of the difference in outcome of germination between populations must be extended to comparative taxa used in trials and the results may not reflect the entire range of variation between the narrow endemics and other taxa. In particular, the two species which responded poorly to the higher incubation temperature, *S. eriocephalum* and *S. parvifolium*, occur in vastly different environments to the two narrow endemics. On the contrary, some species were collected from the same sites (for example *Pomaderris elliptica* and *P. aff. apetala* at Hawley, *S. obovatum* at the Swan River) and are close comparisons, even though their germination responses varied markedly.

All three populations of *Spyridium microphyllum* and the *S. obcordatum* population from Dans Hill were non specific regarding incubation temperature and in this respect had a wider germination response than all other *Spyridium* taxa, except for *S. vexilliferum*, which occurs in a few locations over a wide geographic area in Tasmania, but is common in mainland Australia. *Spyridium obcordatum* from Hawley had significantly higher germination at 12°C. All other taxa except *S. gunnii* germinated better at 12°C.

Time of the year of burning may influence germination potential. Consequently, the two narrow endemics may be disadvantaged if they are able to germinate year round if seedlings which arise after a summer fire are to persist under conditions of continued moisture stress. The ability to avoid germinating under summer temperatures is thought to be an adaptive strategy employed by plants so that seedlings are not vulnerable to summer drought (Thanos & Georgiou 1988; Pierce & Moll 1994). This was not borne out by the experimental results, with common species *Pomaderris elliptica*, *P. apetala* and *P. pilifera* also germinating readily after incubation at 20°C. In terms of the effects on populations, although death of a single post - fire generation is unlikely to significantly deplete the seed bank resource, elimination of the parent population and its offspring followed by invasion of the remaining gap by more competitive widespread species may affect population size and the ability of seedlings to establish after future disturbance.



Dormancy was broken by temperatures within the range recorded for other taxa (Cavanagh 1980; Warcup 1980; Keeley 1987; Thanos & Georgiou 1988; Auld & O'Connell 1991; Auld *et al.* 1991; Kilian & Cowling 1992; Pierce & Moll 1994). The width of the germination niche varied between taxa and between sites. Similar responses have been observed elsewhere (Auld *et al.* 1991). *Spyridium obcordatum* (Hawley population) was relatively narrow in its germination response, producing lower numbers of germinated seed than most of its congeners, other than *S. gunnii*. However, it performed better than some more widespread taxa at 20°C. The Dans Hill *S. obcordatum* population had a wider germination response than nearly all other *Spyridium* populations at 20°C but was variable at the lower incubation temperature, being both wider and more narrow than some other Tasmania endemics. *Spyridium microphyllum* populations were also variable. The Thumbs population had the widest response, the Douglas - Apsley and Swan River populations performed better than their congeners at 20°C. At 12°C, these two populations were either more narrow or equal in their response than most other *Spyridium* taxa. Further experimentation using cold smoke as a potential stimulus may increase germination in taxa with an apparently narrow response, as has been observed elsewhere in Australia (Dixon *et al.* 1994).

Thus, there was little experimental evidence to support the hypothesis that narrow endemics necessarily have a narrow germination niche. Rather, this varies between populations and may have implications for competitive interactions between similar species at individual sites under different seasonal conditions. Whilst *S. obcordatum* at Hawley does have a narrow germination niche relative to the other narrow endemic populations and to other *Spyridium* taxa, the Thumbs population of *S. microphyllum* was one of the more robust *Spyridium* populations used for the trials. Intermediate responses occurred in the Dans Hill, Swan River and Douglas - Apsley populations. All three categories had their counterparts in more widespread taxa.

The ability to accumulate persistent seed banks differs between the two species. *Spyridium microphyllum* seeds are vulnerable to decay in excess of twice the rate of *S. obcordatum* seeds. Seeds were buried close to existing *Spyridium* populations, so inappropriate soil conditions seem an unlikely explanation. *Spyridium microphyllum* seeds can be difficult to assess for probable viability. During the germination trials, some apparently plump and healthy seeds were revealed as unviable after imbibing water, and it is possible that a proportion of the seeds which decayed were not healthy. However, it seems unlikely that such a high proportion would have been missed during preparation of bags. Endosperm predation by micro organisms may explain the high level of decay in *S. microphyllum*. Fungal attack has also been implicated in soil seed loss (Crist & Friese 1993) and seems the most likely explanation. The number of decayed *S. obcordatum* seeds was lower than in the experimental *S. microphyllum* population. Seed loss through decay was quite substantial. It is highly unlikely that unhealthy seeds were mistaken during counting, as *S. obcordatum* seeds are very easy to screen. Seed loss through predation by larger soil fauna increased over time but was equivalent in the two species after two years. An ongoing level of predation would be expected.

Seed loss through the combined agents of decay and predation substantially alter the capacity of the soil seed bank in both species, although this is more substantial in *S. microphyllum* and may contribute to rarity. The failure of buried seeds to germinate without stimulus provides little evidence in support of the widely held belief in the early literature that the actions of micro - organisms break down the seed coat (Baskin & Baskin 1989).

## CHAPTER 4

### GEOGRAPHIC AND BIOCLIMATIC CORRELATES OF RARITY IN *SPYRIDIMUM*

#### Introduction

This chapter is an exploratory analysis of *Spyridium* and compares geographic patterns of distribution of taxa with their climatic distributions. It presents bioclimatic profiles for *Spyridium* taxa and examines rarity in *S. microphyllum* and *S. obcordatum* in this context.

Climatic estimates for locations across Australia regardless of their proximity to meteorological recording stations were made possible by the advent of computer programs such as BIOCLIM and other related procedures (Nix 1986; Adomeit *et al.* 1984, 1987). These techniques fit mathematical surfaces to meteorological data. Their application has been widespread, in fields as diverse as palaeoecology (Markgraf *et al.* 1986; Kershaw & Nix 1988), ecophysiology and biogeography (Busby 1986a; Gibson 1986; Longmore 1986; Nix 1986; Hnatiuk & Maslin 1988; Hill *et al.* 1988; Podger *et al.* 1990; Nix 1991); rare plant habitat prediction (Prober & Austin 1990); phytosociology (Brown 1989); and to predict effects of climate change on the potential distribution of biota (Busby 1988).

#### Methods

##### *Data collection*

Implicit in extracting data from external sources is the risk of misidentifications (Nix 1986; Busby 1991). Anomalies may be evident when records are mapped, or when records with extreme bioclimatic values are detected by scrutiny of the climate profile. By these methods, some control can be exerted over the data. However, care must be taken to avoid eliminating records that relate to real disjunctions. Distortion of the true distributions of taxa by land clearance was of concern in this study, as vegetation containing *Spyridium* is likely to have been cleared since early European settlement. Mapping, in conjunction with old herbarium records, can overcome this problem to some extent.

The distributions of 48 *Spyridium* taxa, including species, subspecies and varieties, in mainland Australia and Tasmania were identified from records held in State Herbaria and from flora survey records stored on electronic data bases in State Government nature conservation agencies. Victorian records were taken entirely from the Department for Conservation and Natural Resources data base. Where possible, general habitat and environmental information was noted. Tasmanian records were extracted from the Tasmanian Herbarium, from flora survey data, from communication with reliable sources and from personal observation. All *S.*

*microphyllum* and *S. obcordatum* populations were verified in the field, as were most records for other Tasmanian *Spyridium* species.

Locations of taxa recorded on herbarium sheets with any degree of accuracy were geocoded by conversion to latitude, longitude and elevation above sea level (in metres) using 1:100,000 or 1:25,000 topographic maps (Kershaw & Nix 1988). Precision was to the nearest minute. A degree of subjective judgement was necessary to determine the reliability of a location. In regions where topographic variation was unremarkable, the problems of accuracy were considered to be less serious than in mountainous terrain where locally steep climatic gradients existed. These problems were overcome to some extent by consultation with botanists or other workers in the field and by examination of the climate profiles. Records with extreme values were considered likely to have arisen from this type of error in areas of high relative relief.

### *Taxonomy*

The credibility of bioclimatic analysis clearly rests on the degree to which species are taxonomically resolved. A revision of *Spyridium* is currently being prepared (K. Thiele, Australian National Herbarium, in prep.). Western Australian species have recently been revised (B. Rye, Western Australian Herbarium, in prep.). As a result of this work, a number of new species have been erected. In particular, Western Australian taxa have changed substantially since publication of the Census of Australian Vascular Plants (Hnatiuk 1990). Consequently, only species currently considered highly likely to be retained in *Spyridium* were used for the analysis. These were identified by K. Thiele as "core" species, sharing the same fruit, aril and disc characteristics. All Tasmanian species were core species.

Recently described or resurrected species which have no core status but which were included in the analysis were *S. tricolor* W. R. Barker & Rye sp. nov., a species with a disjunct distribution in Western Australia (Barker & Rye 1993) and *S. erymnocaulum* W. R. Barker ms, known only from the Eyre Peninsula in South Australia (W. R. Barker pers. comm.). New or resurrected Western Australian endemics include *S. villosum* (Turcz.) Benth.; *S. polycephalum* (Turcz.) Rye ms; *S. glaucum* Rye ms; *S. majoranifolium* (Fenzl) Rye var. *majoranifolium* ms; *S. majoranifolium* var. *pediacum* Rye ms; *S. mucronatum* Rye var. *mucronatum* ms; *S. mucronatum* var. *multiflorum* Rye ms; *S. mucronatum* var. *recurvum* Rye ms; *S. minutum* Rye ms; *S. montanum* Rye ms and *S. glaucum* Rye ms.

Other additions include three species to be transferred from *Cryptandra* (K. Thiele pers. comm.). These are referred to in the text as *S. "burraborang"* (formerly *Cryptandra* species A *sensu* Harden 1990); *S. scortechinii* (= *C. scortechinii* F. Muell.) and *S. buxifolium* (= *C. buxifolia* Fenzl).

Four mainland Australian species previously included under *Spyridium* were not core species and were eliminated (*S. complicatum*, *S. denticuliferum*, *S. divaricatum* and *S. tridentatum*). A further five species, previously considered Western Australian endemics were uncertain, mainly because material had not been

examined (K. Thiele pers. comm.). These were *S. cordatum*, *S. kalganese*, *S. microcephalum*, *S. rotundifolium* and *S. westringifolium*. However, *S. divaricatum*, *S. cordatum* and *S. microcephalum* are recognised in Western Australia (B. Rye, pers. comm.) and were retained. Specimens currently curated as *S. microcephalum/cordatum* which have yet to be described were included as a separate taxon (*S. "micord"*). *Spyridium rotundifolium* is no longer recognised and it was excluded from the analysis. It is likely that at least two more species will be described in Western Australia to accommodate material currently held by the Western Australian Herbarium as *Spyridium* sp. and *Spyridium* sp. Frank Hann, both of which were excluded. One other uncertain species, *S. thymifolium*, occurs in South Australia. An examination of herbarium specimens suggested that it is likely to be retained under *Spyridium* and was included in the analysis.

This confusing situation nevertheless resulted in taxonomic information which was considered relatively reliable for all States, although some anomalies are likely to exist which were not detected by the methods outlined above. Tasmania, Victoria and New South Wales have the fewest species, all of which are clearly distinguished from each other and with the exception of *S. tridentatum* in Victoria, are all core species. There are some problems with members of the genus in South Australia, especially in the *S. halmaturinum* - *S. bifidum* - *S. coactilifolium* complex, which are in need of clarification and may prove to contain 8 - 10 species (W. Barker, pers. comm.). However, their credentials are generally satisfactory. Further taxonomic changes will occur as the Australian Rhamnaceae revision progresses. However, the information obtained was assessed as being suitable for the analysis. Taxonomic details are summarized in Appendix B.

### ***Mapping and distributional classification of taxa***

Data files produced for BIOCLIM input were used to map the distributions of each taxon according to latitude and longitude, at a scale of 1: 7,000,000.

Distributions of *Spyridium* were compared and classified according to their geographic range. Latitudinal and longitudinal ranges for each taxon were converted to kilometres from 1:100,000 topographic maps. A taxon displays narrow endemism if it has a combined north - south and east - west range of less than 100 km, based on the commonly recognised criterion used by Brown *et al.* (1983), Hopper & Muir (1984) and Briggs & Leigh (1988). Some taxa were narrowly endemic in either their north - south or east - west range but were treated separately. The remaining categories were disjunct, where populations occurred in two or more widely separated (more than 100 km apart) regions; and widespread, where a taxon had both a north - south and east - west range of more than 100 km. Taxa restricted within regions (defined below) are referred to as regional taxa. The use of political boundaries to broadly define regions is not intended to imply biogeographic significance but is a convenient means of categorizing taxa which are concentrated in particular areas.

## ***Bioclimatic analysis***

### *Generation of synthetic climate estimates*

Geocoded data were used to generate bioclimatic profiles for *Spyridium* taxa using BIOCLIM Version 2.0 (Busby 1986b), which generates 16 climate parameters for each site where a species occurs (Busby 1988; 1991). To achieve this, the program first produces monthly precipitation and temperature estimates for sites anywhere in mainland Australia and Tasmania, using an algorithm (Wahba & Wendelberger 1980) to fit a set of continuous mathematical surfaces to meteorological data (Nix 1986; Busby 1986a; 1988; 1991). The data represent long term climate records from meteorological stations and the algorithm fits a function of latitude, longitude and elevation to it to produce independent monthly estimates throughout the Australian region (excluding off shore islands). A single surface covers the entire continent and models mean monthly maximum and minimum temperatures from 901 meteorological stations. Mean monthly precipitation is modelled for 19 regional surfaces from 11,000 stations and records are from 1901 to 1975 (Busby 1988, 1991). The authors of BIOCLIM claim that predictive error is less than 10% and 5% for monthly precipitation values and mean maximum and minimum temperatures respectively, although in topographically diverse regions or where meteorological data is sparse, this may increase (Nix 1986). The upgraded version of BIOCLIM is likely to overcome these problems to a large degree but was not available on any external user network at the time of analysis.

The second stage calculates 16 synthetic climate parameters referred to as bioclimatic indices (Nix 1991), from the monthly temperature and precipitation estimates. These are:

1. Mean annual temperature ( $^{\circ}\text{C}$ ).
2. Mean minimum temperature of the coolest month ( $^{\circ}\text{C}$ ).
3. Maximum temperature of the warmest month ( $^{\circ}\text{C}$ ).
4. Annual temperature range ( $^{\circ}\text{C}$ ).
5. Mean temperature of the coolest quarter ( $^{\circ}\text{C}$ ).
6. Mean temperature of the warmest quarter ( $^{\circ}\text{C}$ ).
7. Mean temperature of the wettest quarter ( $^{\circ}\text{C}$ ).
8. Mean temperature of the driest quarter ( $^{\circ}\text{C}$ ).
9. Annual mean precipitation (mm).
10. Mean precipitation of the wettest month (mm).
11. Mean precipitation of the driest month (mm).
12. Coefficient of variation of monthly precipitation (seasonality).
13. Mean precipitation of the wettest quarter (mm).
14. Mean precipitation of the driest quarter (mm).
15. Mean precipitation of the coolest quarter (mm).
16. Mean precipitation of the warmest quarter (mm).

These parameters are generated by default, to indicate conditions relative to the physiological requirements of the target species (Nix 1986, 1991), although other

parameters may be derived from the program. In the case of *Spyridium*, they were considered an appropriate starting point for taxa that were geographically widespread and likely to display a broad range of temperature and precipitation regimes.

The third stage of the program produces a climatic profile for each taxon, referred to as the bioclimate envelope or taxon template (Nix 1986), by ranking all the values in numerical order from all of the sites. The result is the mean and standard deviation of each parameter, as well as the minimum, maximum and 5, 25, 50, 75 and 95 percentile values. These data were used for intrageneric comparisons, following the method of Nix (1986), where values within the 5 and 95 percentile range for all climate parameters are taken as core environments.

BIOCLIM provides cumulative frequency distributions of values for each climate parameter, with departure from normality indicative of potential anomalies in the data (Nix 1986, 1991).

A major restriction with BIOCLIM is that it generates synthetic variables, predicted from known data points and as such is not an exact method. Coincidentally, a number of taxa were recorded from near meteorological stations in Western Australia and South Australia, thus lessening problems with bioclimate prediction likely to arise where meteorological data are scant. The results were in agreement with published climatological accounts of the regions where *Spyridium* occurs.

The program's main advantage is that it can deal with large sets of meteorological data that would otherwise be virtually impossible to obtain and process within the time and financial constraints of most research projects. It also enables the user to extract climate estimates by one standard method, rather than relying on methods which may vary between regions. The only alternative is to collect continuous data at each site, clearly impractical when sites are distributed across southern Australia. Nevertheless, comparisons between synthetic variables for sites which may be geographically widely separated, resulting in differing seasonal regimes, must be carefully scrutinised so that only those variables are used which are likely to indicate climatic differences and true variation. For these reasons, careful examination of individual climate profiles is important prior to further analysis.

#### *Canonical Variates Analysis (CVA)*

Canonical Variates Analysis (CVA) was used to directly compare bioclimatic profiles of taxa. CVA is a robust linear technique which has been widely used to specifically distinguish multivariate differences between populations, groups or classes and has been widely used by archaeologists, palynologists, biogeographers and taxonomists (for example Lampert 1981; Hnatiuk & Maslin 1988; Meadows & Sugden 1991). It maximizes the ratio of the between group sum of squares while minimizing the within group sum of squares of the site scores along the first ordination axis (ter Braak 1987). The ordination axes are linear functions of the original variables (in this case synthetic bioclimatic indices), defined by the

canonical coefficients. Members of different populations have values which are as high or as low as possible, maximizing the distance between them (Sokal & Rohlf 1981).

CVA is used where the same sets of variables are measured on known groups and the purpose of the analysis was to discriminate which variable(s) best differentiate(s) groups. CVA assumes that variables are normally distributed within groups, and that the variances and covariances of these variables are similar. Whereas the first criterion could be largely overcome with transformation of the data, comparisons between taxa with vastly unequal group sizes violated the latter assumptions. Trial runs of the entire *Spyridium* data were unsuccessful and consequently some taxa were subsampled, thus reducing the number of records. These were the widespread species *S. parvifolium*, *S. vexilliferum* var. *vexilliferum*, *S. eriocephalum* var. *eriocephalum* and *S. globulosum*. *Spyridium divaricatum*, which contained only one record, was excluded.

A preliminary analysis of all *Spyridium* taxa identified four main groups confined to geographic regions. Some taxa may occur in more than one region (for example *S. parvifolium*). Regions are:

1. Western Australia.
2. South Australia/western Victoria (west of 142° E).
3. Victoria (east of 142° E)/New South Wales/southeastern Queensland.
4. Tasmania.

This analysis was too broad to examine narrow endemics in the context of regional *Spyridium* flora. Further analyses were carried out on each group of regional taxa to distinguish which bioclimatic variables best discriminated narrow endemics from others.

Group means were plotted for each regional analysis.

### *Bioclimatic Ranges*

The distributions of site records within the ordination space for each taxon for each regional analysis was plotted. The degree of dispersion of populations for each taxon was assessed by comparing the standard deviations from their mean score along each axis. The ranges of taxa compared subjectively. Taxa were then categorised as either bioclimatically relatively widespread (having a broad climatic envelope), if site records were dispersed more than one standard deviation from the mean on either axis, or relatively restricted (having a narrow climatic envelope) if site records were dispersed less than one standard deviation from the mean on both axes.

### *Computer Programs*

The storage and manipulation of data, univariate and multivariate statistical analyses and plotting procedures were carried out using SYSTAT Version 5.03



(Systat Inc. 1993). Maps were produced using the Viridans (1992) software package.

## Results

In the following sections, specific aspects of the geographic and bioclimatic distribution of *Spyridium* are discussed according to region, as results are presented. A more general discussion follows.

### *Geographic distribution*

#### *Herbarium and survey records*

The genus *Spyridium* has a wide range across southern Australia and is distributed from 113° 07' E to 152° 51' E between latitudes of 25° 12' S and 43° 15' S. Excluding Tasmanian taxa, all species except three are concentrated between 32° 00' S and 36° 46' S (Table 4.1). Centres of endemism in *Spyridium* are in Western Australia and South Australia. The former is in the south - west Botanical Province, in the Roe and Eyre subdivisions. In South Australia, *Spyridium* is concentrated in an area which includes Kangaroo Island, Southern Lofty, the York and Eyre Peninsulas, extending across to the southeast of South Australia and the Wimmera region into western Victoria. The distribution of the genus is less condensed in Tasmania with *Spyridium* more or less distributed across the state. In eastern Australia, taxa are dispersed from the Grampians in western Victoria more or less along the Great Dividing Range to the Queensland border (Stanthorpe/Girraween area).

#### *Regional distributions*

Land clearance is likely to have affected the mainland Australian distribution of *Spyridium*. Kangaroo Island still retains approximately 20% of its indigenous vegetation (D. Kraehenbuehl pers. comm.) but even more extensive areas have been cleared elsewhere, especially where distributions coincide with the Eyre Peninsula, Mt Lofty Ranges and South East (Interdepartmental Committee of Vegetation Clearance 1976; Mitchel *et al.* 1981; Lange 1983; Schwerdtfeger 1985).

Land clearance has been extensive in Victoria, including areas where *Spyridium* is concentrated (Bridgewater 1976). Vegetation clearance or related activities have undoubtedly contributed to patterns of species decline in this state, with high numbers of rare, threatened and in particular, depleted taxa recognised in the west (Gullan *et al.* 1990; Scarlett & Parsons 1989).

The wheatbelt of Western Australia has also suffered extensive loss of vegetation (Brown 1989). However, species richness in the vegetation in general is known to

TAXON	LAT MIN	LAT MAX	NORTH SOUTH RANGE (KM)	LONG MIN	LONG MAX	EAST WEST RANG E (KM)
<i>S. divaricatum</i>	25 <sup>0</sup> 12'	25 <sup>0</sup> 12'	0	113 <sup>0</sup> 07'	113 <sup>0</sup> 07'	0
<i>S. glaucum</i>	33 <sup>0</sup> 28'	33 <sup>0</sup> 30'	4	120 <sup>0</sup> 00'	120 <sup>0</sup> 01'	2
<i>S. montanum</i>	34 <sup>0</sup> 22'	34 <sup>0</sup> 23'	2	118 <sup>0</sup> 03'	118 <sup>0</sup> 20'	24
<i>S. oligocephalum</i>	33 <sup>0</sup> 41'	34 <sup>0</sup> 03'	41	118 <sup>0</sup> 31'	119 <sup>0</sup> 40'	97
<i>S. spadiceum</i>	34 <sup>0</sup> 42'	35 <sup>0</sup> 02'	37	117 <sup>0</sup> 51'	117 <sup>0</sup> 55'	6
<i>S. villosum</i>	34 <sup>0</sup> 25'	34 <sup>0</sup> 45'	37	117 <sup>0</sup> 28'	118 <sup>0</sup> 11'	60
<i>S. mucronatum</i> var. <i>multiflorum</i>	33 <sup>0</sup> 05'	33 <sup>0</sup> 36'	57	121 <sup>0</sup> 44'	123 <sup>0</sup> 18'	94
<i>S. majoranifolium</i> var. <i>pediacum</i>	34 <sup>0</sup> 31'	34 <sup>0</sup> 35'	7	118 <sup>0</sup> 02'	118 <sup>0</sup> 13'	15
<i>S. mucronatum</i> var. <i>recurvum</i>	33 <sup>0</sup> 45'	34 <sup>0</sup> 05'	35	118 <sup>0</sup> 16'	119 <sup>0</sup> 58'	143
<i>S. mucronatum</i> var. <i>mucronatum</i>	32 <sup>0</sup> 57'	33 <sup>0</sup> 26'	54	120 <sup>0</sup> 05'	123 <sup>0</sup> 12'	262
<i>S. globulosum</i>	28 <sup>0</sup> 44'	35 <sup>0</sup> 08'	710	114 <sup>0</sup> 37'	126 <sup>0</sup> 28'	995
<i>S. majoranifolium</i> var. <i>majoranifolium</i>	33 <sup>0</sup> 29'	35 <sup>0</sup> 06'	180	117 <sup>0</sup> 41'	123 <sup>0</sup> 17'	470
<i>S. microcephalum</i>	32 <sup>0</sup> 10'	34 <sup>0</sup> 13'	228	117 <sup>0</sup> 47'	126 <sup>0</sup> 18'	715
<i>S. minutum</i>	32 <sup>0</sup> 22'	33 <sup>0</sup> 45'	154	120 <sup>0</sup> 44'	122 <sup>0</sup> 41'	117
<i>S. cordatum</i>	32 <sup>0</sup> 59'	33 <sup>0</sup> 53'	100	119 <sup>0</sup> 23'	123 <sup>0</sup> 38'	357
<i>S. "micord"</i>	33 <sup>0</sup> 32'	34 <sup>0</sup> 12'	74	119 <sup>0</sup> 04'	120 <sup>0</sup> 36'	129
<i>S. polycephalum</i>	32 <sup>0</sup> 24'	33 <sup>0</sup> 59'	176	118 <sup>0</sup> 00'	123 <sup>0</sup> 52'	493
<i>S. erymnocaulle</i>	33 <sup>0</sup> 33'	33 <sup>0</sup> 37'	7	136 <sup>0</sup> 14'	136 <sup>0</sup> 26'	17
<i>S. leucopogon</i>	34 <sup>0</sup> 44'	35 <sup>0</sup> 13'	54	135 <sup>0</sup> 30'	136 <sup>0</sup> 01'	43
<i>S. halmaturinum</i> var. <i>integrifolium</i>	35 <sup>0</sup> 42'	36 <sup>0</sup> 02'	37	136 <sup>0</sup> 34'	137 <sup>0</sup> 08'	48
<i>S. eriocephalum</i> var. <i>glabrisepalum</i>	35 <sup>0</sup> 35'	35 <sup>0</sup> 47'	22	137 <sup>0</sup> 29'	137 <sup>0</sup> 56'	38
<i>S. halmaturinum</i> var. <i>halmaturinum</i>	35 <sup>0</sup> 45'	36 <sup>0</sup> 03'	33	136 <sup>0</sup> 36'	138 <sup>0</sup> 06'	126
<i>S. halmaturinum</i> var. <i>scabridum</i>	35 <sup>0</sup> 43'	35 <sup>0</sup> 53'	19	136 <sup>0</sup> 35'	137 <sup>0</sup> 52'	108
<i>S. tricolor</i>	31 <sup>0</sup> 47'	33 <sup>0</sup> 45'	218	123 <sup>0</sup> 17'	133 <sup>0</sup> 19'	867
<i>S. bifidum</i> var. <i>bifidum</i>	32 <sup>0</sup> 07'	36 <sup>0</sup> 44'	513	135 <sup>0</sup> 14'	141 <sup>0</sup> 51'	472
<i>S. bifidum</i> var. <i>integrifolium</i>	33 <sup>0</sup> 09'	36 <sup>0</sup> 10'	335	134 <sup>0</sup> 16'	140 <sup>0</sup> 27'	519
<i>S. subochreatum</i> var. <i>subochreatum</i>	32 <sup>0</sup> 20'	36 <sup>0</sup> 33'	468	135 <sup>0</sup> 46'	142 <sup>0</sup> 21'	553
<i>S. subochreatum</i> var. <i>laxiusculum</i>	35 <sup>0</sup> 11'	36 <sup>0</sup> 46'	176	139 <sup>0</sup> 14'	140 <sup>0</sup> 22'	95
<i>S. coactilifolium</i>	33 <sup>0</sup> 38'	35 <sup>0</sup> 38'	222	138 <sup>0</sup> 28'	138 <sup>0</sup> 37'	13
<i>S. nitidum</i>	34 <sup>0</sup> 21'	36 <sup>0</sup> 49'	274	135 <sup>0</sup> 27'	140 <sup>0</sup> 30'	424

Table 4.1. Geographic ranges of *Spyridium* taxa.

TAXON	LAT MIN	LAT MAX	NORTH SOUTH RANGE (KM)	LONG MIN	LONG MAX	EAST WEST RANGE (KM)
<i>S. phlebophyllum</i>	30 <sup>0</sup> 20'	33 <sup>0</sup> 04'	303	137 <sup>0</sup> 58'	139 <sup>0</sup> 52'	160
<i>S. phylicoides</i>	31 <sup>0</sup> 49'	36 <sup>0</sup> 04'	472	132 <sup>0</sup> 15'	140 <sup>0</sup> 08'	662
<i>S. spathulatum</i>	33 <sup>0</sup> 39'	36 <sup>0</sup> 21'	300	135 <sup>0</sup> 33'	141 <sup>0</sup> 00'	458
<i>S. thymifolium</i>	35 <sup>0</sup> 00'	36 <sup>0</sup> 32'	170	136 <sup>0</sup> 33'	140 <sup>0</sup> 19'	316
<i>S. vexilliferum</i> var. <i>latifolium</i>	35 <sup>0</sup> 47'	36 <sup>0</sup> 46'	109	136 <sup>0</sup> 48'	140 <sup>0</sup> 25'	304
<i>S. "burrageorum"</i>	34 <sup>0</sup> 09'	34 <sup>0</sup> 17'	14	150 <sup>0</sup> 16'	150 <sup>0</sup> 21'	8
<i>S. buxifolium</i>	32 <sup>0</sup> 02'	33 <sup>0</sup> 22'	150	149 <sup>0</sup> 33'	151 <sup>0</sup> 21'	160
<i>S. scortechinii</i>	28 <sup>0</sup> 35'	36 <sup>0</sup> 43'	900	149 <sup>0</sup> 44'	152 <sup>0</sup> 51'	280
<i>S. cinereum</i>	36 <sup>0</sup> 55'	37 <sup>0</sup> 40'	83	142 <sup>0</sup> 27'	149 <sup>0</sup> 57'	630
<i>S. microphyllum</i>	41 <sup>0</sup> 45'	42 <sup>0</sup> 37'	96	147 <sup>0</sup> 45'	148 <sup>0</sup> 15'	42
<i>S. obcordatum</i>	41 <sup>0</sup> 04'	41 <sup>0</sup> 13'	17	146 <sup>0</sup> 31'	146 <sup>0</sup> 46'	21
<i>S. obovatum</i> var. <i>obovatum</i>	41 <sup>0</sup> 01'	43 <sup>0</sup> 12'	242	147 <sup>0</sup> 11'	148 <sup>0</sup> 20'	97
<i>S. obovatum</i> var. <i>velutinum</i>	41 <sup>0</sup> 56'	43 <sup>0</sup> 05'	128	147 <sup>0</sup> 13'	148 <sup>0</sup> 14'	85
<i>S. ulicinum</i>	41 <sup>0</sup> 27'	43 <sup>0</sup> 15'	200	146 <sup>0</sup> 47'	147 <sup>0</sup> 48'	85
<i>S. gunnii</i>	40 <sup>0</sup> 12'	43 <sup>0</sup> 09'	327	144 <sup>0</sup> 26'	148 <sup>0</sup> 05'	307
<i>S. vexilliferum</i> var. <i>vexilliferum</i>	31 <sup>0</sup> 05'	42 <sup>0</sup> 50'	1304	135 <sup>0</sup> 39'	148 <sup>0</sup> 20'	1065
<i>S. parvifolium</i>	32 <sup>0</sup> 43'	41 <sup>0</sup> 19'	955	137 <sup>0</sup> 15'	149 <sup>0</sup> 58'	1068
<i>S. eriocephalum</i> var. <i>eriocephalum</i>	32 <sup>0</sup> 15'	42 <sup>0</sup> 50'	1175	135 <sup>0</sup> 41'	147 <sup>0</sup> 20'	979

Table 4.1. continued. Geographic ranges of *Spyridium* taxa.

be naturally significantly lower than areas to the north west and south east (Hopper 1979). The high degree of homogeneity of distributions suggested that land clearance, although indisputably influential on the distribution of much of the indigenous flora (Leigh & Briggs 1992), may not have totally altered the distribution of *Spyridium*.

Conversely in Tasmania, some taxa have only been collected relatively recently, suggesting natural rarity and discovery with increased botanical activity in recent times. By comparison, the ranges of other Rhamnaceae which prefer fertile soils, such as *Discaria pubescens*, have been severely modified by agricultural practices and their true distributions are only discernible from close scrutiny of herbarium records.

Most taxa occurred relatively close to the coast and in isolated, topographically elevated regions such as ridges or scarps surrounded by coastal plains. In South Australia there was a strong association between distribution patterns and elevated areas such as the Mount Lofty and southern Flinders Ranges. This pattern was repeated in eastern Australia along the Great Dividing Range. In this respect, *S. microphyllum* and *S. obcordatum* were typical members of the genus over much of their range, as nearly all populations were found on ridges, isolated hilltops or headlands. Some non-endemic taxa were closely associated with coastal environments, as well as being found further inland (for example *S. scortechinii*, *S. vexilliferum*, *S. majoranifolium* var. *majoranifolium*, *S. coactilifolium*), but there were only two species which were probable obligate coastal endemics (*S. globulosum* and *S. divaricatum*).

Western Australian herbarium records and published accounts of vegetation where *Spyridium* occurs, indicated that sites were typically heathland, mallee, mallee - heath or dune scrub (Specht 1972; George *et al.* 1979, Lamont *et al.* 1984; Brown 1989). It was less frequently found in open forest, low woodland or thickets (*sensu* Beard 1984). Vegetation may be dominated by *Eucalyptus*, *Casuarina*, *Melaleuca*, *Acacia*, *Dryandra* or *Banksia*. Soils were highly variable, consisting of shallow sands over clay, deep sands, gravelly sands derived from laterite, sandstone, and granites; or calcareous coastal sands. Other sites were located on sandy loam, loam, or clay loam over limestone, granite or spongolite. *S. villosum* was recorded from acid peaty sand at one site. There were no edaphic endemics, where more than one record was available, other than *S. globulosum*. Taxa also displayed a wide altitudinal range and were located at sites on the southeast coastal plain and Western Australian Plateau, mostly between 20 m and 400 m but occasionally up to 600 m.

South Australian/western Victorian taxa were also predominantly confined to shrub - dominated vegetation on a variety of soil textures and types. These included heath, mallee, mallee - heath, scrub or low shrubland and less commonly, low open woodland or low open forest. The latter were frequently dominated by *Myoporum* or *Casuarina* as well as *Eucalyptus*. Soils consisted of acid or calcareous sands, lateritic gravels, sandy loams, loams and clay loams over clay, limestone, laterite granite and calcrete. There were no edaphic endemics. Altitude

was also variable for all taxa, with an overall range of 20 m to 950 m. The majority of taxa were confined to locations below 300 m.

Tasmanian *Spyridium* also occurred in a number of environments. Taxa were mainly associated with shrub - dominated vegetation or gaps within open forest. One species (*S. vexilliferum* var. *vexilliferum*) was recorded from lateritic sand, a rare soil type in the state. Altitudinal ranges were variable.

There were no environmental data available for New South Wales taxa, although their distributions indicate that they are probably associated with sandstone and granite soils in low open vegetation and woodland. Altitude ranged from near sea level to 1100 m.

### *Distribution of taxa*

Fifteen species, subspecies and varieties of *Spyridium* out of 48 (31%) are narrow endemics. At the species level, eleven out of 37 (29%) have both latitudinal and longitudinal ranges of less than 100 km (Table 4.1).

Western Australia has six narrowly endemic species and two varieties out of a total of 20 taxa (40%): *S. divaricatum* (Fig. 4.1a); *S. glaucum* (Fig. 4.1b); *S. montanum* (Fig. 4.1c); *S. oligocephalum* (Fig. 4.1d); *S. spadiceum* (Fig. 4.1e); *S. villosum* (Fig. 4.1f); *S. mucronatum* var. *multiflorum* (Fig. 4.1g) and *S. majoranifolium* var. *pediacum* (Fig. 4.1h).

*Spyridium divaricatum* was confined to dune scrub near Shark Bay at 20 m and was one of two *Spyridium* taxa distributed in the northern sandplain area. *Spyridium montanum* and *S. villosum* occurred in the Stirling Range area as well as at lower altitudes in sandplain vegetation. The remainder of the taxa occurred mainly in sandplain vegetation, or on rocky ridges or in gullies on a variety of substrates, including sand, gravelly loam, clay loam or clay sand. No taxon displayed any habitat, altitudinal or edaphic specificity, except for *S. mucronatum* var. *multiflorum*, which was restricted to the sandplain, and *Spyridium glaucum*, populations of which were distributed between 320 and 350 m. *Spyridium spadiceum* was the only taxon associated with woodland, with all others a component of heathland, mallee heath or mallee scrub.

South Australia/western Victoria has two narrow endemic species and two narrow endemic varieties, *S. erymnocaulum* (Fig. 4.2a); *S. leucopogon* (Fig. 4.2b), *S. halmaturinum* var. *integrifolium* (Fig. 4.2c) and *S. eriocephalum* var. *glabrisepalum* (Fig. 4.2d), out of a total of 21 taxa (19%).

There was only a limited amount of environmental data available for South Australian taxa. They showed similar edaphic diversity to their Western Australian counterparts, occurring on sand, sandy loam, sandy clay, laterite or limestone in shrub dominated vegetation. Altitudes ranged from 20 m - 200 m for *S. leucopogon* and *S. halmaturinum* var. *integrifolium*; 140 m - 400 m for *S. erymnocaulum* and 10 m - 120 m for *S. eriocephalum* var. *glabrisepalum*.



(a) *S. divaricatum*



(b) *S. glaucum*



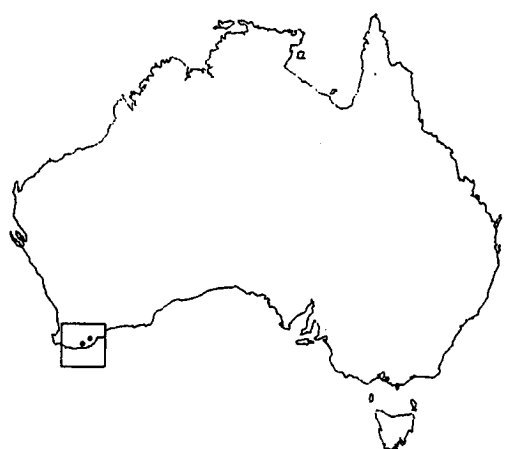
(c) *S. montanum*



(d) *S. oligocephalum*

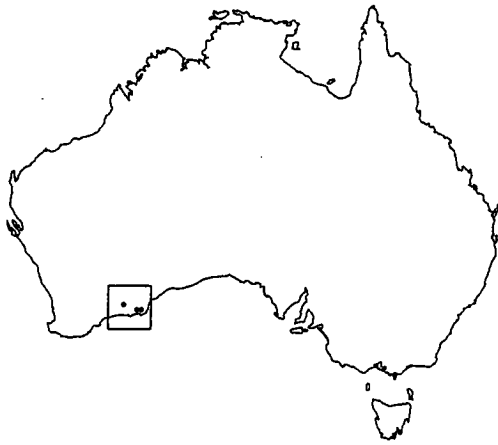


(e) *S. spadiceum*

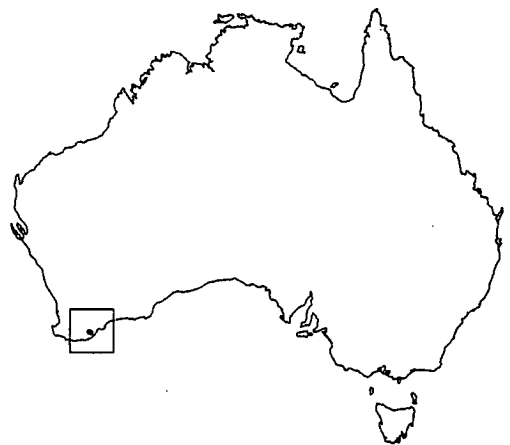


(f) *S. villosum*

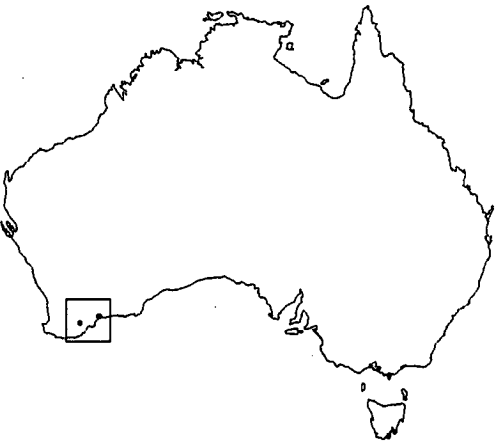
Figure 4.1. The geographic distribution of Western Australian endemics.



(g) *S. mucronatum* var. *multiflorum*



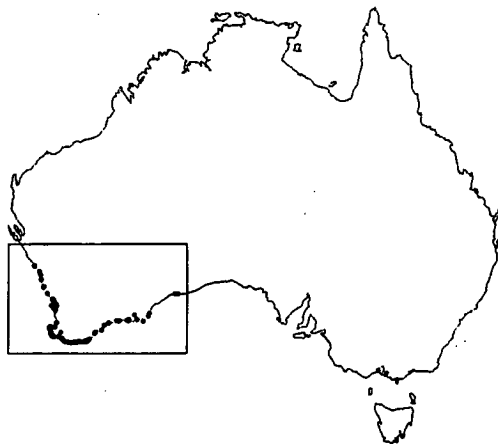
(h) *S. majoranifolium* var. *pediacum*



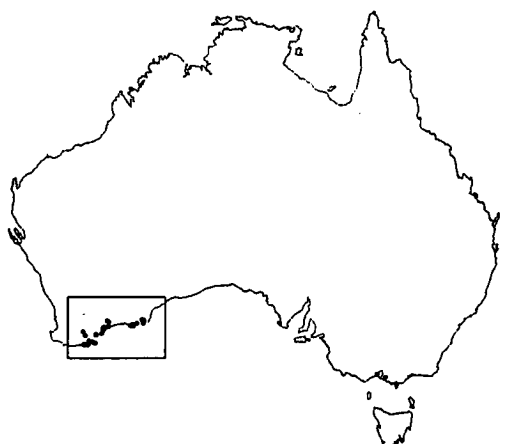
(i) *S. mucronatum* var. *recurvum*



(j) *S. mucronatum* var. *mucronatum*

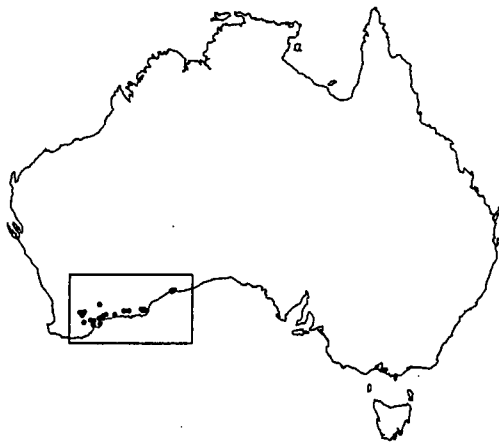


(k) *S. globulosum*

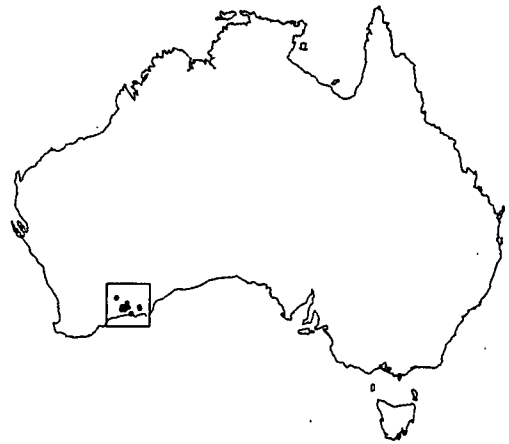


(l) *S. majoranifolium* var. *majoranifolium*

Figure 4.1. continued. The geographic distribution of Western Australian endemics.



(m) *S. microcephalum*



(n) *S. minutum*



(o) *S. cordatum*



(p) *S. "micord"*



(q) *S. polycephalum*

Figure 4.1 continued. The geographic distribution of Western Australian endemics.





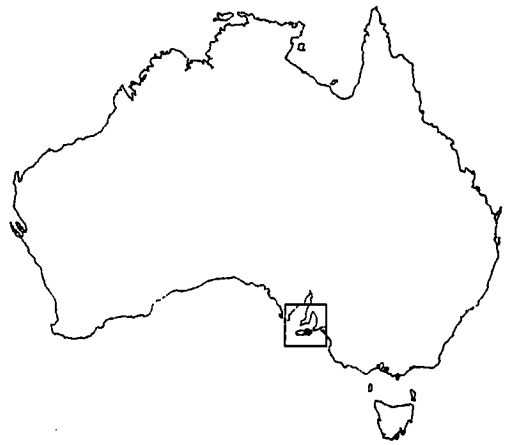
(a) *S. erymnocaule*



(b) *S. leucopogon*



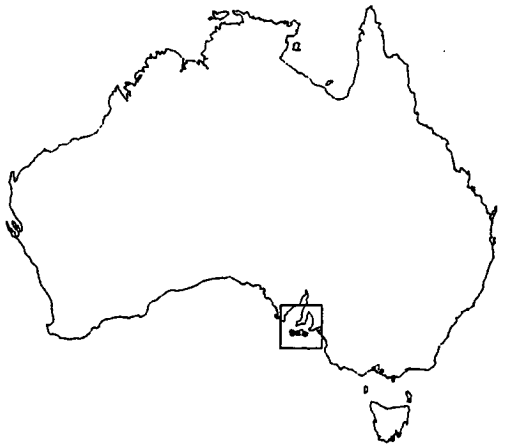
(c) *S. halmaturinum* var. *integrifolium*



(d) *S. eriocephalum* var. *glabrisepalum*

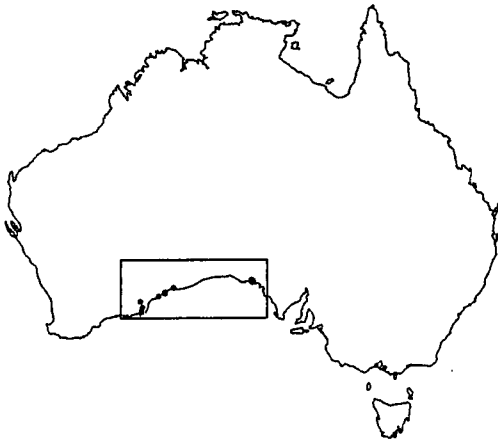


(e) *S. halmaturinum* var. *halmaturinum*



(f) *S. halmaturinum* var. *scabrum*

Figure 4.2. The geographic distribution of South Australian/western Victorian taxa.



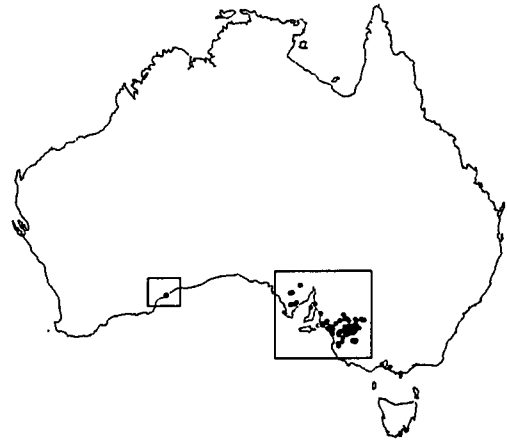
(g) *S. tricolor*



(h) *S. bifidum* var. *bifidum*



(i) *S. bifidum* var. *integrifolium*



(j) *S. subochreatum* var. *subochreatum*



(k) *S. subochreatum* var. *laxiusculum*



(l) *S. coactilifolium*

Figure 4.2 continued. The geographic distribution of South Australian/western Victorian taxa.



(m) *S. nitidum*



(n) *S. phlebophyllum*



(o) *S. phyllicoides*



(p) *S. spathulatum*



(q) *S. thymifolium*



(r) *S. vexilliferum* var. *latifolium*

Figure 4.2. continued. The geographic distribution of South Australian/western Victorian taxa.

Eastern Victoria/New South Wales/southeast Queensland has one narrow endemic, *S. "burraborang"* (Fig. 4.3a), out of a total of 7 taxa (14%).

*Spyridium microphyllum* (Fig. 4.4a) and *S. obcordatum* (Fig. 4.4b) were the only narrow endemics in Tasmania, out of a total of nine taxa (22%). *Spyridium microphyllum* was recorded from gaps within shrubby or heathy eucalypt forest and from shrub - dominated riparian or ridgetop vegetation, mainly on dolerite. *S. obcordatum* occurred in shrubby open eucalypt forest, grassy and shrubby *Allocasuarina* woodland and in coastal heath on a wide range of substrates.

There are also a number of taxa which do not qualify as narrow endemics by the criteria used above, but are restricted either in their east - west or north - south distributions to a range of less than 100 km. These taxa are important because their distributions may indicate a close relationship with topographic or physiographic features, or allude to migration or refugial patterns, and consequently a different biogeographic history to narrowly endemic taxa. These include one species with disjunct populations (*S. cinereum*, Fig 4.3d) and others which may have one very narrow range either latitudinally or longitudinally, compared to a widespread distribution in its other range. In Western Australia, these were: *S. mucronatum* var. *recurvum* (Fig. 4.1i); *S. mucronatum* var. *mucronatum* (Fig.4.1j); *S. cordatum* (4.1o) and *S. microcephalum/cordatum* (= *S. "micord"*, Fig. 4.1 p). South Australian taxa included: *S. halmaturinum* var. *halmaturinum* (Fig. 4.2e); *S. halmaturinum* var. *scabridum* (Fig. 4.2 f); *S. subochreatum* var. *laxiusculum* (Fig. 4.2k); and *S. coactilifolium* (Fig. 4.2l). In Tasmania, *S. obovatum* var. *obovatum* (Fig. 4.4c); *S. obovatum* var. *velutinum* (Fig. 4.4d) and *S. ulicinum* (Fig.4.4e) were restricted in either their latitudinal or longitudinal ranges.

Six species have disjunct distributions: *S. tricolor* (Fig. 4.2g); *S. subochreatum* var. *subochreatum* (Fig. 4.2j); *S. scortechinii* (Fig. 4.3c); *S. cinereum* (Fig. 4.3d); *S. gunnii* (Fig.4.4f) and *S. eriocephalum* var. *eriocephalum* (Fig.4.5c).

Populations of *S. gunnii* are mostly confined to western Tasmania, except for outliers in the southeast and on Flinders Island. *S. tricolor* occurs east and west of the Nullabor Plain, mostly in woodland or mallee communities on sandy soil or sandy loam over limestone (Barker & Rye 1993). It has a localised distribution in South Australia but is more widespread in Western Australia.

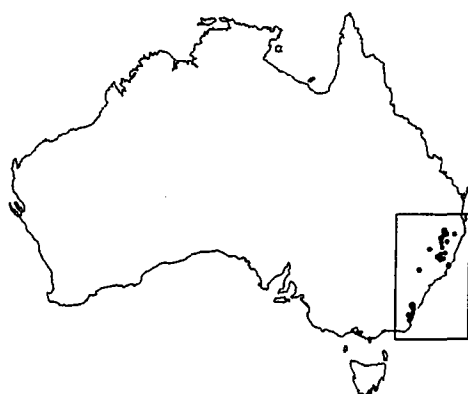
*Spyridium subochreatum* is widespread in heath and mallee in South Australia and Victoria, with two small disjunct populations in open heath west of the Nullabor Plain (Fig. 4.2j). *Spyridium cinereum* occurs in gaps within heathy low woodland in the Grampians in western Victoria and in heathland in eastern Victoria and New South Wales. *Spyridium eriocephalum* has an extensive range, owing to disjunct populations at Risdon, near Hobart; Bacchus Marsh near Melbourne and the Moroka River in south Gippsland, Victoria. However, its main centre of abundance is in heath, mallee shrublands or scrub in semi - arid areas of Victoria and South Australia. Disjunct populations of *S. eriocephalum* in Tasmania occur in gaps within low woodland or mallee type shrubland on locally fertile Aboriginal shell midden sites at Risdon which are also likely to be calcareous. In Victoria, the



(a) *S. "burragorang"*



(b) *S. buxifolium*



(c) *S. scortechinii*



(d) *S. cinereum*

Figure 4.3. The geographic distribution of eastern Victorian/New South Wales/southeastern Queensland taxa.



(a) *S. microphyllum*



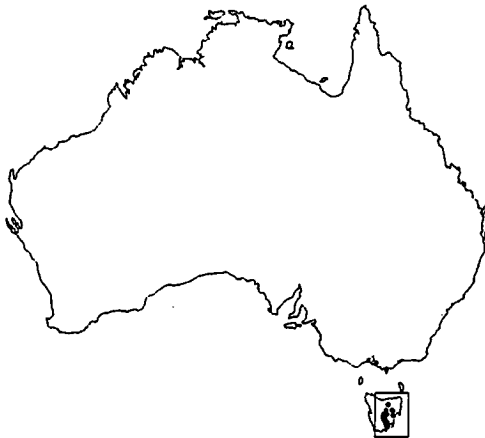
(b) *S. obcordatum*



(c) *S. obovatum* var. *obovatum*



(d) *S. obovatum* var. *velutinum*

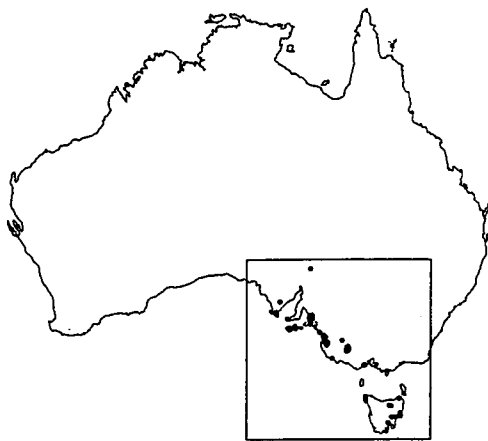


(e) *S. ulicinum*



(f) *S. gunnii*

Figure 4.4. The geographic distribution of Tasmanian endemics



(a) *S. vexilliferum* var. *vexilliferum*



(b) *S. parvifolium*



(c) *S. eriocephalum* var. *eriocephalum*

Figure 4.5. The geographic distribution of taxa widespread in southeastern Australia.

species is confined to disjunct mallee vegetation near Melbourne and to riparian scrub on the Moroka River in eastern Victoria. This is perhaps the most surprising distribution of any *Spyridium* species. There appears to be little similarity between the habitats supporting the three populations.

*Spyridium scortechinii* populations are disjunct between the northern extension of the Great Dividing Range and the New South Wales South Coast and Southern Tablelands. It occurs in open forest between altitudes of 40 and 1100 m.

The most widespread species are a Western Australian endemic, *S. globulosum* (Fig. 4.1k); and southeastern Australian taxa *S. vexilliferum* var. *vexilliferum* (Fig. 4.5a); *S. parvifolium* (Fig. 4.5b); *S. eriocephalum* var. *eriocephalum* (Fig 4.5c). *Spyridium globulosum* is predominantly found on dunes in coastal shrublands or low woodlands from Geraldton to Eyre. *Spyridium vexilliferum* has a very wide range, having been recorded from both coastal and inland environments as diverse as the Grampians, the Flinders Ranges, the Tasmanian Midlands, Kangaroo Island and the coasts of Tasmania, Victoria and South Australia. Throughout most of its range, *S. vexilliferum* prefers low woodland, mallee shrublands or low open vegetation on sandy or gravelly soils.

*Spyridium parvifolium* is widespread in Victoria and eastern South Australia but has a limited distribution in New South Wales and northern Tasmania. Its preferred habitat is woodland or open forest with a seasonally damp, heathy or open shrubby understorey on relatively fertile soils.

### ***Bioclimatic profiles***

The majority of mainland Australian taxa were confined to subhumid or semi - arid mediterranean - type climates. However, sites receive a broad range of mean annual precipitation between 265 mm and 992 mm (Appendix C.1). Tasmanian taxa, some widespread taxa and some regional taxa were distributed in moist, relatively aseasonal or seasonally subdued environments, where rainfall occurs throughout the year under hyperhumid, perhumid or humid conditions. With the exception of *S. gunnii*, all are likely to experience periods of water stress, although there were no taxa which experienced totally dry conditions annually.

*Spyridium microphyllum* sites received on average an annual mean precipitation of 714 mm, while *S. obcordatum* sites received an average of 850 mm per annum (Appendix C.1).

In South and Western Australia, taxa receive summer rainfall generally lower than 16 per cent of annual mean precipitation and frequently down to 10 per cent. In contrast, southeastern Australian taxa may experience up to 22 percent of their annual rainfall during summer. Eastern Australian endemics receive 31-34% of annual mean precipitation during the warmest quarter. The effectiveness of potential moisture availability to plants is more difficult to assess in the absence of evaporation data for sites. For example, most Tasmanian endemics grow in populations on shallow, brown earths where the benefits of heavy rainfall may be



lost even though evaporative losses are likely to be low. By comparison, mainland Australian *Spyridium* generally occur in populations on sandy or gravelly soils which store more moisture but which experience greater evaporation during summer.

Distributions occurred within a range of seasonal regimes, measured as the coefficient of variation of monthly precipitation, with most taxa receiving 30 to 50 per cent of their mean annual rainfall during the coolest quarter. The most seasonal environments supporting *Spyridium* were those of *S. divaricatum* and *S. globulosum* in Western Australia, followed by South Australian taxa. The remainder of Western Australian endemics experienced slightly less seasonal rainfall. Taxa widespread throughout southeastern and eastern Australia occurred in the least seasonal environments. Taxa restricted to eastern Tasmania, including *S. microphyllum*, were confined to areas with rainfall distributed more or less evenly throughout the year, with a subdued maximum in the coolest quarter. The exception was *S. obcordatum*, which experienced a comparatively higher proportion of its rainfall predominantly during winter.

The genus was distributed throughout a range of thermal regimes (Appendix C.2). Although Western Australian *Spyridium* generally occupied sites with the highest mean summer temperatures (19.5°C to 21.7°C), winters were cooler (7.7°C to 11.0°C) and intermediate between Tasmanian (5.6°C to 8.3°C) and South Australian (8.8°C to 12.0°C) winter temperatures. Exceptions were coastal species *S. divaricatum* and *S. globulosum* and the disjunct species *S. tricolor*. Eastern Australian *Spyridium* also experienced cool winters (8.6°C to 9.7°C) but summer means were variable, ranging from warm (*S. scortechinii*, 19.5°C) to hot (*S. buxifolium*, 21.9°C).

In addition to experiencing mild winters, some South Australian *Spyridium*, notably *S. erymnocaulum* and *S. phlebophyllum*, occurred in sites with very high mean summer temperatures (21.4°C and 22.8°C respectively). Annual temperature ranges were generally lowest for Tasmanian and South Australian taxa and highest for Western Australian taxa and eastern taxa. Subdued summer or winter temperatures in Tasmania and South Australia are responsible for this apparent similarity.

### ***Canonical Variates Analysis - full data set***

The first two axes of the ordination adequately summarized between group differences based on bioclimatic variables (Fig. 4.6).

#### ***Axis 1.***

Significant loadings on axis 1 were precipitation of the warmest quarter (0.6) and mean temperature of the driest quarter (-0.5). Groups were consequently separated along this axis on the basis of summer temperature and humidity. The distribution of taxa within the ordination space was somewhat compressed, owing



Taxon symbol	Taxon	Taxon symbol	Taxon	Taxon symbol	Taxon
SDV	<i>S. divaricatum</i>	SLE	<i>S. leucopogon</i>	SBX	<i>S. buxifolium</i>
SGA	<i>S. glaucum</i>	SHI	<i>S. halmaturinum</i> var. <i>integrifolium</i>	SCH	<i>S. scortechinii</i>
SMO	<i>S. montanum</i>	SEG	<i>S. eriocephalum</i> var. <i>glabrisepalum</i>	SCI	<i>S. cinereum</i>
SOL	<i>S. oligocephalum</i>	SHH	<i>S. halmaturinum</i> var. <i>halmaturinum</i>	SMI	<i>S. microphyllum</i>
SPD	<i>S. spadiceum</i>	SHS	<i>S. halmaturinum</i> var. <i>scabridum</i>	SOB	<i>S. obcordatum</i>
SVI	<i>S. villosum</i>	STR	<i>S. tricolor</i>	SOO	<i>S. obovatum</i> var. <i>obovatum</i>
SMM	<i>S. mucronatum</i> var. <i>multiflorum</i>	SBB	<i>S. bifidum</i> var. <i>bifidum</i>	SOV	<i>S. obovatum</i> var. <i>velutinum</i>
SMP	<i>S. majoranifolium</i> var. <i>pediacum</i>	SBI	<i>S. bifidum</i> var. <i>integrifolium</i>	SUL	<i>S. ulicinum</i>
SMR	<i>S. mucronatum</i> var. <i>recurvum</i>	SBS	<i>S. subochreatum</i> var. <i>subochreatum</i>	SGU	<i>S. gunnii</i>
SMU	<i>S. mucronatum</i> var. <i>mucronatum</i>	SBL	<i>S. subochreatum</i> var. <i>laxiusculum</i>	SVV	<i>S. vexilliferum</i> var. <i>vexilliferum</i>
SGL	<i>S. globulosum</i>	SCO	<i>S. coactilifolium</i>	SPA	<i>S. parvifolium</i>
SMA	<i>S. majoranifolium</i> var. <i>majoranifolium</i>	SNI	<i>S. nitidum</i>	SEE	<i>S. eriocephalum</i> var. <i>eriocephalum</i>
SMC	<i>S. microcephalum</i>	SPH	<i>S. phlebophyllum</i>		
SMI	<i>S. minutum</i>	SPL	<i>S. phyllicoides</i>		
SCD	<i>S. cordatum</i>	SPT	<i>S. spathulatum</i>		
MIC	<i>S. microcephalum</i> /cordatum	STH	<i>S. thymifolium</i>		
SPO	<i>S. polycephalum</i>	SVL	<i>S. vexilliferum</i> var. <i>latifolium</i>		
SEY	<i>S. erymnocaulum</i>	SBG	<i>S. "burrageorum"</i>		

Table 4.2. Key to taxon symbols.

distribution of taxa within the ordination space was somewhat compressed, owing to the extreme values for rainfall for the eastern Australian endemics. The majority of mainland Australian endemics comprise a group adapted to warm, dry summers and Tasmanian endemics to a group characterised by relatively mild, moist summers. Taxa endemic to New South Wales/southeastern Queensland experienced warm and humid summer conditions.

*Spyridium obcordatum* populations experience warmer, drier summers than the Tasmanian east coast endemics, placing it equally as close to some mainland Australian taxa, as to the Tasmanian group. *Spyridium microphyllum* occurred in the central area of the Tasmanian group.

#### *Axis 2.*

Taxa were well separated along axis 2. Significant loadings were mean annual temperature (0.6), coefficient of variation of monthly precipitation (-0.6), mean temperature of the coolest quarter (-0.5), mean precipitation of the driest month (0.5) and mean precipitation of the driest quarter (0.5). Tasmanian endemics formed a group having relatively moist summers, low annual temperatures, cold winters and an aseasonal precipitation regime. South Australian and Western Australian endemics formed two clusters denoting mediterranean - type climates, having mild winters temperatures and highly seasonal precipitation. Western Australian endemics were positioned below South Australian taxa, although the former occupied more seasonal environments overall. New South Wales/eastern Queensland taxa were positioned well below Tasmanian and widespread taxa, which is somewhat misleading.

Tasmanian taxa are distinguished from Western Australian and South Australian endemics primarily by having mild, moderately moist summers. Aseasonal precipitation, cold winters and lower overall mean annual temperature also discriminate Tasmanian taxa from their mainland Australian counterparts. Tasmanian endemics and eastern Australian endemics formed discrete clusters, whereas there was some overlap between Western Australian and South Australian taxa.

#### *Bioclimatic ranges - full data set*

Scatter plots of site records for taxa which occurred in more than one region (referred to as trans regional taxa) showed that they were both narrowly and broadly distributed within the bioclimatic envelope. *Spyridium parvifolium*, *S. eriocephalum* and *S. vexilliferum* occur over a wide geographic area in southeastern Australia and were bioclimatically widely distributed. *Spyridium subochreatum* and *S. tricolor* are disjunct between Western Australia and South Australia and were restricted within the ordination space (Fig. 4.7).

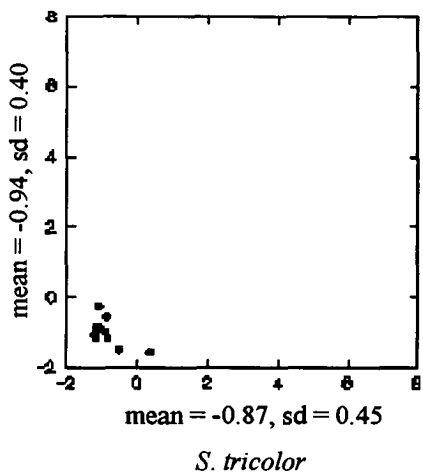
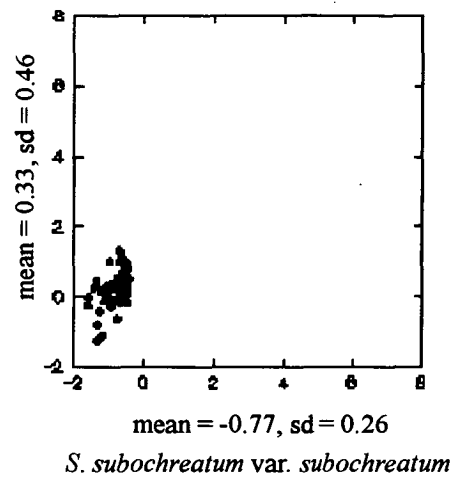
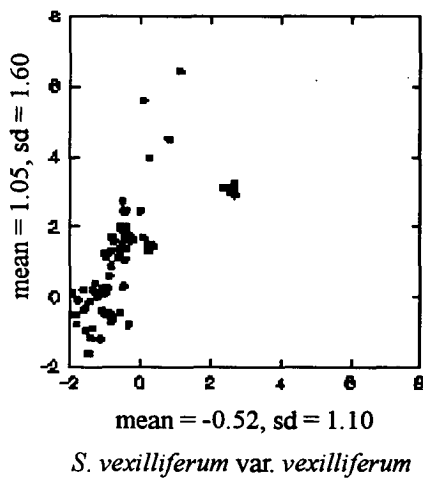
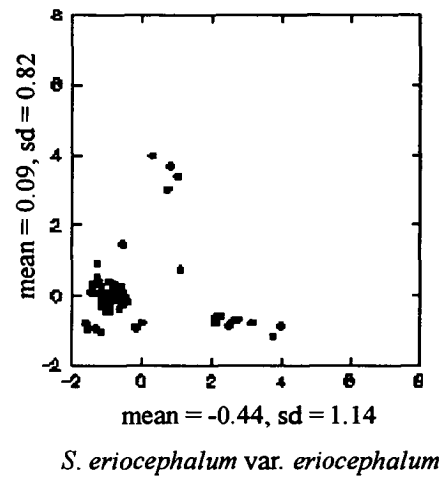
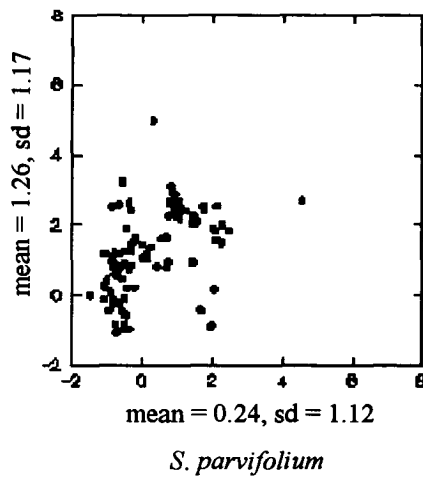


Figure 4.7. Canonical Variates Analysis - full data set, trans regional taxa. The distribution of site records in the ordination space defined by axes 1 and 2.

## Regional analyses

### Bioclimatic profiles - Western Australia

Taxa confined to the Western Australian region experienced mean annual precipitation ranging from 265 mm to 957 mm but were mainly in the driest sites occupied by any *Spyridium* (Appendix C.1). The wide range of precipitation reflects the regional spread of taxa, although rainfall was not evenly distributed between taxa which occurred within the same area, a consequence of the steep rainfall gradients which exist in the southwest province (Beard 1984). The widespread species, *S. globulosum* received the highest rainfall (957 mm per annum), highly variable (sd 281) over its extensive coastal distribution which includes the wet southwest as well as drier areas to the north and east.

Narrow endemics, *S. spadiceum*, *S. villosum*, *S. montanum* and *S. majoranifolium* var. *pediacum*, received mean annual precipitation in excess of 560 mm and up to 939 mm (Appendix C.1). These taxa also occupied sites with the most seasonally pronounced rainfall, with approximately 40 per cent of mean annual precipitation falling during the coolest quarter and only 10 per cent during the warmest quarter. Most of the remainder consists of heavy autumn falls which occur with the onset of low pressure systems. *S. mucronatum* var. *multiflorum* was confined to semi-arid environments with precipitation profiles within the ranges of more widespread taxa (446 mm), and relatively low seasonality. Dry season rainfall comprising 14 per cent of mean annual precipitation. The single *S. divaricatum* record has highly seasonal rainfall which is atypical of its overall arid climate, owing to its proximity to the coast. *Spyridium glaucum* (360 mm) and *S. divaricatum* (265 mm) occupy the driest sites of all *Spyridium* in Western Australia. However, the latter has more seasonal, if scant, winter rainfall by comparison.

Temperature was similarly diverse, with warmest monthly maxima ranging between 27°C and 34.5°C and coolest monthly minima between 7.7°C and 16.8°C (Appendix C.2). These ranges reflect degrees of proximity to the coast and the altitudinal ranges of taxa.

Narrow endemics, including *S. montanum*, *S. spadiceum*, *S. glaucum*, *S. villosum*, *S. oligocephalum* and *S. majoranifolium* var. *pediacum*, were situated in the coolest locations during winter with mean temperatures for the coolest quarter between 7.6°C and 10.8°C (Appendix C.2). The more widespread species *S. polycephalum* also shared this range. During summer most narrow endemics also experienced the lowest mean temperatures in the warmest quarter, ranging between 19.5°C and 20.5°C. These were *S. spadiceum*, *S. majoranifolium* var. *pediacum*, *S. villosum*, *S. montanum* and *S. oligocephalum*. The widespread *S. majoranifolium* var. *majoranifolium* was also within this range. *Spyridium glaucum* was a narrow endemic which occupied sites with cool winters but hot summers, whereas *S. mucronatum* var. *multiflorum* sites experienced mild winters as well as mild summers, within the *Spyridium* range.

In summary, Western Australian narrow endemics occupy a range of bioclimates within the *Spyridium* envelope for the region. Concentrated in the cooler, wetter areas are *S. spadiceum*, *S. montanum*, *S. villosum* and *S. majoranifolium* var. *pediacum*. *Spyridium oligocephalum* and *S. glaucum* receive cool dry winters and warm dry summers. *S. divaricatum* is found on sites which experience cool, moist winters and warm dry summers, with more seasonally pronounced rainfall. *S. mucronatum* var. *multiflorum* is climatically unremarkable, having a similar profile to most widespread regional taxa. These are generally intermediate to the narrow endemics in winter wet, summer dry environments over a range of moisture and temperature regimes, some of which are coincident with those experienced by restricted taxa and some of which are mutually exclusive.

#### *Canonical Variates Analysis - Western Australia*

Between group differences were adequately summarized by the first two axes (Fig. 4.8).

##### Axis 1

Taxa were best discriminated on the basis of mean precipitation in the wettest month (-0.8); mean precipitation in the wettest quarter (-0.8); mean precipitation in the coolest quarter (-0.8); mean annual precipitation (-0.7) and seasonality (-0.7). Taxa were distributed along a gradient representing the most seasonal climates with the wettest Western Australian winters, to climates with lower winter rainfall and less pronounced seasonality.

##### Axis 2

Significant loadings on axis 2 were mean temperature of the coolest quarter (0.6); mean temperature of the wettest quarter (0.6) and mean minimum temperature of the coolest month (0.5). Consequently, taxa were separated on the basis of winter temperatures, although they were generally poorly separated along this axis. Remote from the main group was *S. montanum*.

#### *Bioclimatic ranges - Western Australia*

Scatter plots of all sites for each taxon showed that many Western Australian *Spyridium* taxa were climatically narrowly distributed while some were broadly distributed.

Six narrow endemics were bioclimatically widespread and one was restricted within the bioclimatic profile. The former were *S. glaucum* (Fig 4.9a), *S. montanum* (Fig 4.9b), *S. spadiceum* (Fig 4.9d), *S. villosum* (Fig 4.9e), and to a lesser extent *S. oligocephalum* (Fig 4.9c) and *S. mucronatum* var. *multiflorum*

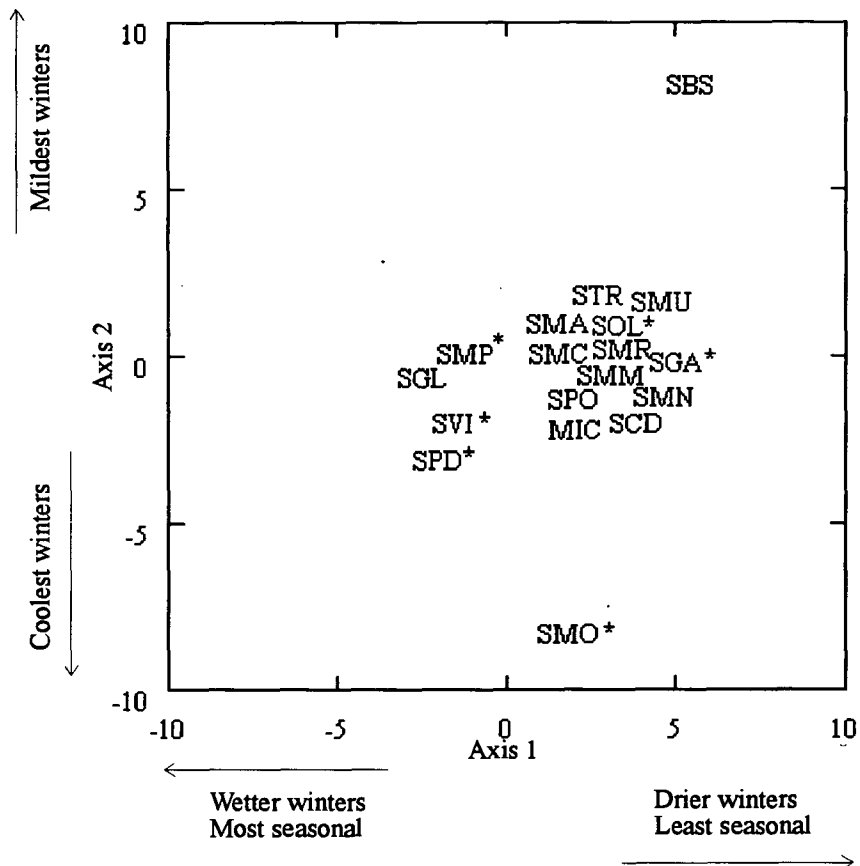
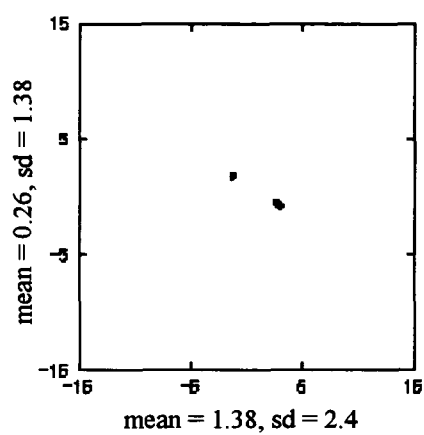
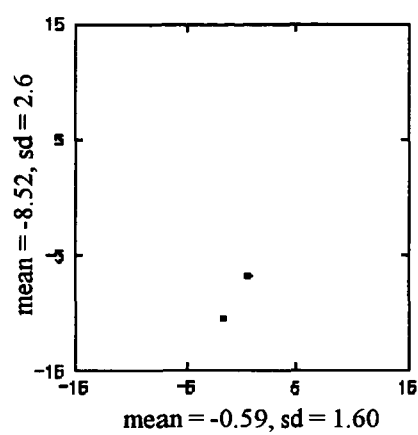


Figure 4.8. Canonical Variates Analysis - Western Australia. The distribution of taxa in the ordination space. Asterisks denote narrow endemics. See Table 4.2 for a key to taxon symbols.

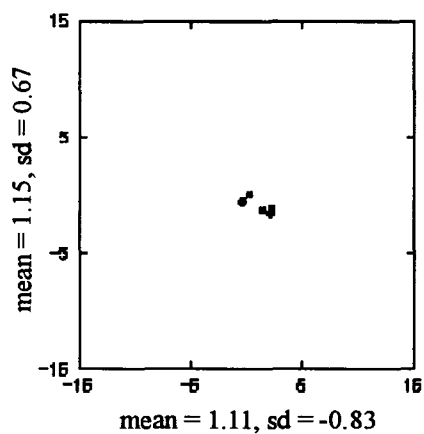




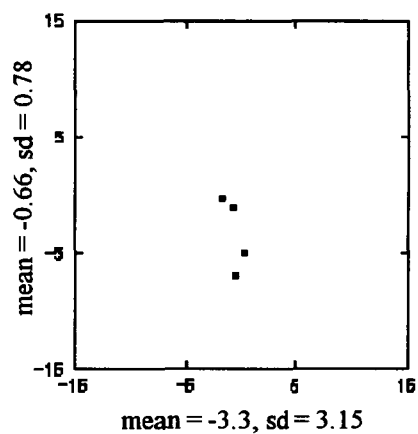
(a) *S. glaucum*



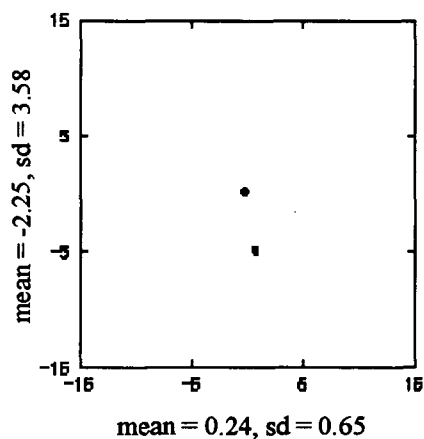
(b) *S. montanum*



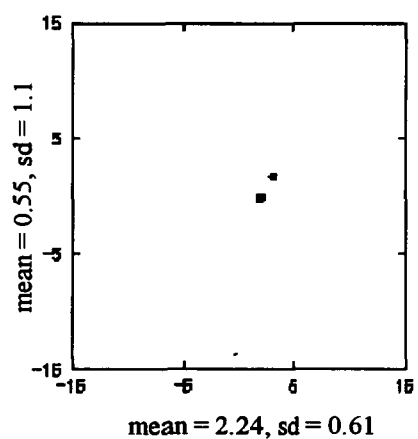
(c) *S. oligocephalum*



(d) *S. spadiceum*

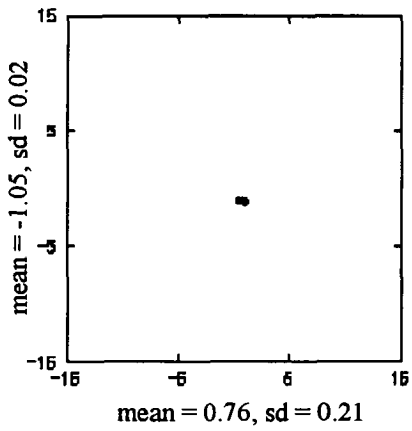


(e) *S. villosum*

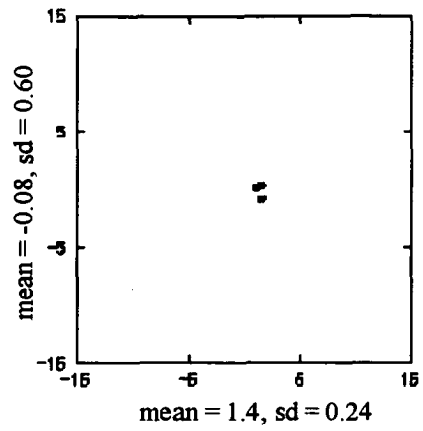


(f) *S. mucronatum* var. *multiflorum*

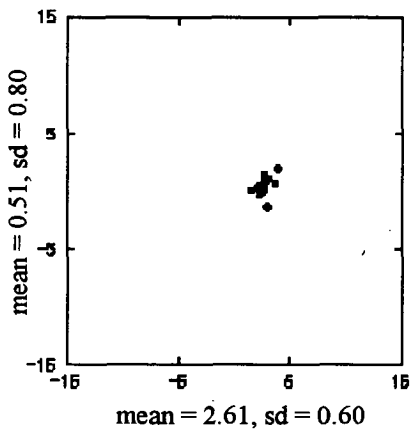
Figure 4.9. Canonical Variates Analysis - Western Australia. Scatter plots showing the distribution of site records in the ordination space defined by axes 1 and 2.



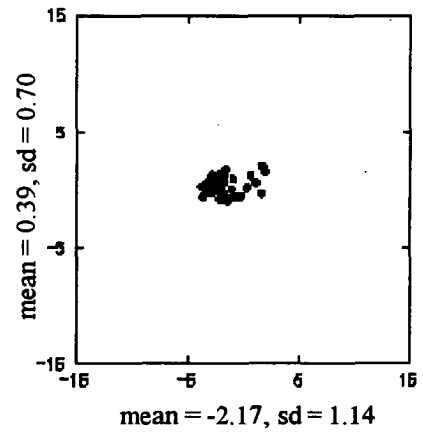
(g) *S. majoranifolium* var. *pediacum*



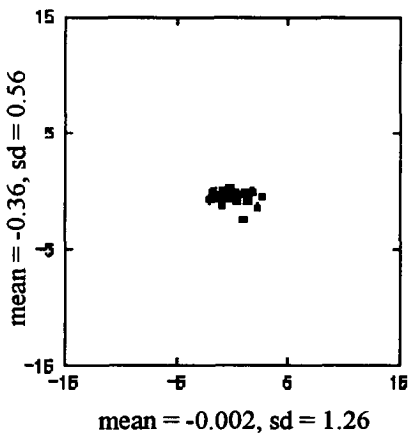
(h) *S. mucronatum* var. *recurvum*



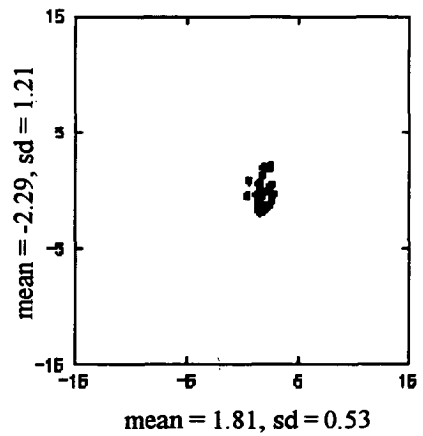
(i) *S. mucronatum* var. *mucronatum*



(j) *S. globulosum*



(k) *S. majoranifolium* var. *majoranifolium*



(l) *S. microcephalum*

Figure 4.9 continued. Canonical Variates Analysis - Western Australia. Scatter plots showing the distribution of site records in the ordination space defined by axes 1 and 2.

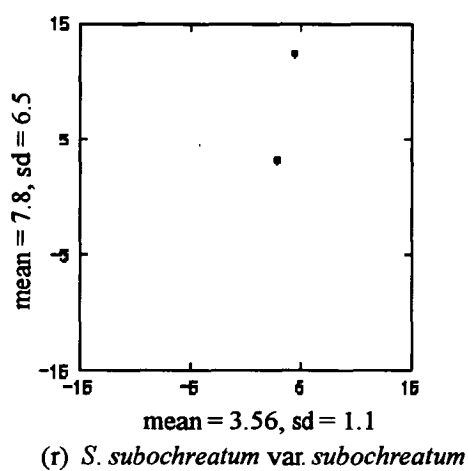
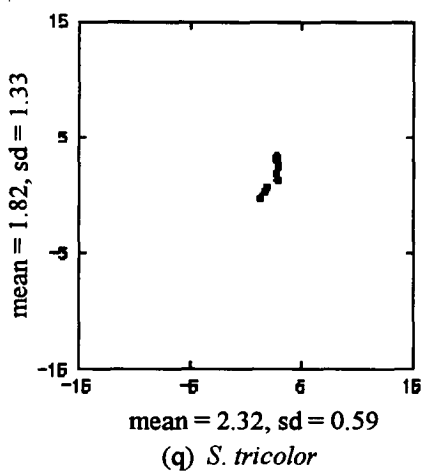
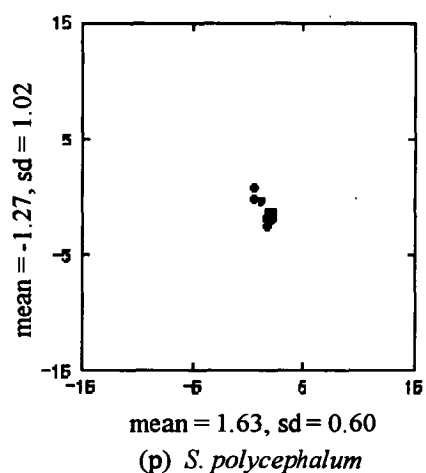
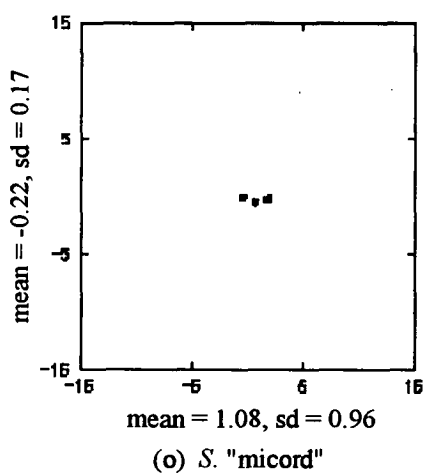
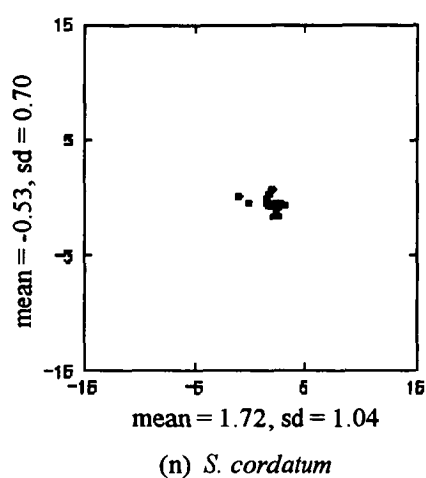
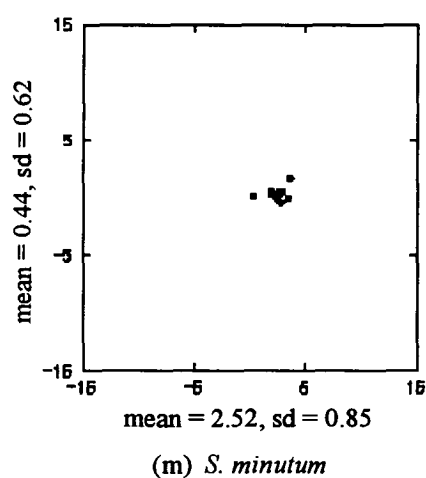


Figure 4.9 continued. Canonical Variates Analysis - Western Australia. Scatter plots showing the distribution of site records in the ordination space defined by axes 1 and 2.

lesser extent *S. oligocephalum* (Fig 4.9c) and *S. mucronatum* var. *multiflorum* (Fig 4.9f). The remaining narrow endemic *S. majoranifolium* var. *pediacum* was bioclimatically restricted (Fig. 4.9g).

There were seven taxa that were geographically and bioclimatically widespread. These were *S. globulosum* (Fig. 4.9j), *S. majoranifolium* (Fig. 4.9k), *S. microcephalum* (Fig. 4.9l), *S. cordatum* (Fig. 4.9n) and *S. polycephalum* (Fig. 4.9p). Taxa which were geographically widespread but bioclimatically restricted were *S. mucronatum* var. *recurvum* (Fig. 4.9h), *S. mucronatum* var. *mucronatum* (Fig. 4.9i), *S. "micord"* (Fig. 4.9o) and *S. minutum* (Fig. 4.9m).

*Spyridium tricolor* and *S. subochreatum*, two taxa with populations which are disjunct between Western Australia and eastern Australia, but which are geographically narrow in the west, were locally bioclimatically widespread within the region (Figs. 4.9 q & r).

#### *Bioclimatic profiles - South Australia/western Victoria*

Taxa endemic to the South Australian and western Victorian region received mean annual precipitation ranging between 318 mm and 764 mm (Appendix C.1). However, the majority (11) were within the 500 to 700 mm isohyets and unlike Western Australian and Tasmanian endemics, there were no taxa recorded from comparatively wet environments. The coefficient of variation of monthly precipitation was highest for South Australian/western Victorian taxa overall, except for *S. phlebophyllum*, which was mainly restricted to arid sites in the Flinders Ranges and northeastern regions, and *S. subochreatum* var. *subochreatum*. They are, therefore the most "mediterranean" of all *Spyridium* species, confined to a semi - arid climate where no taxon experienced rainfall in excess of 800 mm per annum, a pronounced winter rainfall mostly in excess of 40 per cent of mean annual precipitation and summer rainfall which was approximately 10 per cent of mean annual precipitation.

The four narrow endemics occupied drier sites during most of the year but most experienced relatively wet winters (Appendix C.1). *Spyridium erymnocaulum* was recorded from sites receiving an average of only 148 mm of winter rain, which was 37 per cent of the mean annual precipitation of 399 mm. Summers were also dry (55 mm in the warmest quarter) but consisted of 14 per cent of mean annual precipitation, making the two sites where it occurs only moderately seasonal and semi - arid to arid, being located in the winter rainshadow belt of the north eastern Eyre Peninsula, but receiving some orographic rainfall during summer because of the proximity of sites to the Cleve Hills.

*Spyridium leucopogon* is endemic to the southern Eyre Peninsula, northwest of the Port Lincoln area. Sites were semi - arid (502 mm rainfall per annum) and highly seasonal, experiencing dry summers (46 mm or 9 per cent of mean annual precipitation) and moderately wet winters (232 mm, 46 per cent of total). Sites receive rain bearing westerly winds during winter although the rainfall profile for the area indicates slightly lower winter precipitation than the broader region in

which they are situated (Schwerdtfeger 1985), indicating the significance of rain from the southwest during spring (Gentilli 1972) and the possibility of mild local rainshadow effects during winter.

The Kangaroo Island endemics *S. eriocephalum* var. *glabrisepalum* and *S. halmaturinum* var. *integrifolium*, received moderate winter rainfall for the region (230 and 307 mm) and dry summers during which 10 - 11 per cent of mean annual precipitation (524 and 665 mm) falls on populations (57 and 64 mm). Sites were semi - arid and highly seasonal with 44 - 46 per cent of rain falling in winter. *S. eriocephalum* var. *glabrisepalum* is restricted to the rainshadow belt of the low lying southeast (Gentilli 1972), whereas *S. halmaturinum* var. *integrifolium* experiences a broader rainfall range.

Temperatures for most South Australian/western Victorian *Spyridium* sites showed relatively little variation between mean annual minima and maxima and had the lowest range of any *Spyridium*, except for some Tasmanian taxa (Appendix C.2). Winters were generally mild and summers warm to very warm. Mean temperature for the coolest quarter ranged between 8.8°C and 12.0°C. Mean temperature for the warmest quarter ranged between 18.4°C and 22.8°C.

*Spyridium erymnocaula* experienced mean winter temperatures (10.4°C) in the cooler end of the range occupied by South Australian taxa, but sites were among the warmest in the state during summer (21.3°C). *Spyridium leucopogon* occurred in sites with very mild mean temperatures for the coolest quarter (12.0°C) and warm summers (20.3°C). The difference in warmest month maxima, 29.5°C and 26.4°C respectively, is a result of differing effects of potentially cooling easterlies passing over Spencer Gulf during summer. Whereas *S. erymnocaula* populations are probably sheltered by the Cleve Hills, *S. leucopogon* populations are less protected from their cooling effect. The proximity of *S. eriocephalum* var. *glabrisepalum* and *S. halmaturinum* var. *integrifolium* populations to the coast ensured very mild temperatures during winter (11.7°C and 11.8 °C) and summer temperatures in the cooler end of the state range (18.9°C and 18.4 °C).

In summary, the area occupied by *Spyridium* in South Australia/western Victoria is climatically diverse in its range of rainfall and temperature regimes, including three mediterranean sub - climates as well as near arid and subhumid climates. However, in spite of the existence of steep gradients, the rainfall and temperature minima and maxima are limited in comparison to those experienced by Western Australian taxa. Three of the four narrow endemics occupy the driest sites, but not exclusively, and have no common temperature requirements, although three occur in sites which are among some of the warmest in the state during winter and have highly seasonal precipitation.

#### *Canonical Variates Analysis - South Australia/western Victoria*

The first two axes of the ordination adequately summarized between group differences (Fig. 4.10). Kangaroo Island taxa formed a relatively discrete cluster and were slightly separated from the remainder of groups. The remaining taxa

were scattered throughout the ordination space. Narrow endemics occurred within the bioclimatic range of most widespread taxa.

### Axis 1

The most significant loadings along axis 1 were mean precipitation in the wettest month (0.7), wettest quarter (0.7) and coolest quarter (0.7); mean annual precipitation (0.6); seasonality (0.8); mean temperature in the warmest quarter (-0.6) and mean maximum temperature in the warmest month (-0.7); and mean annual temperature range (-0.6). These identified sites scattered along a gradient describing warm summers and dry winters at the proximal end of the axis, to highly seasonal, wet winter environments with cooler summers.

### Axis 2

Axis 2 represented a combined temperature and rainfall gradient, ranging from cool winters with taxa at the distal end experiencing some summer rain, to taxa experiencing mild winters and dry summers. Significant loadings were mean temperature in the coolest quarter (-0.6); mean precipitation in the driest month (0.6) and mean precipitation in the driest quarter (0.6).

### *Bioclimatic ranges - South Australia/western Victoria*

The narrow endemic *S. erymnocaula* was bioclimatically widely distributed (Fig. 4.11a). The remaining three narrow endemics (*S. leucopogon*, *S. halmaturinum* var. *integrifolium* and *S. eriocephalum* var. *glabrisepalum*) had narrow bioclimatic distributions, being highly concentrated within the ordination space (Figs. 4.11b, c & d). The disjunct taxon *S. tricolor* which has a restricted distribution in the region was also bioclimatically widespread (Fig. 4.11t).

Most widespread taxa were also bioclimatically restricted. These were *S. halmaturinum* var. *halmaturinum* (Fig. 4.11e), *S. halmaturinum* var. *scabridum* (Fig. 4.11f), *S. bifidum* var. *integrifolium* (Fig. 4.11h), *S. nitidum* (Fig. 4.11j), *S. phyllicoides* (Fig. 4.11l), *S. thymifolium* (Fig. 4.11n) and *S. vexilliferum* var. *latifolium* (Fig. 4.11o). *Spyridium parvifolium*, a trans regional species, was bioclimatically restricted in the region (Fig. 4.11r).

Widespread taxa which were also bioclimatically widespread were *S. bifidum* var. *bifidum* (Fig. 4.11g), *S. subochreatum* var. *laxiusculum* (Fig. 4.11i), *S. phlebophyllum* (Fig. 4.11k), *S. coactilifolium* (Fig. 4.11j), *S. spathulatum* (Fig. 4.11m), *S. subochreatum* (Fig. 4.11p), *S. eriocephalum* (Fig. 4.11q) and *S. vexilliferum* (Fig. 4.11s).

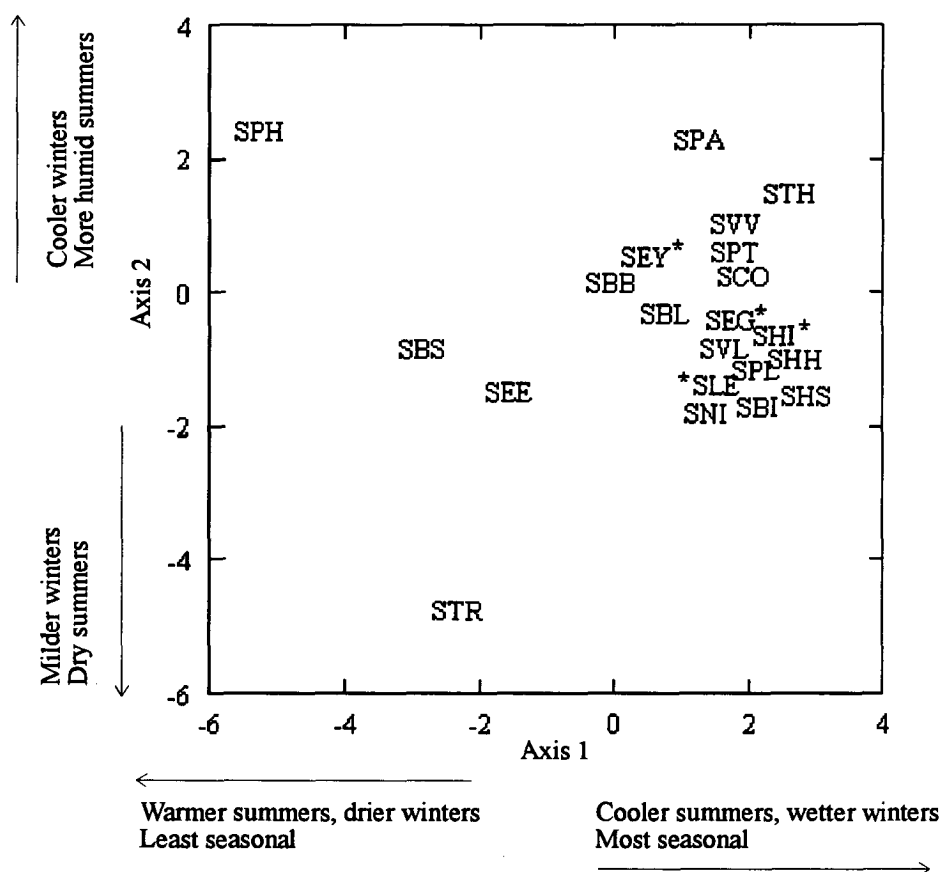


Figure 4.10. Canonical Variates Analysis - South Australia/western Victoria. The distribution of taxa in the ordination space. Asterisks denote narrow endemics. See Table 4.2 for a key to taxon symbols.

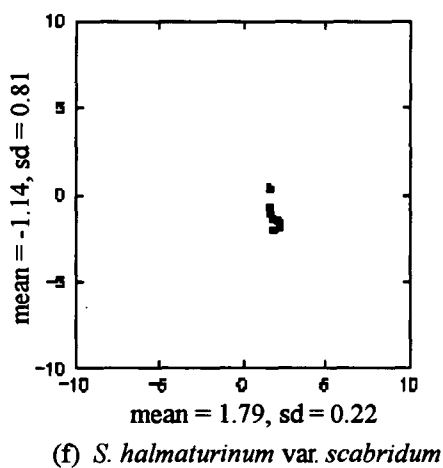
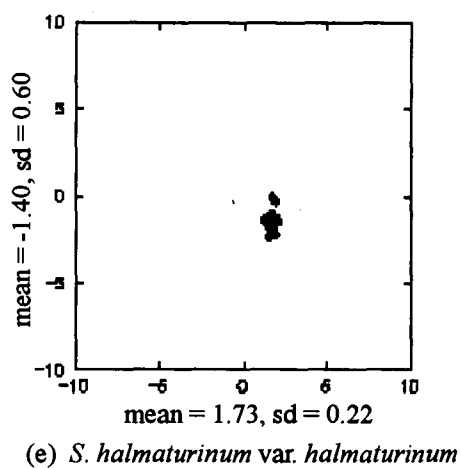
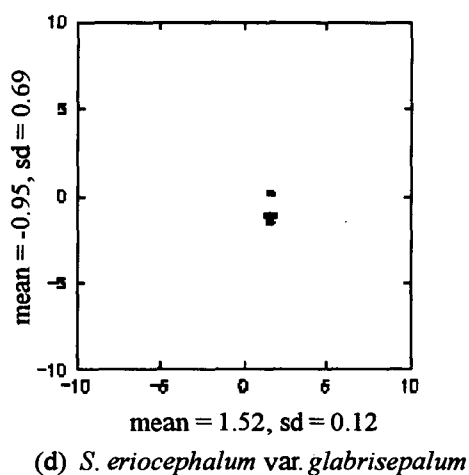
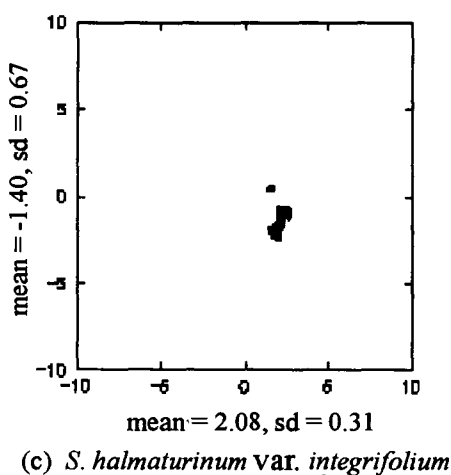
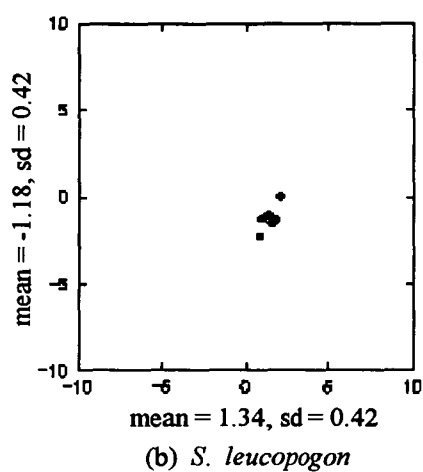
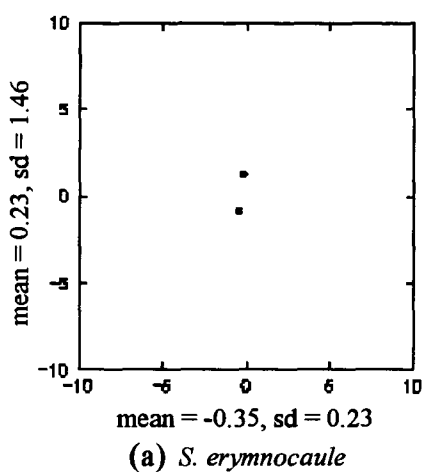
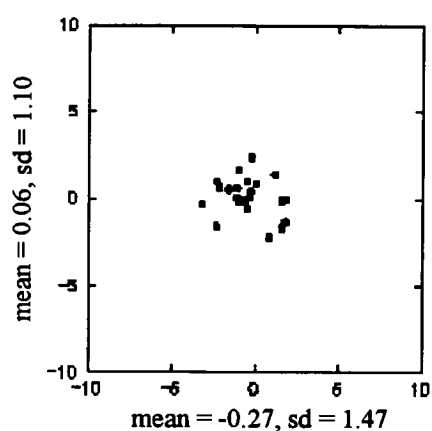
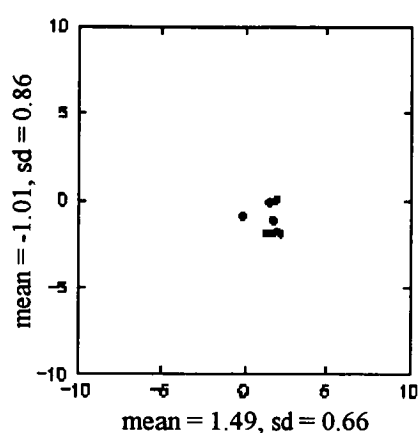


Figure 4.11. Canonical Variates Analysis - South Australia/western Victoria. Scatter plots showing the distribution of site records in the ordination space defined by axes 1 and 2.

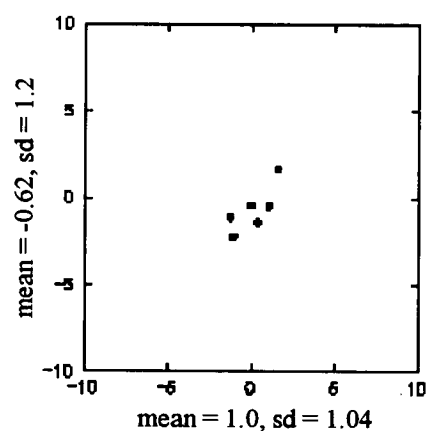




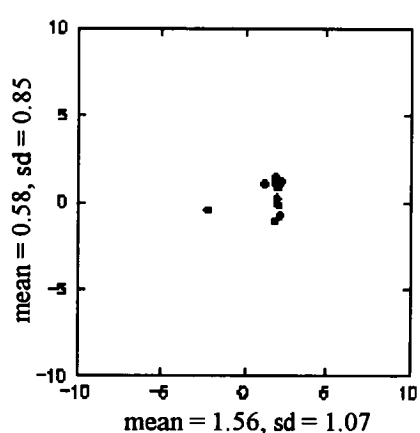
(g) *S. bifidum* var. *bifidum*



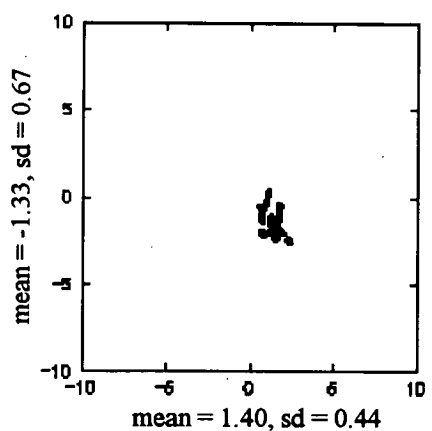
(h) *S. bifidum* var. *integrifolium*



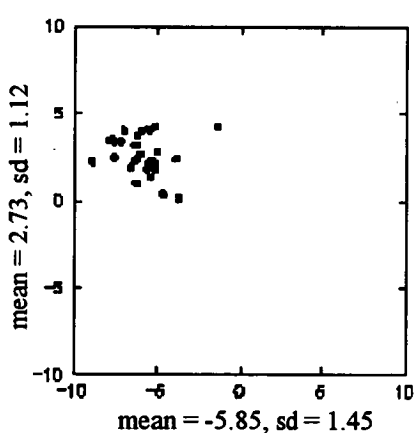
(i) *S. subochreatum* var. *laxiusculum*



(j) *S. coactilifolium*

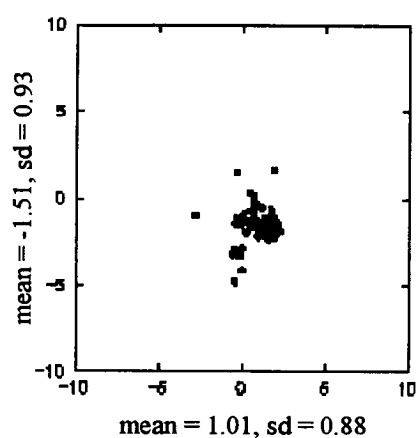


(l) *S. nitidum*

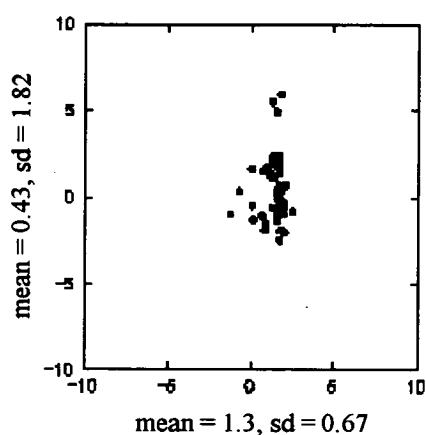


(k) *S. phlebophyllum*

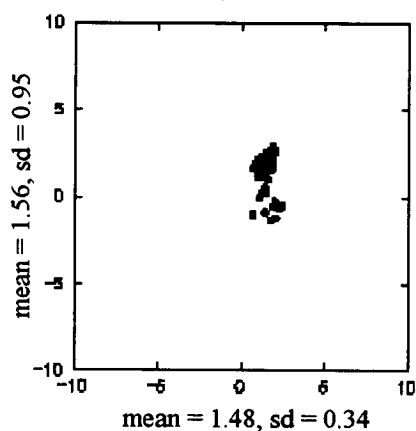
Figure 4.11 continued. Canonical Variates Analysis - South Australia/western Victoria. Scatter plots showing the distribution of site records in the ordination space defined by axes 1 and 2.



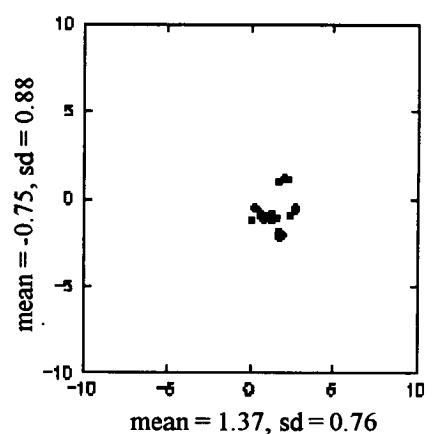
(l) *S. phlyicoides*



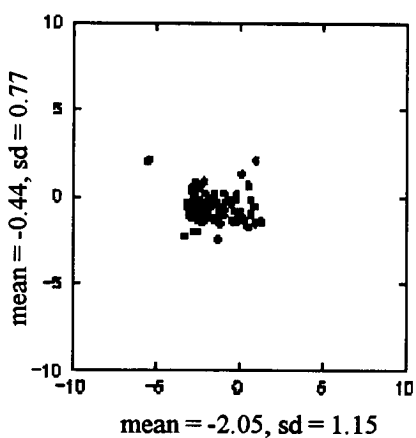
(m) *S. spathulatum*



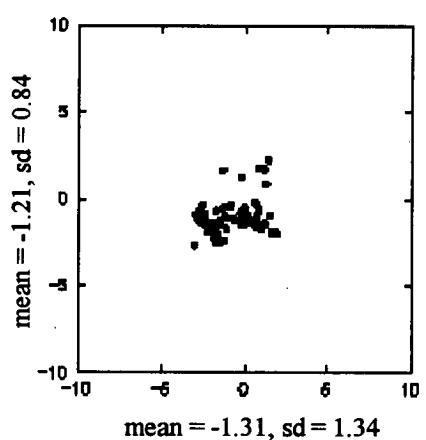
(n) *S. thymifolium*



(o) *S. vexilliferum* var. *latifolium*

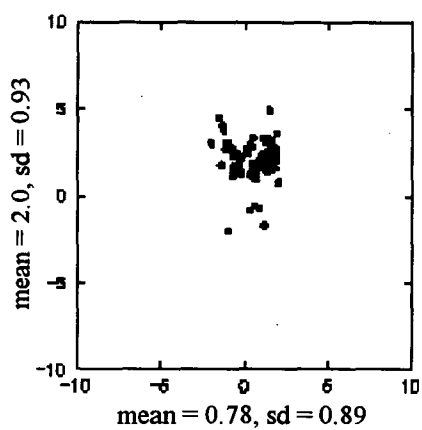


(p) *S. subochreatum* var. *subochreatum*

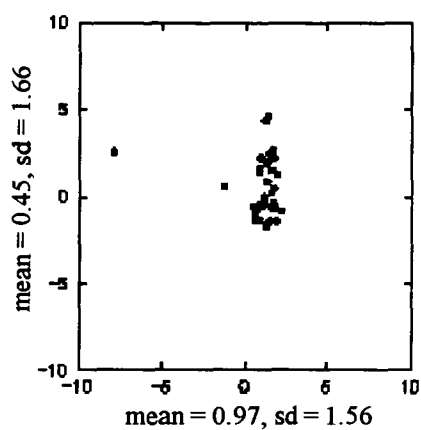


(q) *S. eriocephalum* var. *eriocephalum*

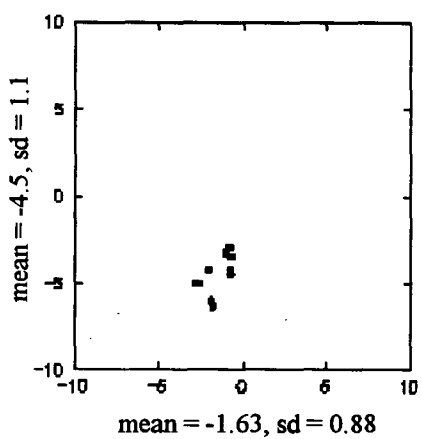
Figure 4.11 continued. Canonical Variates Analysis - South Australia/western Victoria. Scatter plots showing the distribution of site records in the ordination space defined by axes 1 and 2.



(r) *S. parvifolium*



(s) *S. vexilliferum* var. *vexilliferum*



(t) *S. tricolor*

Figure 4.11 continued. Canonical Variates Analysis - South Australia/western Victoria. Scatter plots showing the distribution of site records in the ordination space defined by axes 1 and 2.

### *Bioclimatic profiles - eastern Victoria/New South Wales/southeastern Queensland*

Mean annual precipitation ranged from 520 to 1,020 mm for the seven species which occur in this region (Appendix C.1). Wettest months are in the warmest quarter, when sites receive approximately 30% of rain, for *Spyridium scortechinii*, *S. buxifolium* and *S. "burraborang"*. However, these sites are still relatively moist throughout the year and receive substantial amounts of moisture during winter (15 - 20% of mean annual precipitation). The remainder of taxa occur in climates having a subdued winter maximum. All receive approximately 30% of mean annual precipitation during winter. Rainfall seasonality was moderately low in this region overall.

*Spyridium "burraborang"* sites experience mean annual precipitation of 807 mm per year, and are drier than those of *S. scortechinii* (940 mm) and wetter than *S. buxifolium* sites (641 mm), the two geographically closest species.

Taxa experience variable annual mean temperatures (12.3°C - 16.1°C). The coolest of these was *S. vexilliferum*, reflected its predominantly southern coastal distribution. *Spyridium "burraborang"* had an annual mean temperature of 15.5°C. Minimum temperatures in the coolest month ranged from -2.7°C to 6.4°C, with *Spyridium "burraborang"* experiencing 2.6°C. Annual temperature ranges were high for all taxa (26.5°C - 17.2°C). Summer temperatures ranged from hot (*S. eriocephalum*, 30.6°C) to warm (*S. vexilliferum*, 22.1°C). *Spyridium "burraborang"* was in the upper portion of this range at 27.8°C (Appendix C.2).

In summary, eastern taxa formed two groups. The New South Wales group (*S. "burraborang"*, *S. buxifolium* and *S. scortechinii*) experience warm to hot, humid summers and cool moist winters. The remainder of taxa, except *S. "burraborang"*, are concentrated primarily in Victoria, where summers are drier and cooler, with a subdued winter precipitation maximum. *Spyridium "burraborang"*, has a climatic profile midway between the two more widespread taxa.

### *Canonical Variates Analysis - eastern Victoria/New South Wales/southeastern Queensland*

#### Axis 1

Taxa were best discriminated on the basis of temperature during the driest to wettest quarters (Fig. 4.12). Significant loadings on axis 1 were mean temperature of the wettest quarter (0.5) and mean temperature of the driest quarter (-0.4). The three eastern endemics, *S. buxifolium*, *S. scortechinii* and *S. "burraborang"* occupied the distal end of the axis representing hot, humid summers and cool to mild winters with lower precipitation. The remainder of taxa occurred in summer dry/winter wet regions.

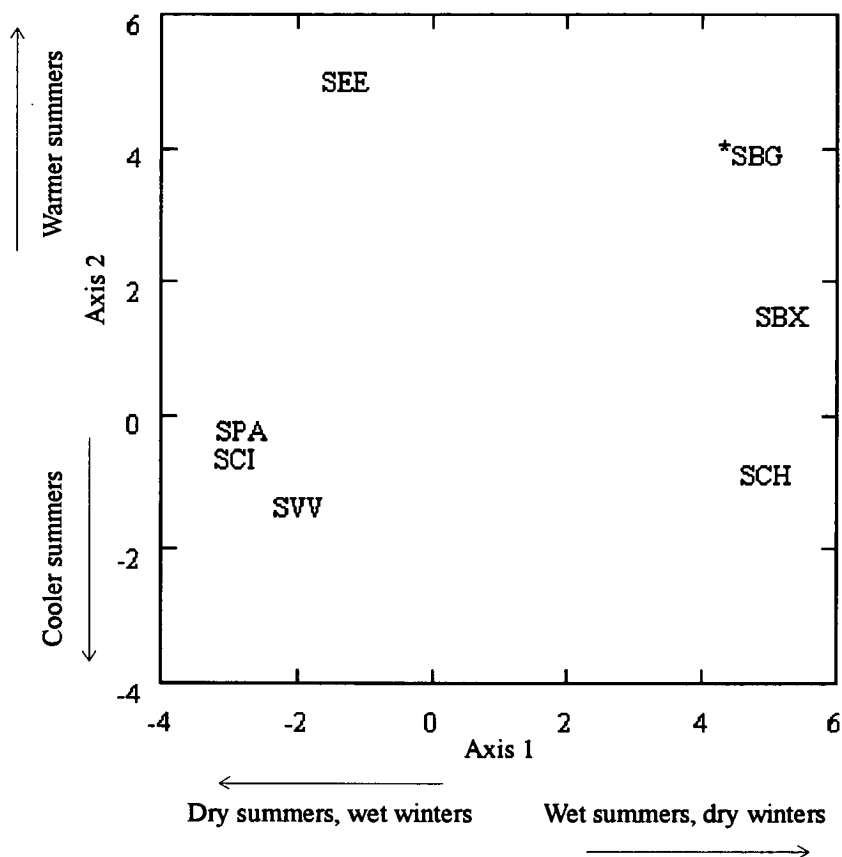


Figure 4.12. Canonical Variates Analysis - New South Wales/eastern Victoria/southeastern Queensland. The distribution of taxa in the ordination space. The asterisk denotes a narrow endemic. See Table 4.2 for a key to taxon symbols.

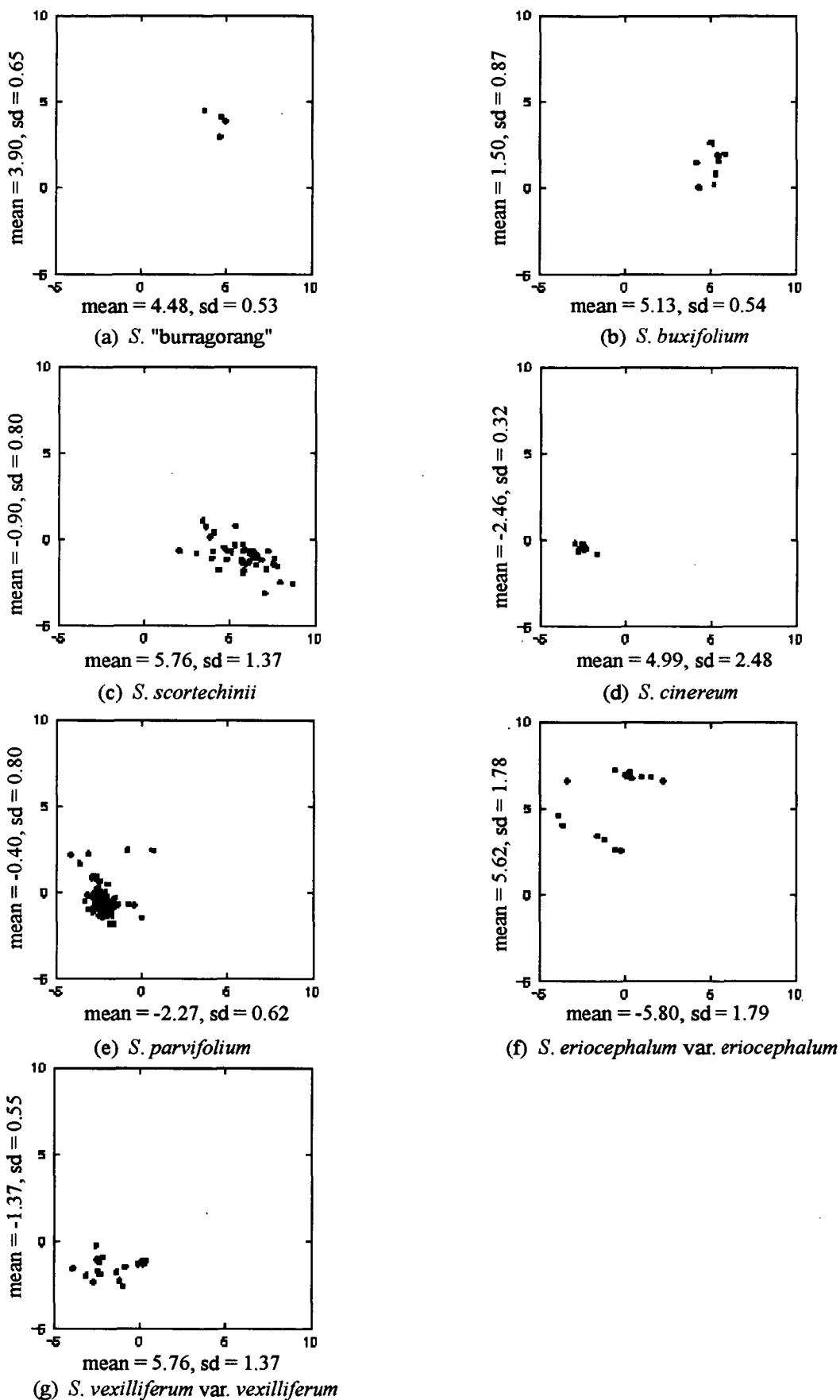


Figure 4.13. Canonical Variates Analysis - eastern Victoria/New South Wales/southeastern Queensland. Scatter plots showing the distribution of site records in the ordination space defined by axes 1 and 2.

## Axis 2

This axis represented a gradient of summer temperatures (Fig. 4.12). Significant loadings were mean temperature of the warmest quarter (0.6) and mean maximum temperature of the warmest month (0.6). The disjunct taxon *Spyridium eriocephalum* was at the distal end of axis 2, with the majority of populations occurring in semi - arid regions. The remainder of taxa experienced lower summer maxima.

### *Bioclimatic ranges - - eastern Victoria/New South Wales/southeastern Queensland*

The narrow endemic *S. "burraborang"* was narrowly dispersed within the eastern bioclimatic range (Fig. 4.13a).

Widespread taxa varied in their bioclimatic distributions. Bioclimatically widespread taxa were *S. scortechinii* (Fig. 4.13c), and the trans - regional species *S. vexilliferum* (Fig. 4.13g), which were distributed across a range of temperatures for the wettest quarter. *Spyridium eriocephalum* occupied a wide climatic envelope on both axes, as might be expected from its disjunct distribution between northeast and southern Victoria (Fig. 4.13f).

Widespread taxa which were bioclimatically restricted were *S. buxifolium* (Fig. 4.13b) and *S. cinereum* (Fig. 4.13d), which is disjunct between southeastern Victoria and the Grampians, and the trans - regional species *S. parvifolium* (Fig. 4.13e).

### *Bioclimatic profiles - Tasmania*

Tasmanian sites were the wettest in Australia (714 mm to 2175 mm), although similar values of mean annual precipitation were shared with some narrow Western Australian endemics (*S. villosum*, *S. montanum* and *S. spadiceum*). Distributions were frequently scattered and occurred over steep environmental gradients. Consequently a wide range of values were contained within each profile, indicated by large standard deviations (Appendix C.1). *Spyridium gunnii* sites were located in temperate hyperhumid and perhumid environments and *S. ulicinum* in temperate perhumid or humid locations. All other taxa, including *S. obcordatum*, experienced temperate humid conditions, although *S. microphyllum* sites were borderline subhumid/humid (*sensu* Gentilli 1972).

Tasmanian sites had the least seasonal rainfall regime of any *Spyridium* sites in Australia. *Spyridium microphyllum* populations experienced the lowest seasonality (12.3) and *S. obcordatum* the highest (30.2). Most rain fell during winter, however rainfall maxima were not confined to the coolest month at all sites. Significant falls caused by easterly weather originating over the Tasman Sea occurred during December on the central east coast, effecting populations of *S. microphyllum*, *S. obovatum* var. *obovatum* and *S. obovatum* var. *velutinum*.

*Spyridium obcordatum* populations differed mainly in this respect, with the onset of dry conditions during this time of the year. *Spyridium microphyllum* occupied the driest sites overall, experiencing the lowest mean annual (714 mm) and winter (185 mm) rainfall but dry to moderately moist summers (160 mm). However, increased rainfall was experienced by the most elevated population at Bald Hill (640 metres above sea level). *Spyridium obcordatum* populations received moderate mean annual rainfall (850 mm) and good winter falls (302 mm) but the driest summers (133 mm) of all the Tasmanian *Spyridium* populations.

Temperature profiles for Tasmanian endemics reflected their latitudinal position (Appendix C.2). Sites were substantially cooler than their mainland counterparts with an intermediate mean annual temperature range and low winter temperatures offset by mild summers. The two narrow endemics experienced the mildest winters of all Tasmanian taxa and the warmest summers although *S. microphyllum* sites were slightly cooler and more humid than those where *S. obcordatum* was recorded. The Bald Hill population of *S. microphyllum* was substantially cooler than all others.

Some closely related taxa differed in their climatic distributions. *Spyridium obovatum* var. *velutinum* had a more similar climate to *S. microphyllum* than to *S. obovatum* var. *obovatum*, which occurred in moister, more seasonal and slightly warmer sites. However, the two also frequently occur together. *Spyridium gunnii* and *S. ulicinum* had unique bioclimates and have geographic distributions which are exclusive to the rest of the genus in Tasmania. The former occupies cool and wet sites predominantly on the west coast but also in the southeast and on Flinders Island in Bass Strait. *Spyridium ulicinum* occurs in cool, moist and frequently elevated areas predominantly in the southeast of the state, with one outlying population at Ben Lomond in the north eastern highlands.

The two narrow endemics, *S. obcordatum* and *S. microphyllum* have little in common, either geographically or bioclimatically and although they experience similar winter and summer temperatures, there is a marked difference in precipitation regimes. It is likely that this difference has significance by extending the growing season for *S. microphyllum* into mid summer.

Rain bearing easterly weather in late spring and early summer cuts short any period of potentially prolonged moisture stress which might be experienced by *S. microphyllum* populations during the late summer months. *S. obcordatum* sites are more directly affected by the pattern of travelling anticyclones from the west and the related cool south westerly airstream, influential across southern Australia. A wetter and more pronounced winter rainfall regime and a more prolonged period of summer drought characterise these sites and align *S. obcordatum* with taxa distributed in parts of western Victoria, southeastern South Australia and Western Australia.



## Canonical Variates Analysis - Tasmania

### Axis 1

There were no significant loadings on axis 1. Taxa were widely separated into two groups consisting of one outlying taxon, *S. vexilliferum* and all other taxa, which were compressed at the opposite end of the axis (Fig. 4.14). Consequently the first axis was not considered further.

### Axis 2

Mean precipitation of the wettest month (0.6), wettest quarter (0.6) and coolest quarter (0.5) were correlated with axis 2, representing a gradient of winter rainfall. *Spyridium gunnii* occupied the wettest sites and taxa confined to eastern Tasmania occupied the driest sites (Fig. 4.14).

### Axis 3

Axis 3 represented a gradient relating to summer rainfall. Significant loadings were mean precipitation of the driest month (-0.7), driest quarter (-0.7), warmest quarter (-0.6); and mean annual precipitation (-0.6). *Spyridium obcordatum* experienced the driest summers and *S. gunnii* the wettest. Taxa confined to eastern Tasmania were also concentrated within the ordination space on this axis (Fig. 4.14).

## Bioclimatic ranges - Tasmania

Both *S. microphyllum* and *S. obcordatum* were narrowly restricted within the regional bioclimate, defined by axes 2 and 3 (Figs. 4.15a & b).

Taxa with a broader geographic distribution which were also bioclimatically widespread were *Spyridium obovatum* var. *obovatum* (Fig. 4.15c), *S. ulicinum* (Fig. 4.15e) and *S. gunnii* (Fig. 4.15f). The trans regional species *S. parvifolium*, which has a restricted distribution in northern Tasmania, was bioclimatically borderline between wide and restricted in the region (Fig. 4.15g).

Geographically widespread but bioclimatically restricted taxa were *S. obovatum* var. *velutinum* (Fig. 4.15d) and *S. vexilliferum* (Fig. 4.15h). The latter are at the edge of its range in Tasmania and it might be expected that the range of bioclimates available to them is narrower than on mainland Australia. *Spyridium eriocephalum* is represented at only one site in Tasmania, putting it in the category of bioclimatically restricted and at the edge of its range in the state.

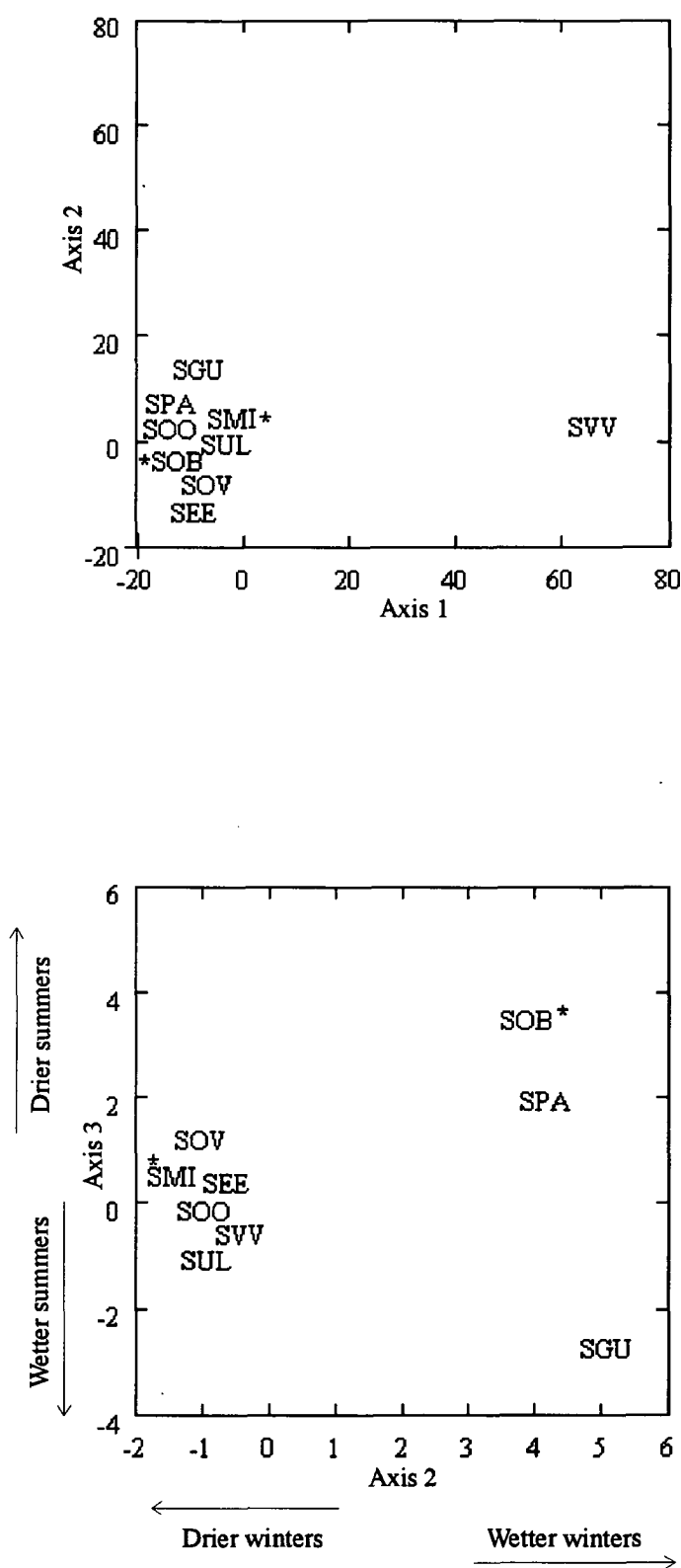


Figure 4.14. Canonical Variates Analysis - Tasmania. The distribution of taxa in the ordination space. Asterisks denote narrow endemics. See Table 4.2 for a key to taxon symbols.

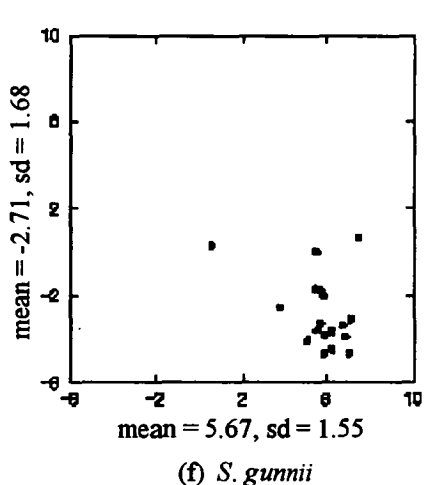
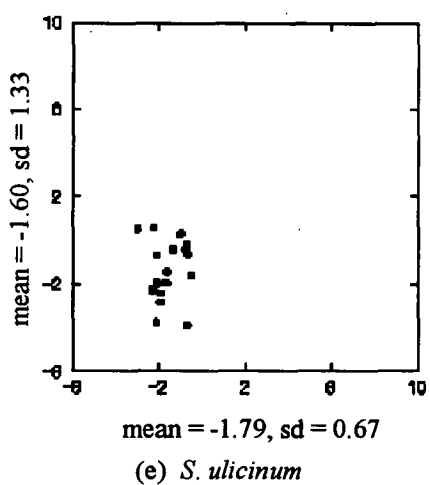
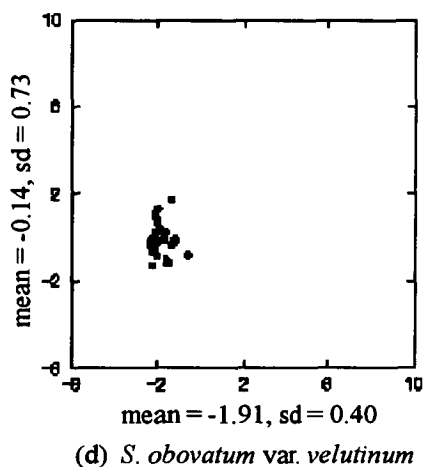
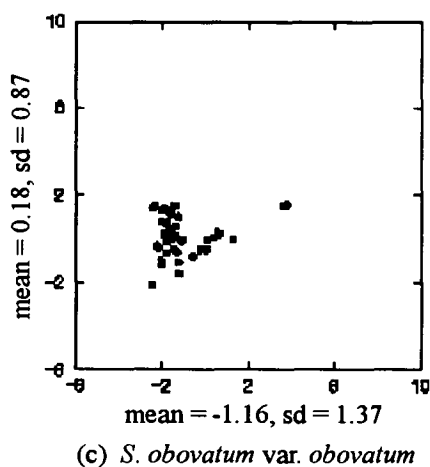
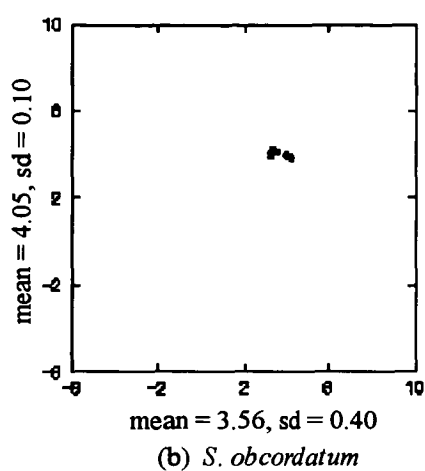
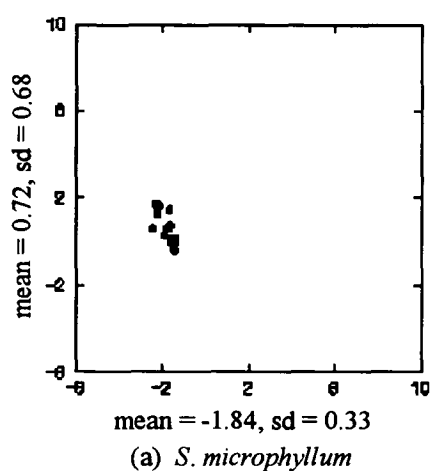


Figure 4.15. Canonical Variates Analysis - Tasmania. Scatter plots showing the distribution of site records in the ordination space defined by axes 2 and 3.

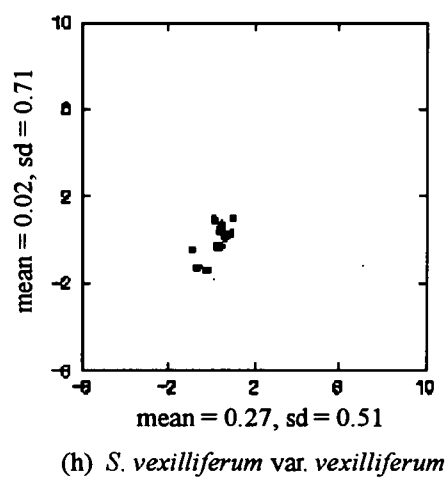
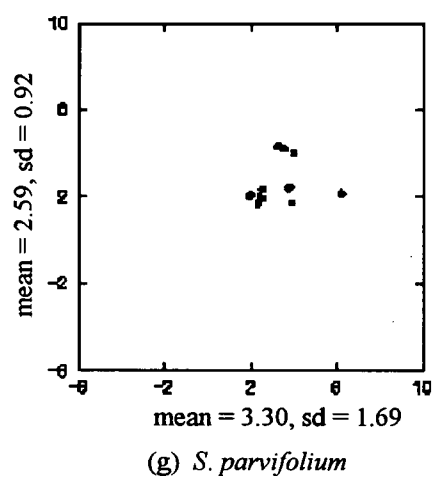


Figure 4.15 continued. Canonical Variates Analysis - Tasmania. Scatter plots showing the distribution of site records in the ordination space defined by axes 2 and 3.

## Discussion

### *Geographic evidence for rarity and narrow endemism in Spyridium*

The foregoing analysis revealed some discernible patterns of geographic distribution in the genus. These include:

1. Concentrated distributions and nodes of species richness in particular regions.
2. With the exception of obligate coastal taxa, most had no preference for any single topographic feature but were associated with elevated areas and/or coastal or near coastal environments.
3. With the exception of *S. globulosum*, taxa had no edaphic preference.
4. Some disjunct populations occurred in widely varying environments.
5. Taxa were primarily associated with heathland or shrubland and, less frequently, with woodland or forest.

"Nodes of species richness" (George *et al.* 1979: p. 220) in Western Australia occur in the same areas as mallee and sand plain vegetation ("kwongan" *sensu* Pate & Beard 1984), and are major centres of species diversity. They harbour a number of neoendemics and relictual taxa and are regarded as refugia from both past marine incursions and their edaphic consequences, as well as periods of aridity (Diels 1906 in Beard 1984; Marchant 1973; George *et al.* 1979; Hopper 1979, 1992).

The high number of endemic *Spyridium* taxa in South Australia is not in keeping with the State's flora, which is generally comprised of a mixture of taxa also found in either Western Australia or in Victoria (Specht 1972; Boardman 1986). Conversely, there are only two species with populations which are disjunct between South Australia and Western Australia. The flora of Kangaroo Island has a relatively high endemic component (5%, D. Kraehenbuehl pers. comm.) and *Spyridium* is particularly abundant in this region. Approximately 2.5% of the flora of the Eyre Peninsula are endemic to the region (Lange & Lang 1985), as are the flora of the Mt Lofty Ranges (D. Kraehenbuehl pers. comm.). These areas have long been recognised as refugia (Crocker & Wood 1947; Specht 1972; Boardman 1986).

The Great Dividing Range is an important topographic feature in eastern Australia, incorporating a wide range of topographic features which include deep gullies and elevated plateaux. Narrow endemics include taxa belonging to major families but also to other genera in the Rhamnaceae (*Pomaderris*, *Discaria*). It is also considered a major migratory pathway (Burbidge 1960). Similarly, the Grampians Range in Victoria is noted for its high levels of endemism and biodiversity (Lunt 1990).

Tasmanian taxa have different degrees of association with centres of endemism. The central east coast contains high concentrations of narrow endemics (Kirkpatrick & Brown 1984a & b), including sites where *S. microphyllum* and *S. obovatum* were recorded. *S. obovatum* also occurs in the far southeast, an area

also noted for narrow endemism and recognised as a refugial centre (Ladiges *et al.* 1983; Kirkpatrick & Brown 1984a & b; Davies 1974; Potts & Reid 1985a). Sites where *S. obcordatum* is located in northern Tasmania are associated with three other narrow endemics known from the region (*Tetratheca gunnii*, *Pimelea filiformis* and *Epacris virgata*). Other species which are at the edge of their range in Tasmania and which have been recorded with *S. obcordatum* include *Mitrasacme paradoxa*, *Angianthus preissianus*, *Ajuga australis*, *Hydrocotyle callicarpa*, *Hypoxis vaginata* var. *brevistigma*, *Microtis arenaria*, *Stylidium inundatum*, *Stylidium perpusillum*, *Lasiopetalum baueri*, *Lepidosperma viscidum*, *Pomaderris oraria* ssp. *oraria* and *Triglochin centrocarpum* (Askey-Doran & Fry 1994; Coates unpub. data). To the west, *Spyridium gunnii* is associated with edaphic endemics on ultramafic substrates and other restricted taxa at sites elsewhere in the state (Gibson *et al.* 1992; pers. obs.). *S. ulicinum* also tends to occur with other endemics in eastern Tasmania (Coates unpub. data).

An apparent lack of edaphic, altitudinal or topographic preference was shared by most narrow endemics in the genus. Although there was a strong association with elevated areas, there were populations in most taxa which occurred in both this environment as well as on sites at lower altitude.

There was a strong association between *Spyridium* and shrub - dominated vegetation in western and southern regions. Shrubland ranged from mallee or heathland to riparian or dune scrub and less commonly in forest. By contrast, there was a tendency for taxa in eastern Australia to occur in forest, particularly more widespread species such as *S. parvifolium*.

The absence of Tasmanian taxa from coastal plains or coastal heathland on recent sediments in northern and eastern Tasmania suggests confinement to refugia. *Spyridium obcordatum* occurs close to the coast but is restricted to elevated headlands or hill tops. Populations are well separated from each other and are absent from lowland coastal heaths on siliceous sands. This may also signify a preference for more fertile soils. *S. microphyllum*, although qualifying as a narrow endemic, is disjunct within its range with an outlying population separated from all other populations by a distance of over 50 kilometres which also suggests a once wider range. The few populations all occur on ridges or along river banks.

Taxa distributed in the south and southwest of mainland Australia are also associated with coastal and near coastal environments and may have been more widespread during lowered sea levels, suggesting that active migration was taking place in the past.

#### *Bioclimatic evidence for rarity and narrow endemism in Spyridium*

*Spyridium* is not restricted edaphically or topographically and although it is generally confined to the mediterranean belt across southern Australia, it occupies a broad range of mediterranean climate types. The term mediterranean includes a number of subclimates in warm and temperate, subhumid or semi - arid regions. In general, hot dry summers and cool wet winters characterise the mediterranean

climate, with a large proportion of annual precipitation occurring during cooler months, a period of five to eight months duration. Mediterranean climates also experience a dry season lasting between one and eight months, where this period coincides with the longest days (Gentili 1972). Consequently, subclimates within the broader mediterranean group are classified by the length, temperature and humidity of their dry season as warm and dry or extra dry (xerothermomediterranean); long dry season or short dry season (thermomediterranean) and moderate or mesomediterranean (Gentili 1972; Beard 1984). The dry season, when moisture is limiting for plant growth, is the critical period for determining subclimate type.

In Tasmania, *Spyridium* also occupy a wide range of climates but taxa do not have similar climatic requirements to narrow endemics elsewhere. In the analysis, some Tasmanian taxa were discriminated from all others on the basis of summer and winter precipitation.

Tasmanian endemics are presently confined to environments having cool temperatures and a relatively short period of summer drought. *Spyridium* in Tasmania is certain never to have experienced temperatures similar to those experienced by populations on mainland Australia. However, following deglaciation of the Tasmanian Central Highlands at 25,000 BP and the movement of anticyclones further to the south, a steep precipitation gradient was established from west to east (Colhoun 1978). A rainshadow effect was created when the moist westerly airstream was blocked and increased continentality favoured more seasonal rainfall and temperature regimes, compared to the prevailing maritime climate (Colhoun 1978). Consequently, *Spyridium* may have been favoured climatically in Tasmania and eastern Australia during this period, assuming that taxa were already established in these regions.

*Spyridium* can be divided into four classes on the basis of geographic and bioclimatic distribution. These classes can be used as a foundation to construct hypotheses to explain rarity within the genus.

1. Geographically restricted and climatically restricted.

These taxa include: *Spyridium majoranifolium* var. *pediacum* in Western Australia; *S. leucopogon* *S. halmaturinum* var. *integrifolium* and *S. eriocephalum* var. *glabrisepalum* in South Australia; *S. "burraborang"* in eastern Australia; *S. obcordatum* and *S. microphyllum* in Tasmania.

2. Geographically restricted and climatically widespread.

These taxa include: *S. glaucum*; *S. montanum*; *S. spadiceum*; *S. villosum*; and to a lesser extent *S. oligocephalum* and *S. mucronatum* var. *multiflorum* in Western Australia, and *Spyridium erymnocaulum* in South Australia.

3. Geographically widespread and climatically widespread.

These taxa include: *S. globulosum*; *S. majoranifolium*; *S. microcephalum*; *S. cordatum* and *S. polycephalum* in Western Australia. *S. subochreatum* var. *laxiusculum*; *S. bifidum*; *S. phlebophyllum*; *S. coactilifolium* and *S. spathulatum* in South Australia. *Spyridium vexilliferum*; *S. parvifolium*; *S. subochreatum* and *S.*

*eriocephalum* in southeastern Australia. *Spyridium scortechinii* in eastern Australia; *Spyridium obovatum*; *S. gunnii* and *S. ulicinum* in Tasmania. Trans regional taxa were *S. parvifolium*, *S. eriocephalum* and *S. vexilliferum*.

4. Geographically widespread and climatically restricted.

These taxa include: *S. mucronatum* var. *recurvum*; *S. mucronatum*; *S. "micord"* and *S. minutum* in Western Australia. *Spyridium halmaturinum*; *S. halmaturinum* var. *scabridum*; *S. nitidum*; *S. thymifolium*; *S. vexilliferum* var. *latifolium*; *S. phyllicoides* and *S. bifidum* var. *integrifolium* in South Australia; *S. cinereum* and *S. buxifolium* in eastern Australia; *S. obovatum* var. *velutinum* in Tasmania. Trans regional taxa were *S. subochreatum* and *S. tricolor*.

The four categories are analogous to the typology for rare species proposed by Rabinowitz (1981), excluding the population size component and being applied to common taxa as well as rare taxa. Four categories are proposed where bioclimates indicate habitat preference.

1. Taxa which have a narrow range and occur in a specific habitat = geographically and climatically restricted.
2. Taxa which have a narrow range but occur in several habitats = geographically restricted but climatically widespread.
3. Taxa which have a large range in several habitats = geographically widespread and climatically widespread.
4. Taxa which have a large range in a specific habitat = geographically widespread and climatically restricted.

Frequently hypothesized causes of rarity (Drury 1974; Harper 1981; Fiedler 1986; Fiedler & Ahouse 1992) can now be applied in order to construct hypotheses regarding the current distribution of *Spyridium* taxa, by comparing narrow endemics to widespread taxa. A general lack of edaphic or topographic specificity in the taxa in the genus precludes restriction to rare habitats.

Narrow endemics which are climatically restricted may be either neoendemics or palaeoendemics. They may have narrow physiological requirements, drastically reduced ranges or had inadequate time for dispersion. Interspecific competition may confine narrow endemics within restricted climates.

Narrow endemics which are climatically widespread may occupy fragmented portions of former ranges. This is likely to have resulted from environmental change fragmenting previously continuous distributions. Land clearance may have also resulted in narrow endemism although it would be expected that this pattern would not be confined to Western Australia.

Taxa which are geographically and climatically widespread are the generalists of the genus. These taxa are able to exploit a wide range of habitats and are possibly competitive (*sensu* Grime 1979). At the edge of their range, taxa such as *S. parvifolium*, *S. eriocephalum* and *S. vexilliferum* take on some of the attributes of rare species.



Geographically widespread and climatically narrow taxa occur in habitats that occur frequently and are geographically widespread. These may also be poor competitors within unfavourable bioclimates.

The geographic and climatic evidence showed that *Spyridium microphyllum* and *S. obcordatum* are narrow endemics which occupy narrow climatic niches but do not differ in this latter respect from some widespread taxa. Consequently, the two rare species may not be confined to a habitat wholly defined by climatic parameters. However, although *Spyridium microphyllum* has a similar bioclimate to other central eastern Tasmanian taxa, it occupies the driest sites of all Tasmanian *Spyridium* taxa. This suggests that its distribution may be limited by the number of climatically suitable sites available in the region. Further analysis is needed to determine the frequency of sites occupied by *S. microphyllum* as well as common taxa.

*Spyridium obcordatum* sites differed from most other Tasmanian *Spyridium* taxa. They were most similar to an uncommon non - endemic species, *S. parvifolium*. In this respect, *S. obcordatum* sites had closer affinities with some southeastern Australian taxa.

It is impossible to determine whether geographic restriction resulting from climatic constraints is a cause of rarity, or a consequence of rarity. In this context, the most likely explanations for rarity in light of the foregoing analysis are *S. microphyllum* and *S. obcordatum* are recently diverged, having had inadequate time for dispersal or alternatively, have drastically reduced ranges. Poor competitive ability, in addition to, or because of narrow physiological tolerances, may also be a cause of rarity.

The disjunct distributions of *S. microphyllum* suggest that it was formerly more widespread, with populations now restricted to sites which are the driest of all *Spyridium* sites in Tasmania. *Spyridium microphyllum* was mainly recorded from sites having warm summers, and relatively mild winter temperatures. Consequently, *S. microphyllum* is likely to be rare because of a much reduced geographic range combined with an inability to compete under moister climatic regimes.

The geographic and climatic evidence for *Spyridium obcordatum* and its ability to exploit a wide range of habitats within a narrow climatic envelope suggests it is not restricted by narrow physiological requirements, but may have had insufficient time for dispersal, assuming the availability of suitable habitat outside its present range. Alternatively, its range may also have been drastically reduced. *Spyridium obcordatum* occupied sites having the most seasonal rainfall regime in Tasmania and in this respect was more similar to some mainland Western Australian taxa.

## CHAPTER 5

### ENVIRONMENTAL DETERMINANTS OF RARITY IN *SPYRIDIMUM MICROPHYLLUM* AND *SPYRIDIMUM OBCORDATUM* POPULATIONS

#### Introduction

This chapter tests the hypothesis that *S. microphyllum* and *S. obcordatum* are restricted by environmental conditions as indicated by their qualitative environmental realised niches (Austin *et al.* 1990). Its objective is to establish whether *S. microphyllum* and *S. obcordatum* populations form part of distinct phytosociological assemblages occupying distinct environments.

The concept of the niche is frequently used in ecology to explain co - existence of organisms within plant or animal communities (Christiansen & Fenchel 1977). The concept of the fundamental niche of a species was defined by Hutchinson (1957) and further developed by MacArthur & Levins (1967) and Levins (1968) as the multidimensional environmental space bounded by biotic and abiotic variables within which an organism is able to successfully complete its life history. Competitive exclusion may reduce the space occupied by a species to its realised niche, which can vary according to the number and abundance of competitors and predators ( Solbrig & Solbrig 1979; Newman 1982).

Austin (1987) and Austin *et al.* (1990) demonstrated that although the response of a species to a resource gradient is often assumed to be Gaussian, this is not necessarily the case. Rather, maximum abundance may be attained where conditions are optimal along an environmental gradient and the species' distribution may be asymmetric. This would be particularly relevant when considering species which are confined to refugia, where environmental conditions are not necessarily optimal. In such places, competitive, widespread species are possibly excluded by marginal site conditions. Others have discussed niche theory while emphasising its application to "stable" vegetation (Newman 1982). However, such models are considered clearly inappropriate for the analysis of Australian vegetation types where recurrent disturbance usually precludes the establishment of climax communities (Noble & Slatyer 1977, 1980).

The distributions of rare species frequently imply confinement to realised niches. This situation may arise in response to environmental forcing factors, such as climate change or land use change, or as a result of physiological requirements, as is frequently found in serpentine endemics (Kruckeberg 1986, 1987). Cropper (1993) and Scarlett & Parsons (1993) cite several examples of disjunct taxa in the Australian flora which share the same habitats as narrowly restricted taxa. Habitat which supports rare species commonly consists of open, rocky environments, where light availability is high and where moisture is limiting. Localized disturbances which create open conditions for seedling establishment are also frequently linked with rarity (Cropper 1993; Scarlett & Parsons 1993) and are known to be strongly associated with rare Rhamnaceae taxa in Tasmania (Coates 1991). However, environmental conditions may be surrogates for other phenomena or may indirectly signify poor

competitive performance. For example, Baskauf & Eickmeier (1994) found that in spite of their restriction to open environments, rare *Echinacea* species were not restricted as a result of inferior photosynthetic response when compared to a widespread congener. Similarly, Kruckeberg & Rabinowitz (1985) found little evidence to support the notion that rare species have narrow ecological requirements in comparison to widespread taxa. Hence, factors which appear to explain rarity in a taxon do not necessarily reveal underlying reasons for rarity and are not necessarily correlated with geographic distribution and abundance.

Confinement to a rare habitat is a commonly postulated hypothesis for rarity which has been addressed in a number of rare plant studies in Australia and overseas (see Kruckeberg & Rabinowitz 1985; Prober & Austin 1991). The main difficulty with applying this theory to the study of rarity lies in defining what constitutes a rare habitat. In a particularly clear example using mathematical models describing climatic variables, Prober & Austin (1991) successfully predicted the occurrence of habitat thought to support the target taxon (*Eucalyptus paliformis* L. Johnson *et* Blaxell). This approach was not suitable in this study because too few *S. microphyllum* and *S. obcordatum* sites existed to acquire a suitable amount of data to construct a predictive envelope.

A further problem to consider in an analysis of rarity is the degree to which seed dispersal might influence populations. In this case, the widely separated nature of the target populations suggested that a comparison of habitats containing a rare *Spyridium* and adjacent vegetation where *Spyridium* was absent addressed this problem. This approach also minimized the influences of gamma diversity or differing site disturbance histories, considered problematic in explaining genuine differences between sites with and without the rare taxon, but widely separated (Prober & Austin 1991). It was thought that because the two species were shrubs rather than trees, their occurrences might be significantly influenced by the above factors. Consequently, a synecological comparison was also made between sites with the same rare species.

## Methods

A phytosociological survey aimed to identify habitat which supported *S. microphyllum* and *S. obcordatum*, to establish whether this habitat was floristically different from adjacent areas where they were absent, and to determine whether this difference was significantly influenced by unique environmental conditions. The latter areas were considered to be broadly representative of plant assemblages in the vicinity of rare *Spyridium* populations.

## Site selection

### *Spyridium microphyllum*

Three sites were sampled, all of which were underlain by dolerite. The Douglas - Apsley (41° 50' 30" S 148° 14' 16" E) and Thumbs (42° 36' 29" S 147° 53' 30" E) sites occurred at an altitude of 200 m with a south westerly aspect. Both sites were rocky ridges. The Swan River (41° 54' 15" S 148° 04' 45" E) sites were at 30 m with west, north west or easterly aspects, with *S. microphyllum* populations distributed along the river's edge. Populations at a similar altitude on the St Pauls River (41° 49' 15" S 147° 45' 30" E) were visited. However, weed invasion and disturbance were extreme and only a species list was compiled.

### *Spyridium obcordatum*

Two sites were sampled at Dans Hill (41° 11' 28" S 146° 46' 15" E), where vegetation with and without *S. obcordatum* occurred on ultramafic rocks (Dans Hill 1). Ultramafics supporting *S. obcordatum* also occurred adjacent to areas of Tertiary gravels where it was absent (Dans Hill 2). Both sites were at an altitude of 55 m with a south westerly aspect on low forested hills. At Hawley (41° 09' 01" S 146° 31' 02" E) one population occurred on an isolated dolerite hilltop at an altitude of 65 m, facing north west. Adjacent vegetation was on Tertiary sands. The Asbestos Range population (41° 06' 30" S 146° 39' 00" E) was on a coastal headland consisting of Precambrian schist at an altitude of 50 m with a westerly aspect. *S. obcordatum* also occurs on dolerite at nearby Greens Beach. However, the site was recently heavily disturbed. A species list was obtained although the collection of useful environmental data was not possible.

## Vegetation survey

Transects consisting of contiguously placed 5 metre x 5 metre quadrats were placed through representative populations. Stands occurred as more or less discrete groups so that it was possible to extend each transect into areas where each species was either very sparse or absent, but still had the same aspect as the target population and the same angle of slope. In each quadrat the presence of all vascular plant species was recorded.

Environmental attributes were recorded for each quadrat. These included altitude, geology, aspect, slope, topography and years since fire. The latter two were recorded as classes. Eight topographic classes represented ridge top, upper slope, mid slope, lower slope (non riparian), river edge, rock plate, rock plate perimeter and scree slope. Fire history (years since fire, estimated by ring counts) was represented by five classes consisting of 0 - 5 years, 5-10 years, 10 - 20 years, more than 20 years but with charcoal present and more than 20 years with charcoal absent. Life form categories were treated as variables which might indirectly indicate environmental conditions. Percentage projected foliage cover was subjectively estimated and

assigned a Braun Blanquet cover class for trees, tall shrubs, low shrubs (excluding *S. microphyllum* and *S. obcordatum*), herbs, grass, graminoids, ferns, litter, surface rock, exposed bedrock and bare ground. The mid points of cover classes were used in statistical analyses. These were: 1 (<1% ) = 0.5%; 2 (1 - 5%) = 2.5%; 3 (6 - 25% ) = 15%; 4 (26 - 50%) = 37.5%, 5 (51 - 75%) = 62.5; 6 (> 75%) = 87.5%. The height of each stratum was also recorded. Soil depth was measured with a stiff wire rod in five places in the quadrat (centre and close to each corner). The mean soil depth as well as the maximum and minimum depths were used for analysis. However, the presence of randomly exposed bedrock made it unlikely that absolute values were consistently recorded. Soil samples from below 2 centimetres were oven dried at 40°C and passed through 1.2 and 0.5 mm brass sieves. Soil pH was measured from a solution comprising equal parts of soil and distilled water using an electronic pH meter. Soil texture was estimated according to the method of Northcote (1979). At the Thumbs, some quadrats were extremely rocky and soil sampling was not possible. Quadrats with missing data were excluded from statistical calculations.

### *Data analysis*

#### *Phytosociology*

The Bray - Curtis coefficient was used to compute compositional dissimilarities between all pairs of quadrats for each data set for each species. *S. microphyllum* and *S. obcordatum* were excluded from the analysis so that their presence would not bias the outcome of the ordination. The dissimilarity matrix was ordinated, using non metric multidimensional scaling (NMDS). NMDS is a "robust" ordination method, having the ability to recover compositional dimensions associated with underlying environmental gradients (Minchin 1987). It derives an ordination in a specified number of dimensions so that the distance between samples has the best possible rank order fit with their input dissimilarities (Bowman & Minchin 1987; Faith & Norris 1989; Kantvilas & Minchin 1989). This is interpreted as minimum stress, a measure of how closely the configuration of samples in the ordination space matches the input dissimilarities. Ten random starting configurations were specified in order to achieve the optimal solution, as the algorithm may not achieve this with one start.

A second analysis comprised individual ordinations was carried out in four dimensions on quadrats from each transect, so that site specific environmental trends could be examined and compared with those from the other sites.

The floristic composition of quadrats which contained *Spyridium* were compared with those where it was absent on the basis of their rank Bray - Curtis dissimilarities. The test was used to compute the average distance between pairs of samples within each group, compared to the average distance of each pair of samples between groups (Clarke 1993). The significance of the test statistic (R) was determined by the randomization test (Hope 1968; Sokal & Rohlf 1981) using 1,000 permutations and effecting a two - tailed test. Samples are randomly assigned to either group and the null hypothesis rejected if the recalculated spread of values for R lie outside its real

value (Clarke 1993). This procedure is free of statistical assumptions regarding the distribution of data. Results were considered significant at the 95% confidence level.

### *Environmental correlates*

Correlations were used to test relationships between environmental variables and to explore these in relation to their possible effects on the niche prediction procedure. Of concern were significantly correlated variables causing problems associated with multicollinearity. An artificial binary variable (S.MICRO?; S.OBCORD?) was generated for correlations between presence/absence of either species and environmental variables. Pearsons product - moment correlation coefficient was calculated and probabilities determined using 1,000 randomised permutations to assess the significance of the deviation of  $r$  from a random distribution. Correlations were considered significant at the 95% confidence level.

### *Niche prediction*

The probability of occurrence of *S. microphyllum* and *S. obcordatum* on the basis of one or more environmental variables was predicted using logistic regression, a specialised form of Generalized Linear Modelling (GLM) for binary data. This is a general regression technique which allows linear model building without assuming normal distribution of the errors (McCullagh & Nelder 1983; Austin *et al.* 1990; ter Braak & Looman 1987; Agresti 1990; Christensen 1990). Categorical, binary and continuous variables can be used and there does not need to be a simple linear relationship between the response and predictor variables. This technique has largely been made possible by advances in statistical theory and computer software (Austin *et al.* 1990), although it has been criticised as lacking in flexibility (Yee & Mitchell 1991). The model has three components: the response variable (presence of *S. microphyllum* or *S. obcordatum*) assumed to have distributions belonging to the exponential family; a set of predictor variables, and a monotone link function, in this case the logistic function, which is suitable when the response variable has a binomial distribution (Agresti 1990; Christensen 1990). The probability of occurrence of the response variable is determined by the sum of effects of the predictor variables (Austin *et al.* 1990). Goodness of fit of the model is determined by the likelihood ratio test (scaled deviance) which is asymptotically chi - squared, with degrees of freedom equal to the difference between the total number of parameters and the number in the final model (Yee & Mitchell 1991; Vincent & Haworth 1983).

Environmental variables were used as predictor variables and observations containing missing values were excluded. Interactive combinations of variables were also excluded, as the most parsimonious model was sought which best described the predicted niche (Vincent & Haworth 1983; Margules & Nicholls 1987). Each predictor variable was fitted separately to identify which accounted for the greatest change in scaled deviance. A policy was adopted whereby variables directly describing environmental conditions were initially used to build the final model, rather than indirect variables which are more likely to be a consequence of environmental conditions. The former were pH, average, maximum and minimum soil depth, surface

rock cover and exposed bedrock cover. Indirect variables were tree, tall shrub and shrub height and cover, and herb, grass, graminoid, fern cover, litter cover and bare ground cover. It was debatable whether bare ground cover was a result of other factors, such as litter cover, or whether it directly defined habitat because of its role in seedling establishment or fuel loadings within vegetation. Consequently, bare ground cover and indirect variables were used if no model could be built using direct variables, that is, if there were no apparent environmental predictors from the data available.

A predictive model was built for each site using a forward stepwise procedure, carried out interactively. A forward procedure is recommended by Austin *et al.* (1990) rather than backward stepping as only a subset of the environmental data was used for the analysis and did not constitute a "maximal" model. Stepwise procedures are often referred to as "the most abused computerised statistical technique ever devised" and require careful scrutiny of correlations between variables as well as prior knowledge (Yee & Mitchell 1991; Wilkinson *et al.* 1992: p. 185). The predictor with the lowest scaled deviance was fitted to the model first, then combined with the next most significant. A number of combinations were examined by adding and subtracting variables, until a model was built which adequately described the environmental niche of the target species, indicated by the lowest scaled deviance, achieved without "over fitting" after ten iterations.

### *Computer programs*

Data storage, manipulation and computation were carried out using DECODA (Minchin 1991), which incorporates a program for NMDS. Correlations and logistic regression were undertaken using SYSTAT Version 5.03 (Systat Inc. 1993) and GLIM (Royal Statistical Society 1985) respectively. Analysis of dissimilarities was computed by ANOSIM, written by P. Minchin, University of Melbourne (1993, unpublished).

## **Results**

Ordinations of pooled data revealed that quadrats from each site were floristically distinct from each other in both species' cases (Figs. 5.1 & 5.2). Three dimensional solutions were accepted for each data set. NMDS achieved a minimum stress of 0.106281 from all ten starts for the *S. microphyllum* quadrats and 0.109575 from nine starts for the *S. obcordatum* quadrats. Both ordinations separated sites into clusters, reflecting field observations that there was a large degree of floristic difference between transects and that comparisons using pooled data were unlikely to reveal site specific trends. Consequently, separate ordinations were undertaken for each site, thereby enabling between and within site comparisons.

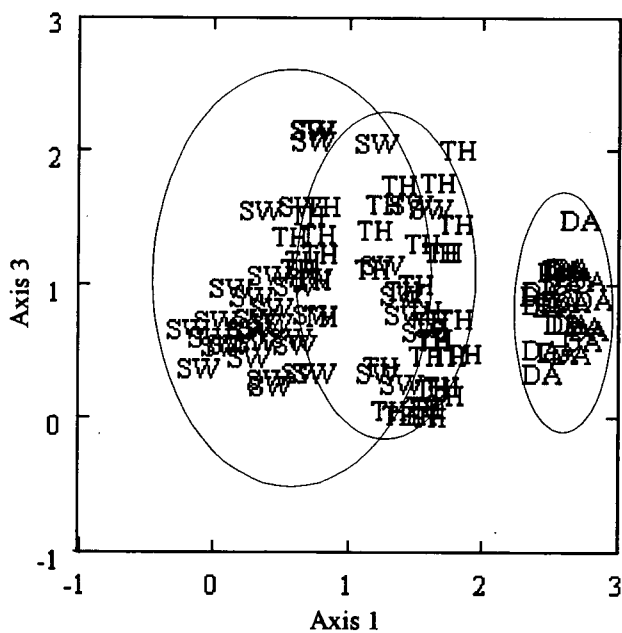
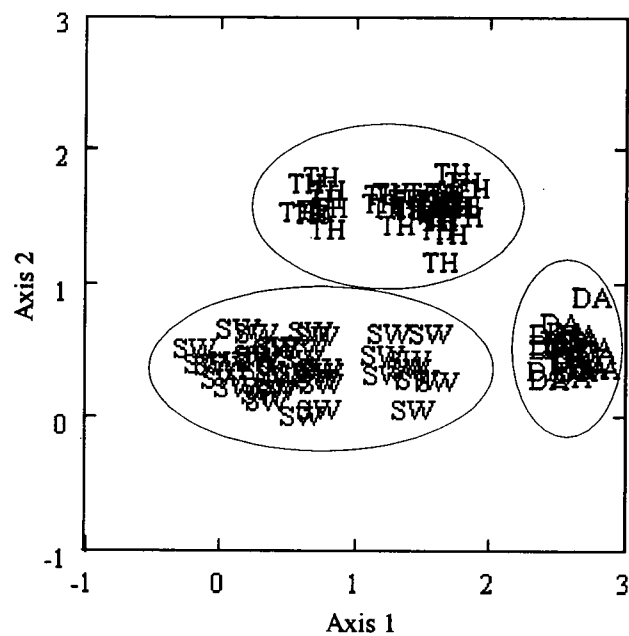


Figure 5.1. Scatterplots in 3 dimensions of the first NMDS for pooled data from *S. microphyllum* sites. DA = Douglas - Apsley; TH = Thumbs; SW = Swan River.



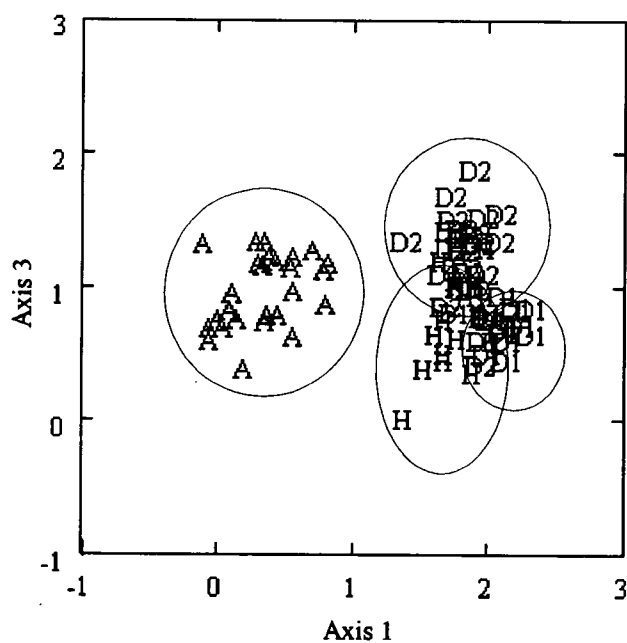
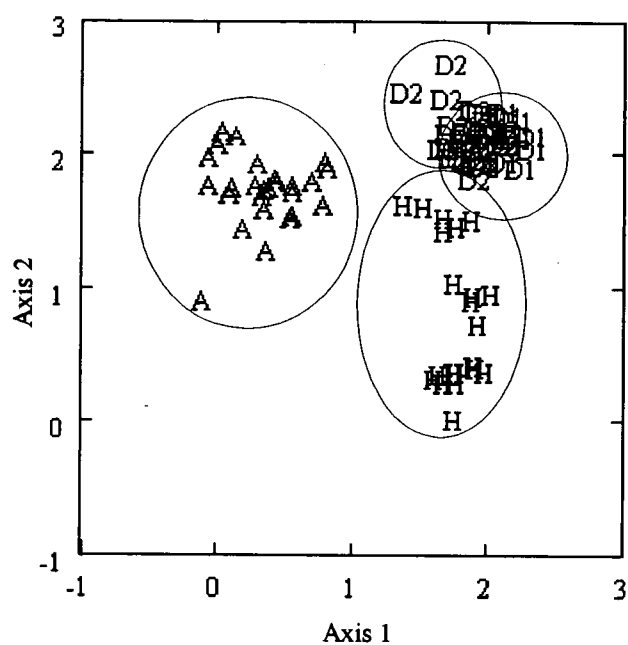


Figure 5.2. Scatterplots in 3 dimensions of the first NMDS for pooled data from *S. obcordatum* sites. A = Asbestos Range; H = Hawley; DH1 = Dans Hill 1  
DH2 = Dans Hill 2.

## *Spyridium microphyllum*

A two dimensional solution was accepted for ordinations of quadrat data from the Douglas - Apsley, Thumbs and Swan River transects. NMDS attained a minimum stress of 0.199445 from 3 of the 10 random starts for the Douglas - Apsley quadrats indicating a relatively poor solution; 0.168872 from all 10 starts for Swan River quadrats and 0.132693 from all 10 starts for the Thumbs quadrats.

### *Douglas - Apsley site*

Sampling at this site consisted of 25 quadrats placed over one transect, with *S. microphyllum* present in 19 quadrats. Rare Tasmanian endemics comprised a significant proportion of the species recorded and included *Leptospermum grandiflorum*, *Epacris apsleyensis*, *Pultenaea selaginoides* and *Eucalyptus barberi*. Analysis of dissimilarities did not distinguish quadrats with *S. microphyllum* as significantly different floristically from those without *S. microphyllum*, although quadrats appeared reasonably well separated in the ordination space ( $R = 0.1693$ ;  $P < 0.10$ ; Fig. 5.3).

Vegetation consisted of open - shrubland and tall closed - scrub, mainly composed of Tasmanian endemic species. The former was dominated by the mallee, *Eucalyptus barberi*, over an understorey of shrubs to 1 m high (Plate 5.1 a & b). This stratum was predominantly *S. microphyllum*, *Epacris apsleyensis* and *Leptospermum grandiflorum*. Two other associations were identified: *Hakea megadenia* - *L. grandiflorum* tall closed - scrub with a sparse second stratum of shrubs common to the first community. A third community consisted of *H. megadenia* or *L. grandiflorum* - *S. obovatum* var. *obovatum* tall closed - scrub. *Spyridium microphyllum* occurred in all three associations, but was infrequent and extremely sparse in tall closed - scrub. The differences between dominant taxa in tall closed - scrub where *S. microphyllum* was sparse or absent and in open - shrubland dominated by *S. microphyllum* was primarily physiognomic rather than floristic.

The site was recently undisturbed but debris encountered during sampling suggested that it had experienced disturbance in the past. Fires were evident from soil charcoal while a nearby area was burnt by a low intensity patch fire in the last two years. *Spyridium microphyllum* seedlings were observed colonising bare ground at the edge of tall shrubland, but there were few mature plants nearby. Soil colour varied from dark greyish brown fine sandy clays or loams to dark grey loams. Soils were shallow overall but also highly variable within a quadrat, depending on its relative rockiness. Average and minimum soil depth were negatively correlated with cover of exposed bedrock.

There were positive relationships between *S. microphyllum* and low shrub cover and between *S. microphyllum* and species richness. Both variables were significantly correlated (Table 5.1). The relationship between *S. microphyllum* and tall shrub cover was not as strong as expected, mainly because a few *S. microphyllum* plants occurred in the closed - scrub communities, suggesting some ability to survive in shaded vegetation where gaps in the canopy existed, or at the edge of the community.



Plate 5.1a. Douglas - Apsley. *Spyridium microphyllum* low open - shrubland, with emergent *Eucalyptus barberi*. Tall closed - scrub is present in the background, and open eucalypt forest in the far background.



Plate 5.1b. Douglas - Apsley. *Spyridium microphyllum* low open - shrubland, with emergent *E. barberi* and *Hakea megadenia* in the foreground, at the boundary of tall closed- scrub.

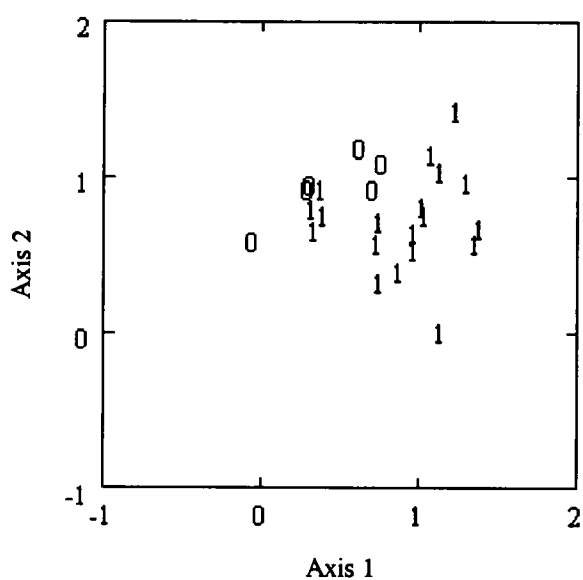


Figure 5.3. Douglas Apsley. The distribution of quadrats in the ordination space of the second NMDS, showing quadrats with *S. microphyllum* (1) and those without (0) *S. microphyllum*.

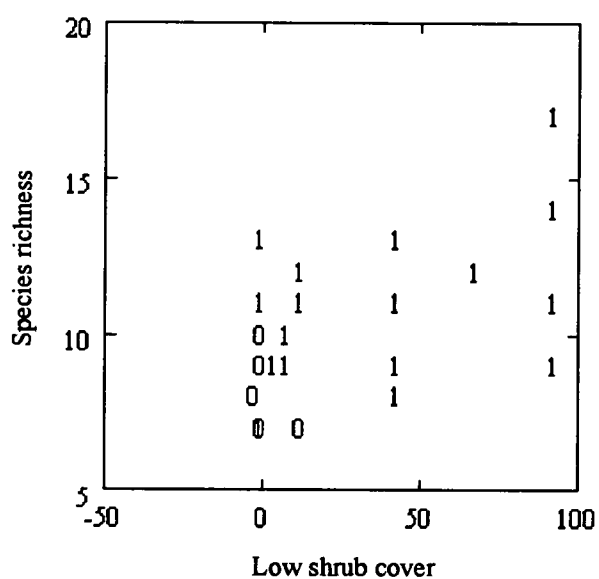


Figure 5.4. Douglas - Apsley. The distribution of quadrats according to low shrub cover and species richness, showing quadrats with *S. microphyllum* (1) and those without *S. microphyllum* (0).

	S.MICRO?	pH	Average soil depth	Maximum soil depth	Minimum soil depth	Tall shrub height	Tall shrub cover	Low shrub height
pH	-0.100(0.80)							
Average soil depth	0.004(1.00)	-0.386(0.08)						
Maximum soil depth	0.168(0.40)	-0.375(0.06)	0.938(0.00)					
Minimum soil depth	-0.164(0.40)	-0.038(0.88)	0.665(0.001)	0.535(0.003)				
Tall shrub height	-0.235(0.20)	0.072(0.74)	0.398(0.04)	0.264(0.22)	0.443(0.04)			
Tall shrub cover	-0.347(0.09)	0.189(0.40)	0.420(0.04)	0.244(0.25)	0.684(0.00)	0.653(0.00)		
Low shrub height	-0.348(0.14)	-0.150(0.53)	-0.257(0.20)	-0.301(0.14)	-0.136(0.65)	-0.354(0.13)	-0.231(0.30)	
Low shrub cover	0.478(0.01)	-0.001(1.00)	-0.145(0.50)	0.052(0.82)	-0.371(0.06)	-0.347(0.08)	-0.596(0.002)	-0.170(0.50)
Herb cover	0.166(0.71)	0.051(0.85)	-0.075(0.75)	0.106(0.64)	-0.069(0.72)	-0.434(0.02)	-0.327(0.12)	-0.076(0.32)
Grass cover	-0.187(0.44)	-0.238(0.20)	0.330(0.12)	0.396(0.05)	0.109(0.59)	0.069(0.74)	0.171(0.41)	-0.111(0.67)
Graminoid cover	0.280(0.15)	-0.356(0.08)	0.159(0.48)	0.323(0.10)	-0.207(0.35)	-0.005(0.97)	-0.378(0.06)	-0.151(0.41)
Fern cover	0.115(0.77)	0.035(0.93)	-0.103(0.66)	-0.081(0.70)	-0.140(0.84)	-0.058(0.67)	-0.219(0.27)	-0.053(0.59)
Litter cover	-0.331(0.11)	0.185(0.40)	0.296(0.16)	0.125(0.53)	0.485(0.01)	0.368(0.08)	0.754(0.00)	-0.060(0.91)
Surface rock cover	0.198(0.40)	-0.229(0.27)	0.090(0.66)	0.092(0.66)	-0.253(0.23)	-0.017(0.94)	0.032(0.87)	-0.069(0.43)
Bed rock cover	0.231(0.31)	0.003(0.99)	-0.468(0.02)	-0.381(0.06)	-0.661(0.00)	-0.412(0.05)	-0.481(0.02)	0.247(0.27)
Bare ground cover	0.095(0.64)	-0.318(0.13)	0.197(0.38)	0.247(0.24)	0.028(0.15)	0.051(0.82)	0.078(0.70)	-0.158(0.54)
Species richness	0.513(0.006)	-0.140(0.50)	0.049(0.81)	0.287(0.16)	-0.254(0.22)	-0.256(0.23)	-0.475(0.02)	-0.184(0.34)

Table 5.1. Correlations and 2-tail probabilities from 1000 random permutations between environmental variables at the Douglas - Apsley site (degrees of freedom = 24).



	Low shrub cover	Herb cover	Grass cover	Graminoid cover	Fern cover	Litter cover	Surface rock cover	Bedrock cover	Bare ground cover
<b>Grass cover</b>	-0.306(0.16)	0.221(0.34)							
<b>Graminoid cover</b>	0.594(0.002)	-0.022(0.98)	0.134(0.49)						
<b>Fern cover</b>	0.345(0.18)	-0.060(0.51)	-0.102(0.97)	0.520(0.06)					
<b>Litter cover</b>	-0.391(0.04)	-0.366(0.05)	-0.071(0.70)	-0.482(0.01)	-0.241(0.26)				
<b>Surface rock cover</b>	-0.108(0.63)	-0.109(0.55)	0.276(0.18)	-0.002(1.00)	-0.027(0.93)	-0.150(0.46)			
<b>Bedrock cover</b>	-0.003(1.00)	0.050(0.90)	0.009(0.85)	-0.175(0.41)	0.035(0.96)	-0.363(0.09)	0.326(0.11)		
<b>Bare ground cover</b>	0.042(0.85)	0.107(0.77)	0.411(0.03)	0.417(0.04)	0.237(0.18)	-0.129(0.53)	-0.130(0.52)	-0.424(0.036)	
<b>Species richness</b>	0.624(0.00)	0.479(0.009)	0.123(0.56)	0.520(0.01)	0.036(0.97)	-0.601(0.00)	-0.027(0.90)	0.024(0.921)	0.245(0.23)

Table 5.1 continued.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	27.56	24			
pH	27.31	23	0.25	1	ns
Average soil depth	27.55	23	0.25	1	ns
Maximum soil depth	26.81	23	0.00	1	ns
Minimum soil depth	26.91	23	0.74	1	ns
Surface rock cover	26.44	23	1.11	1	ns
Exposed bedrock cover	26.25	23	1.31	1	ns
Bare ground cover	27.32	23	0.24	1	ns
Tree height	27.55	23	0.00	1	ns
Tree cover	27.55	23	0.00	1	ns
Tall shrub height	26.00	23	1.55	1	ns
Tall shrub cover	24.42	23	3.13	1	ns
Low shrub height	24.94	23	2.62	1	ns
Low shrub cover	17.16	23	10.40	1	**
Herb cover	26.40	23	1.15	1	ns
Grass cover	26.75	23	1.15	1	ns
Graminoid cover	24.91	23	2.65	1	ns
Fern cover	23.00	23	0.56	1	ns
Litter cover	24.70	23	2.86	1	ns
Species richness	17.43	23	10.13	1	**

Table 5.2. Results of individual models for the Douglas - Apsley site.

Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ ; ns = not significant.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	27.55	24			
+ shrub cover	17.16	23	10.40	1	**
+ species richness	12.32	22	15.24	1	***

Table 5.3. Final model for the Douglas - Apsley site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ .

Estimate	se	Parameter
-8.52		constant
0.16	0.13	low shrub cover
0.87	0.50	species richness

Table 5.4. Parameter estimates for the final model at the Douglas - Apsley site.  
Se = standard error.

Quadrat no.	S.MICRO?	Shrub cover	Species richness	Estimated predicted probability
1				
2	1	6	17	1.00
3	1	6	14	1.00
4	1	2	13	0.96
5	1	6	11	1.00
6	1	5	12	1.00
7	1	6	17	1.00
8	1	5	12	1.00
9	1	4	13	1.00
10	1	4	8	0.99
11	1	6	9	1.00
12	0	2	9	0.43
13	0	2	7	0.12
14	0	0	8	0.17
15	1	3	10	0.87
16	1	2	7	0.12
17	1	3	12	0.99
18	1	3	9	0.59
19	1	2	11	0.81
20	1	4	11	0.99
21	1	4	9	0.99
22	0	2	10	0.64
23	1	3	11	0.97
24	1	3	9	0.74
25	0	3	7	0.51
26	0	2	7	0.12

Table 5.5. Estimated predicted probabilities of occurrence of *S. microphyllum* at the Douglas - Apsley site, according to values for shrub cover (back transformed to their Braun Blanquet cover classes) and species richness (number of species per quadrat). Cover classes: 1 = <1%; 2 = 1-5%; 3 = 5-25%; 4 = 25-40%; 5 = 50-75%; 6 = >75%.



However, the two were significantly negatively correlated at the 90% confidence limit. Tall shrub communities were associated with high litter cover, decreased cover of exposed bedrock and increasingly deeper soils (Table 5.1), whereas low shrubland was species rich, with low litter levels, but positively correlated with an increase in graminoid cover (Table 5.1). Higher cover values were recorded from low shrubland for *Lepidosperma inops* and *Gahnia rodwayi*, small sedges which can commandeer relatively large patches of bare ground, especially after burning.

The presence of *S. microphyllum* could not be significantly predicted by any single direct variable or by any combination of direct environmental variables. Its niche was well defined by a combination of low shrub cover and species richness (Tables 5.2 - 5.5; Fig. 5.4). This is likely to be a consequence of fire history.

High cover of sedge species in quadrats containing *S. microphyllum* also suggests a localised fire event. Charcoal was recorded in all quadrats. Each community appeared to represent a different age class. Ring counts of dominant species indicated at least three broad age classes were present. Assuming annual growth rings, *S. obovatum* var. *obovatum* (tall closed - scrub) was aged at 16 - 18 years, 28 - 35 years and 64 years. *Leptospermum grandiflorum* (tall closed - scrub) was 16 - 18 years and 35 years and 46 years old. *Spyridium microphyllum* (low shrubland) plants were 16 - 18 years and 37 years. All three species are killed by fire but regenerate *en masse* following disturbance, although the two tall shrub species regenerate continuously at low levels and *S. microphyllum* at an extremely low level.

Distribution patterns of tall and low shrubland were easily recognisable from air photographs (1949 & 1988). There was a marked change in vegetation patterns, with a change from a distinct but more evenly distributed vegetation to a discontinuous mosaic of communities, suggesting that the site has experienced patchy or spot fires within the last 40 years. The ring counts provide supportive evidence of a history of patch burning for at least 60 years. It is likely that low open - shrubland regenerated after fire from existing soil stored seed banks within tall shrublands.

#### *Thumbs site*

*Spyridium microphyllum* co-occurred at this site with the rare Tasmanian endemics *Helichrysum lycopodioides* and *Epacris marginata*, although the latter was not recorded in quadrats. The rare narrow Tasmanian endemic *Deyeuxia apsleyensis* occurred in the quadrats without *S. microphyllum*. Quadrats with *S. microphyllum* were significantly different floristically from those without *S. microphyllum* ( $R = 0.65$ ,  $P < 0.0001$ ; Fig. 5.5).

Three transects consisting of 40 quadrats spanned three different plant associations. *S. microphyllum* was present in 23 quadrats. Low open - shrubland was confined to patches associated with the perimeter of exposed bedrock (Plate 5.2a). This was dominated by *S. microphyllum*, *Helichrysum lycopodioides*, *Hibbertia riparia* and *Epacris tasmanica*. Dry sclerophyll forest dominated by *Eucalyptus pulchella* with a sparse understorey of *Cyathodes divaricata*, *Lomatia tinctoria*, *Acacia genistifolia*, *Poa rodwayi* and *Lepidosperma ensiforme* occurred adjacent to shrubland (Plate



Plate 5.2a. Thumbs. *Spyridium microphyllum* low open - shrubland (centre) at the perimeter of exposed dolerite bedrock. *Callistemon pallidus* is at the bottom left hand side of the frame.



Plate 5.2b. Thumbs. *Eucalyptus pulchella* open forest (background) adjacent to *S. microphyllum* low open - shrubland (approximate centre). Vegetation in the foreground consists of *Epacris tasmanica*, *Hibbertia riparia* and *Lepidosperma laterale*, common components of the understorey of open forest shallow, rocky soils between open forest and open rock plate.

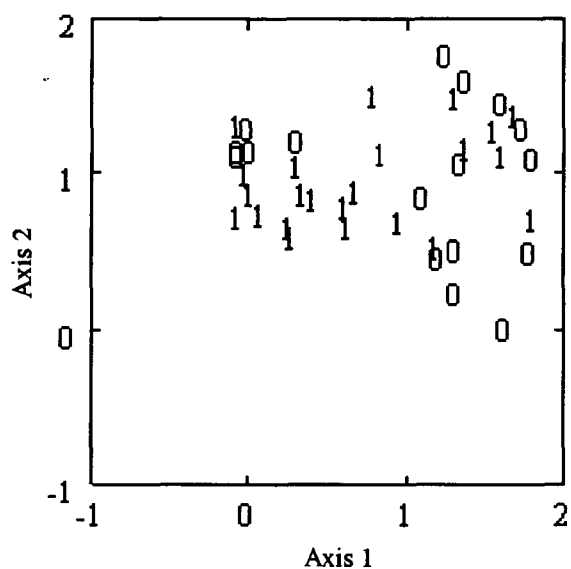


Figure 5.5. Thumbs. The distribution of quadrats in the ordination space of the second NMDS, showing quadrats with (1) and without (0) *S. microphyllum*.

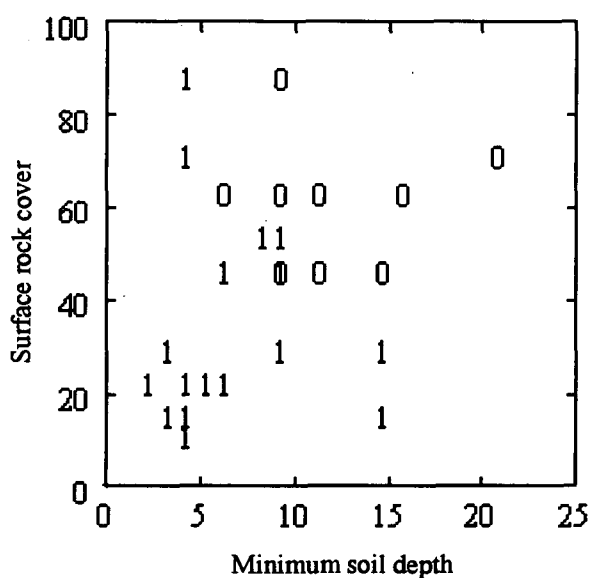


Figure 5.6. Thumbs. The distribution of quadrats according to minimum soil depth and surface rock cover, showing quadrats with *S. microphyllum* present (1) and those where *S. microphyllum* is absent (0).



	<b>S.MICRO?</b>	<b>pH</b>	<b>Average soil depth</b>	<b>Maximum soil depth</b>	<b>Minimum soil depth</b>	<b>Tree height</b>	<b>Tree cover</b>	<b>Tall shrub height</b>	<b>Tall shrub cover</b>
<b>pH</b>	-0.320(0.05)								
<b>Average soil depth</b>	-0.524(0.00)	-0.191(0.23)							
<b>Maximum soil depth</b>	-0.454(0.007)	-0.182(0.32)	0.918(0.00)						
<b>Minimum soil depth</b>	-0.600(0.00)	-0.139(0.44)	0.846(0.00)	0.679(0.00)					
<b>Tree height</b>	-0.877(0.00)	0.066(0.72)	0.653(0.00)	0.544(0.001)	0.756(0.00)				
<b>Tree cover</b>	-0.945(0.00)	0.137(0.43)	0.626(0.00)	0.537(0.00)	0.705(0.00)	0.966(0.00)			
<b>Tall shrub height</b>	0.256(0.22)	0.070(0.61)	-0.143(0.42)	-0.243(0.16)	-0.109(0.51)	-0.288(0.08)	-0.281(0.17)		
<b>Tall shrub cover</b>	0.255(0.22)	0.079(0.60)	-0.093(0.60)	-0.218(0.20)	-0.097(0.57)	-0.288(0.11)	-0.281(0.10)	0.966(0.00)	
<b>Low shrub height</b>	0.541(0.00)	-0.060(0.71)	-0.388(0.02)	-0.260(0.12)	-0.507(0.002)	-0.616(0.00)	-0.588(0.00)	0.500(0.02)	0.3669(0.06)
<b>Low shrub cover</b>	0.385(0.03)	-0.169(0.33)	-0.184(0.29)	-0.001(0.99)	-0.289(0.09)	-0.455(0.008)	-0.424(0.01)	-0.173(0.33)	-0.1787(0.32)
<b>Herb cover</b>	0.124(0.54)	0.018(0.82)	-0.176(0.27)	-0.167(0.35)	-0.169(0.31)	-0.140(0.70)	-0.136(0.95)	-0.061(0.66)	-0.0606(0.71)
<b>Grass cover</b>	-0.376(0.02)	-0.047(0.80)	0.294(0.08)	0.201(0.27)	0.403(0.02)	0.402(0.02)	0.362(0.05)	-0.138(0.43)	-0.1464(0.37)
<b>Graminoid cover</b>	-0.370(0.03)	-0.151(0.37)	0.580(0.00)	0.625(0.00)	0.419(0.02)	0.341(0.05)	0.400(0.02)	-0.133(0.47)	-0.1271(0.44)
<b>Litter cover</b>	-0.809(0.00)	0.197(0.27)	0.574(0.00)	0.461(0.003)	0.693(0.00)	0.836(0.00)	0.835(0.00)	-0.272(0.11)	-0.2620(0.14)
<b>Surface rock cover</b>	-0.531(0.001)	0.351(0.04)	0.426(0.02)	0.384(0.03)	0.361(0.03)	0.392(0.03)	0.461(0.005)	0.185(0.28)	0.1409(0.40)
<b>Bedrock cover</b>	0.261(0.12)	0.015(0.94)	-0.525(0.00)	-0.523(0.001)	-0.497(0.001)	-0.339(0.04)	-0.289(0.09)	0.062(0.72)	0.0259(0.91)
<b>Bare ground cover</b>	0.331(0.04)	-0.181(0.23)	-0.362(0.04)	-0.346(0.04)	-0.317(0.05)	-0.352(0.02)	-0.347(0.02)	0.123(0.49)	0.0893(0.74)
<b>Species richness</b>	-0.126(0.46)	-0.154(0.41)	0.428(0.006)	0.393(0.02)	0.308(0.07)	0.203(0.23)	0.191(0.27)	0.108(0.53)	0.1638(0.35)

Table 5.6. Correlations and 2-tail probabilities from 1000 random permutations between environmental variables at the Thumbs site (degrees of freedom = 34).

	Low shrub height	Low shrub cover	Herb cover	Grass cover	Graminoid cover	Litter cover	Surface rock cover	Bedrock cover	Bare ground cover
<b>Herb cover</b>	0.198(0.26)								
<b>Grass cover</b>	0.051(0.81)	-0.151(0.36)							
<b>Graminoid cover</b>	-0.398(0.02)	-0.143(0.41)	-0.275(0.08)						
<b>Litter cover</b>	-0.041(0.81)	00.181(0.28)	-0.136(0.49)	0.193(0.25)					
<b>Surface rock cover</b>	-0.586(0.00)	-0.351(0.03)	-0.110(0.60)	0.558(0.002)	0.309(0.05)				
<b>Bedrock cover</b>	0.130(0.48)	-0.094(0.59)	-0.261(0.11)	0.017(0.93)	0.389(0.02)	0.357(0.04)			
<b>Bare ground cover</b>	0.311(0.07)	-0.284(0.11)	0.223(0.24)	-0.286(0.10)	-0.341(0.03)	-0.453(0.01)	-0.278(0.11)		
<b>Species richness</b>	0.150(0.32)	-0.098(0.60)	-0.017(0.82)	-0.125(0.53)	-0.340(0.05)	-0.372(0.02)	-0.432(0.006)	0.361(0.02)	
	-0.144(0.41)	-0.174(0.31)	0.249(0.15)	-0.086(0.62)	0.261(0.11)	0.101(0.54)	0.181(0.31)	-0.363(0.03)	-0.224(0.22)

Table 5.6 continued.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	45.00	34			
pH	40.90	33	4.11	1	*
Average soil depth	34.85	33	10.16	1	**
Maximum soil depth	37.56	33	7.44	1	**
Minimum soil depth	30.36	33	14.64	1	***
Surface rock cover	34.00	33	11.01	1	***
Exposed bedrock cover	42.42	33	2.59	1	ns
Bare ground cover	NC	33	-	1	-
Tree height	12.72	33	32.29	1	***
Tree cover	NC	33	-	1	-
Tall shrub height	41.38	33	3.62	1	ns
Tall shrub cover	41.38	33	3.62	1	ns
Low shrub height	21.90	33	23.10	1	***
Low shrub cover	38.67	33	6.34	1	*
Herb cover	44.15	33	0.85	1	ns
Grass cover	39.69	33	5.31	1	*
Graminoid cover	40.19	33	4.81	1	*
Fern cover	45.00	33	0.00	1	ns
Litter cover	17.37	33	27.63	1	***
Species richness	44.45	33	0.56	1	ns

Table 5.7. Results of individual models for the Thumbs site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ ; ns = not significant; NC = no convergence.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	27.55	34			
+ minimum soil depth	30.36	33	14.64	1	***
+ surface rock cover	17.54	32	20.01	1	***

Table 5.8. Final model for the Thumbs site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ .

Estimate	se	Parameter
20.14	8.60	constant
-1.10	0.48	minimum soil depth
-0.17	0.08	surface rock cover

Table 5.9. Parameter estimates for the final model at the Thumbs site. Se = standard error.

Quadrat no.	S.MICRO?	Minimum soil depth	Surface rock cover	Estimated predicted probability
1	0	12	4	0.330
2	0	14	4	0.050
3	0	12	4	0.330
4	1	14	4	0.470
5	1	14	3	0.900
6	1	10	4	0.990
7	1	10	4	0.810
8	1	5	5	0.940
9	1	5	3	1.000
10	1	7	4	0.990
11	1	5	5	0.940
12	1	4	4	1.000
13	1	7	3	1.000
14	1	6	3	1.000
15	1	9	5	0.770
16	0	10	5	0.200
17	0	12	5	0.030
18	0	10	4	0.810
19	0	15	5	0.001
20	0	20	5	0.000
21	0	10	5	0.200
22	0	10	6	0.004
23	1	10	5	0.530
24	1	4	3	1.000
25	1	10	4	0.810
26	1	5	6	0.470
27	1	5	3	1.000
28	1	3	3	1.000
29	1	6	3	1.000
30	1	5	3	1.000
31	1	5	3	1.000
32	1	5	3	1.000
33	1	10	5	0.530
34	0	7	5	0.870
35	0	12	5	0.030

Table 5.10. Estimated predicted probabilities of occurrence of *S. microphyllum* (Thumbs), according to values for minimum soil depth (cm) and surface rock cover, where 1 = <1%; 2 = 1-5%; 3 = 5-25%; 4 = 25-40%; 5 = 50-75%; 6 = >75%.

5.2b). *S. microphyllum* was absent from this type of vegetation, other than at the boundary of forest and shrubland. Tall shrubland was dominated by *Callistemon pallidus*, *Notelaea ligustrina*, *Beyeria viscosa* or *Hakea lissosperma*, emergent over *Epacris tasmanica*, *Hibbertia riparia*, *Dianella tasmanica* or *L. ensiforme*.

These patches varied from relatively open to dense thickets and were associated with jumbled boulder slopes probably of periglacial origin (Davies 1974; Colhoun 1978). The second stratum frequently comprised a dense shrub and graminoid layer and *S. microphyllum* was generally absent. Soils were dark grey to brown fine sandy loams.

No evidence of any recent fire was observed in the quadrats. Ring counts revealed an age of 14 years for the *S. microphyllum* population and for the associated *Helichrysum lycopodioides* population. However, a spot fire had burnt and killed 8 mature plants at the edge of a nearby *S. microphyllum* population, some three years prior to the survey. Twelve seedlings were evident within 1.5 metres of parent plants but had not invaded adjacent undisturbed vegetation. There was no evidence of forest taxa regenerating within the burnt *S. microphyllum* population. No *S. microphyllum* seedlings were recorded in any quadrat.

Correlations indicated that *S. microphyllum* was confined to a habitat distinguished by shallow soils and low open vegetation on open ground relatively free of litter (Table 5.6). *Spyridium microphyllum* was negatively correlated with closed, damp tall shrubland on slopes covered by jumbled boulders (represented by surface rock cover), overlying deep soils (Table 5.6). These communities provided an interesting component of the vegetation continuum and were the wettest of the three communities described. They consisted of a dense, multilayered assemblage of *Beyeria viscosa* and *Notelaea ligustrina*, *Lepidosperma ensiforme* and *Dianella tasmanica*, which are usually associated with damper environments. The latter two species are common in eastern Tasmania and, possessing rhizomes, are able to take advantage of damp crevices in rocky substrates.

Minimum soil depth and surface rock cover provided the most parsimonious model describing the realised niche of *S. microphyllum* (Fig. 5.6; Tables 5.7 - 5.10).

Quadrats with and without *S. microphyllum* were well separated on the basis of bare ground cover and tree cover, but when these were added to the model, prevented it from reaching convergence, mainly owing to the small data set.

#### *Swan River site*

Thirty - nine quadrats were recorded along the Swan River. At times the zone suitable for sampling was quite narrow and the data comprised a number of short transects which were pooled for analysis. *S. microphyllum* occurred in 16 quadrats. Analysis of dissimilarities distinguished quadrats with *S. microphyllum* as significantly different floristically from those without *S. microphyllum* at the Swan River ( $R = 0.22$ ;  $P < 0.005$ ; Fig. 5.7).

Four broad vegetation assemblages were identified. Grassy open forest, dominated by *Eucalyptus pulchella* and occasionally *E. viminalis* occupied the area above the





Plate 5.3a. Swan River. Slopes above the river supporting riparian scrub, open riparian shrubland containing *S. microphyllum* (centre) and grassy *Eucalyptus pulchella* - *E. viminalis* open forest with an understorey of *Melaleuca pustulata* (far background).



Plate 5.3b. Swan River. Upper slopes of the Swan River supporting *Callitris rhomboidea* - *Melaleuca pustulata* open - scrub (background) above *M. pustulata* - *Acacia mucronata* tall closed riparian scrub.

river (Plate 5.3a & b). *S. microphyllum* was absent from this community. The understorey was very sparse and consisted of scattered individuals of *Acacia dealbata*, *A. mearnsii*, *Melaleuca pustulata* or, occasionally, *Bursaria spinosa*. *Melaleuca pustulata* also formed local thickets. In general, the ground was rocky, with *Poa rodwayi* and *Lepidosperma laterale* dominant. The soils were brown clay loams.

The second community was open riparian shrubland which occurred in rocky areas close to the river's edge (Plate 5.3a). The vegetation consisted of *M. pustulata* dominated shrubland, with species such as *Acacia mucronata*, *Spyridium obovatum* var. *obovatum*, *Allocasuarina littoralis*, *Hakea megadenia*, *Callistemon pallidus*, *Acacia genistifolia* and *Micrantheum hexandrum*. *Callitris oblonga* and *Callistemon sieberi* were sporadically recorded from this community. It tended to be rockier, drier and generally more open than the tall closed riparian scrub. *Spyridium microphyllum* occurred throughout the community. Soils were dark brown silty clay alluvium or clay loam.

A third community comprised *Melaleuca pustulata* - *Acacia mucronata* tall closed riparian scrub (Plate 5.3b). Cover of exposed bedrock was relatively low in these quadrats. Species commonly recorded in this community were *Callistemon sieberi*, *C. pallidus*, *Pomaderris apetala*, *Leptospermum lanigerum* and *Lepidosperma ensiforme*. *Spyridium microphyllum* was sometimes present in gaps or at the boundary between the two. Herbaceous exotics were also relatively frequent within this vegetation. Soils were dark reddish brown silty clay loams.

A fourth community consisted of *Callitris rhomboidea* - *Melaleuca pustulata* open - scrub on rocky slopes at the boundary of open forest and open riparian vegetation (Plate 5.3b). Additional species were, *M. pustulata*, *S. obovatum* var. *obovatum*, *S. obovatum* var. *velutinum*, *Leptospermum grandiflorum*, *Calytrix tetragona*, *Lasiopetalum micranthum* and *S. microphyllum*. Soils were brown to dark brown silty, sandy clay loam.

Fire history appears to have been variable. In grassy open forest above the flood zone, *Melaleuca pustulata* individuals were 15 - 17 years old and *Acacia dealbata* was 10 - 12 years old, indicating two possible fires at these times. A range of ages were apparent in riparian shrubland at various positions along transects. This may be expected in an environment prone to floods of different amplitudes. *Melaleuca pustulata* individuals were 15, 17 and 25 years old, *Spyridium obovatum* var. *obovatum* individuals were 10, 15 and 36 years old; while those of *S. microphyllum* were 21 years and 35 years old. In *Callitris rhomboidea* scrub *M. pustulata* individuals were 15 years old, *Spyridium obovatum* var. *velutinum* individuals were 23 and 35 years old. *Spyridium microphyllum* individuals were 24 years, 35 years and 45 years old.

Some ages corresponded to high flood levels (in excess of 5 metres above average) for the Swan River, which occurred 5, 9, 10, 13, 15, 17, 20, 21, 23 and 24 years ago (Hydro Electricity Commission records 1964 - 1993). However, these are impossible to separate from the patch fires which are frequently lit along the river bank by people and no further attempt was made to correlate the two types of disturbance.

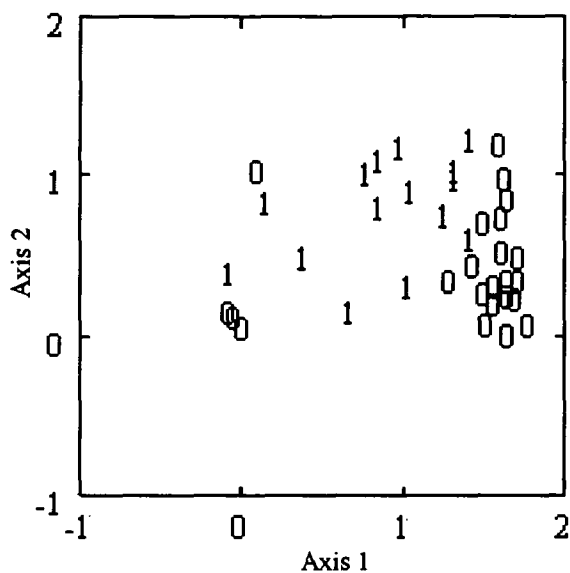


Figure 5.7. Swan River. The distribution of quadrats in the ordination space of the second NMDS, showing quadrats with *S. microphyllum* (1) and without *S. microphyllum* (0).

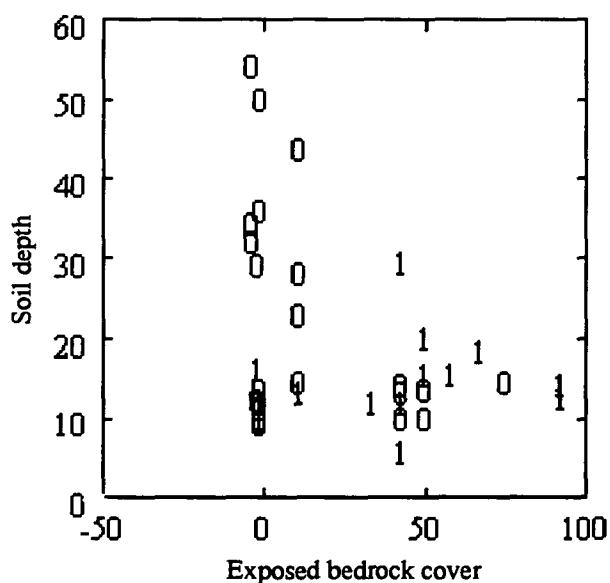


Figure 5.8. Swan River. The distribution of quadrats according to exposed bedrock cover and soil depth, showing quadrats with *S. microphyllum* (1) and those where *S. microphyllum* is absent (0).

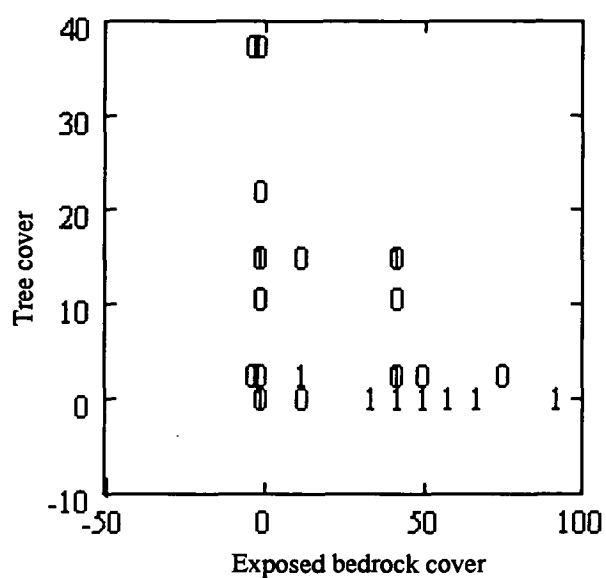


Figure 5.9a. Swan River. The distribution of quadrats according to exposed bedrock cover and tree cover. Quadrats with *S. microphyllum* present (1) and absent (0) are indicated.

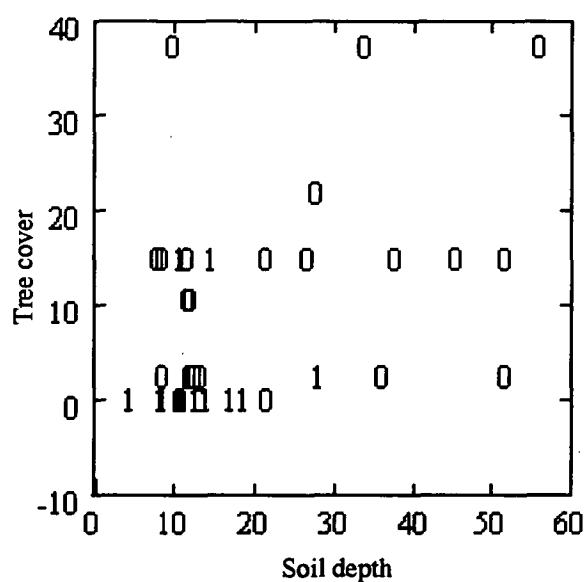


Figure 5.9b. Swan River. The distribution of quadrats according to soil depth and tree cover. Quadrats with *S. microphyllum* present (1) and absent (0) are indicated.

	<b>S.MICRO?</b>	<b>pH</b>	<b>Average soil depth</b>	<b>Maximum soil depth</b>	<b>Minimum soil depth</b>	<b>Tree height</b>	<b>Tree cover</b>	<b>Tall shrub height</b>	<b>Tall shrub cover</b>
<b>pH</b>	0.101(0.58)								
<b>Average soil depth</b>	-0.377(0.02)	-0.122(0.45)							
<b>Maximum soil depth</b>	-0.383(0.02)	0.003(0.99)	0.823(0.00)						
<b>Minimum soil depth</b>	-0.296(0.08)	-0.016(0.93)	0.858(0.00)	0.522(0.006)					
<b>Tree height</b>	-0.628(0.00)	-0.045(0.79)	0.338(0.04)	0.343(0.03)	0.166(0.32)				
<b>Tree cover</b>	-0.466(0.003)	-0.389(0.01)	0.401(0.004)	0.350(0.03)	0.328(0.03)	0.382(0.02)			
<b>Tall shrub height</b>	-0.225(0.18)	-0.143(0.39)	0.185(0.30)	0.272(0.12)	0.049(0.76)	0.344(0.03)	-0.070(0.66)		
<b>Tall shrub cover</b>	0.225(0.16)	0.213(0.19)	-0.155(0.35)	-0.097(0.55)	-0.110(0.55)	-0.248(0.13)	-0.035(0.81)	-0.094(0.57)	
<b>Low shrub height</b>	0.240(0.13)	0.099(0.56)	-0.440(0.004)	-0.472(0.004)	-0.328(0.04)	0.147(0.37)	-0.304(0.07)	-0.031(0.87)	-0.062(0.71)
<b>Low shrub cover</b>	0.451(0.001)	0.099(0.57)	-0.367(0.02)	-0.454(0.005)	-0.271(0.13)	-0.453(0.008)	-0.504(0.002)	-0.302(0.06)	0.092(0.59)
<b>Herb cover</b>	-0.155(0.36)	-0.117(0.48)	0.154(0.35)	0.148(0.39)	0.039(0.83)	0.227(0.16)	0.203(0.23)	0.273(0.10)	-0.159(0.34)
<b>Grass cover</b>	-0.393(0.009)	-0.104(0.54)	0.062(0.69)	0.004(0.99)	0.056(0.74)	0.222(0.19)	0.177(0.30)	0.251(0.14)	-0.275(0.10)
<b>Graminoid cover</b>	-0.232(0.15)	0.044(0.81)	-0.076(0.65)	0.010(0.94)	-0.152(0.36)	0.333(0.04)	0.106(0.55)	-0.167(0.32)	0.051(0.79)
<b>Fern cover</b>	-0.203(0.26)	-0.031(0.86)	-0.226(0.18)	-0.154(0.34)	-0.239(0.16)	0.215(0.19)	-0.174(0.28)	0.062(0.75)	-0.214(0.20)
<b>Litter cover</b>	-0.493(0.004)	-0.032(0.86)	0.345(0.02)	0.232(0.17)	0.411(0.003)	0.227(0.20)	0.291(0.08)	0.244(0.13)	0.152(0.36)
<b>Surface rock cover</b>	0.064(0.71)	0.008(0.97)	-0.481(0.002)	-0.446(0.002)	-0.438(0.004)	0.128(0.42)	-0.248(0.14)	0.081(0.63)	-0.157(0.34)
<b>Bed rock cover</b>	0.372(0.02)	-0.032(0.86)	-0.381(0.02)	-0.333(0.04)	-0.304(0.05)	-0.194(0.25)	-0.438(0.00)	-0.193(0.25)	-0.075(0.66)
<b>Bare ground cover</b>	0.043(0.82)	0.055(0.75)	0.132(0.45)	0.208(0.19)	0.011(0.96)	-0.027(0.86)	-0.108(0.53)	-0.088(0.63)	0.154(0.40)
<b>Species richness</b>	-0.188(0.24)	0.056(0.72)	-0.091(0.61)	-0.084(0.63)	-0.174(0.30)	0.341(0.05)	-0.093(0.58)	0.313(0.05)	-0.200(0.22)

Table 5.11. Correlations and 2-tail probabilities from 1000 random permutations between environmental variables at the Swan River site (degrees of freedom = 37).

	Low shrub height	Low shrub cover	Herb cover	Grass cover	Graminoid cover	Fern cover	Litter cover	Surface rock cover	Bed rock cover
Low shrub cover	0.174(0.30)								
Herb cover	-0.149(0.38)	-0.278(0.08)							
Grass cover	-0.135(0.43)	-0.204(0.24)	0.506(0.001)						
Graminoid cover	0.369(0.02)	-0.024(0.89)	-0.467(0.002)	-0.044(0.80)					
Fern cover	0.326(0.05)	0.172(0.30)	0.125(0.48)	0.224(0.18)	0.141(0.40)				
Litter cover	-0.341(0.04)	-0.276(0.09)	0.383(0.02)	0.400(0.01)	-0.193(0.24)	0.073(0.67)			
Surface rock cover	0.371(0.02)	0.224(0.18)	-0.219(0.19)	-0.113(0.49)	0.060(0.71)	0.340(0.04)	-0.194(0.24)		
Bed rock cover	0.292(0.06)	0.496(0.002)	-0.583(0.00)	-0.468(0.002)	0.201(0.24)	0.185(0.28)	-0.475(0.003)	0.425(0.01)	
Bare ground cover	-0.021(0.90)	0.033(0.84)	-0.291(0.07)	-0.269(0.10)	0.102(0.56)	-0.068(0.68)	-0.416(0.01)	-0.018(0.93)	-0.124(0.45)
Species richness	0.210(0.19)	0.020(0.92)	0.291(0.06)	0.273(0.09)	0.108(0.54)	0.374(0.02)	-0.003(0.99)	0.093(0.57)	0.007(0.97)
Bare ground cover									
Species richness	-0.332(0.04)								

Table 5.11 continued.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	51.97	39			
pH	50.62	38	1.35	1	ns
Average soil depth	46.97	38	4.99	1	*
Maximum soil depth	46.81	38	5.16	1	*
Minimum soil depth	48.17	38	3.81	1	ns
Surface rock cover	51.64	38	0.33	1	ns
Exposed bedrock cover	46.10	38	5.89	1	*
Bare ground cover	51.83	38	0.14	1	ns
Tree height	34.54	38	17.43	1	***
Tree cover	41.29	38	10.70	1	**
Tall shrub height	50.83	38	1.14	1	ns
Tall shrub cover	49.59	38	2.38	1	ns
Low shrub height	48.33	38	3.64	1	ns
Low shrub cover	42.68	38	9.29	1	**
Herb cover	51.53	38	0.44	1	ns
Grass cover	46.14	38	5.83	1	*
Graminoid cover	50.27	38	1.70	1	ns
Fern cover	50.65	38	1.32	1	ns
Litter cover	43.16	38	8.82	1	**
Species richness	51.71	38	0.27	1	ns

Table 5.12. Results of individual models for the Swan River site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ ; ns = not significant.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	51.97	38			
+ exposed bed rock cover	46.08	37	5.90	1	**
+ average soil depth	43.33	36	8.64	1	**
+ tree cover	38.38	35	13.59	1	***

Table 5.13. Final model for the Swan River site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ .

Estimate	se	Parameter
0.47	0.098	constant
0.02	0.017	exposed bedrock cover
-0.04	0.045	average soil depth
-0.13	0.068	tree cover

Table 5.14. Parameter estimates for the final model at the Swan River site. Se = standard error.



Quadrat no.	S.MICRO?	Exposed bedrock cover	Average soil depth	Model 1 Estimated predicted probability (bedrock + soil depth)	Tree cover	Model 2 Estimated predicted probability (bedrock+soil depth + tree cover)
1	0	2	50.0	0.04	3	0.030
2	0	3	14.6	0.35	0	0.540
3	0	3	28.0	0.19	3	0.090
4	0	3	43.6	0.08	3	0.050
5	0	2	36.0	0.09	3	0.050
6	0	2	50.0	0.04	2	0.130
7	1	4	29.4	0.29	2	0.410
8	1	4	20.0	0.48	0	0.630
9	0	0	32.0	0.11	4	0.003
10	0	0	54.0	0.03	4	0.001
11	1	2	9.5	0.35	0	0.530
12	1	2	10.0	0.34	0	0.530
13	0	3	23.0	0.25	3	0.110
14	0	2	11.2	0.32	4	0.008
15	0	0	34.4	0.10	2	0.210
16	1	2	12.2	0.31	0	0.500
17	1	3	13.2	0.37	2	0.470
18	0	2	9.2	0.35	3	0.140
19	0	2	13.4	0.29	3	0.200
20	1	4	5.8	0.64	0	0.720
21	0	4	14.0	0.52	2	0.570
22	1	4	12.0	0.55	3	0.230
23	0	3	23.0	0.25	0	0.450
24	1	6	14.0	0.81	0	0.830
25	1	6	12.4	0.83	0	0.840
26	0	4	13.0	0.53	3	0.330
27	0	4	13.0	0.53	3	0.220
28	0	4	13.4	0.58	2	0.620
29	0	5	14.6	0.72	2	0.710
30	1	5	15.4	0.61	0	0.700
31	1	2	16.2	0.26	3	0.110
32	1	4	15.4	0.55	0	0.670
33	1	4	11.8	0.49	0	0.630
34	0	4	9.8	0.64	2	0.650
35	0	4	10.0	0.58	3	0.240
36	0	2	29.0	0.13	3	0.030
37	1	5	18.2	0.62	0	0.720
38	0	2	12.2	0.31	0	0.500

Table 5.15. Estimated predicted probabilities of occurrence of *S. microphyllum* (Swan River), according to model 1 and model 2, where 1 = <1%; 2 = 1-5%; 3 = 5-25%; 4 = 25-40%; 5 = 50-75%; 6 = >75%.



*Spyridium microphyllum* seedlings were observed in two areas which had been burnt less than a year before. These patches consisted of an area approximately five metres in diameter and a larger area, approximately 15 metres in diameter. There were in excess of 50 seedlings confined to ash beds of burnt litter within a one metre radius of single fire - killed mature plants, and more than 200 seedlings within a 1 metre radius of four mature plants growing close together also killed by fire. *Lasiopetalum micranthum* and *Correa reflexa* seedlings were also evident. A single *S. microphyllum* plant situated upslope at the edge of the burnt area had resprouted, suggesting the fire had been relatively cool.

Correlations indicated that even though a wide range of habitats existed at this site, *S. microphyllum* populations were associated with specific features of the environment. There was a strong negative relationship between *S. microphyllum* and tree height, tree cover, litter cover, grass cover and soil depth. There was a positive correlation between *S. MICRO?* and low shrub cover and exposed bedrock, reflecting its occurrence in open vegetation on shallow rocky soils (Table 5.11). Correlations between low shrub cover and bedrock cover indicated a close relationship between shrubby vegetation and rockiness (Table 5.11).

The probability of occurrence of *S. microphyllum* was significantly predicted by a combination of exposed bedrock cover and average soil depth (Tables 5.12 - 5.15; Fig. 5.8). The results suggest that *S. microphyllum* is confined to the upper riparian zone by shallow rocky soils which are unable to support tree dominated vegetation. However, estimated predicted probabilities were relatively low for the majority of quadrats containing *S. microphyllum* (Table 5.15). Suitable habitat also existed in some quadrats where *S. microphyllum* was absent. The addition of tree cover significantly improved the model fit in most cases (Table 5.15), showing that *S. microphyllum* is generally favoured in areas where trees are excluded (Figs. 5.9a & b), although in two quadrats *S. microphyllum* was associated with moderate tree cover (< 25%).

#### *St Pauls River site*

Vegetation along the St Pauls River was badly degraded as a result of invasion by introduced exotics. The original riparian community had been substantially reduced by clearing and burning of vegetation for agricultural purposes or road maintenance (Plate 5.4a & b). Remnants indicate it was formerly grassy *Eucalyptus ovata* riparian woodland. It is now reduced to occasional emergent individuals over a tall understorey of riparian shrubs and small trees such as *Callitris oblonga*, *Dodonaea filiformis*, *Leptospermum lanigerum*, *Acacia axillaris*, *A. dealbata* and *Bursaria spinosa*. The ground layer was predominantly *Poa labillardieri* var. *acris*, *Themeda triandra*, *Diplarrena moraea*, *Lomandra longifolia*, *P. hookeri*, *Danthonia* spp. and *Ehrharta stipoides*, with *Acaena echinata* and *Plantago varia* in drier areas. Vegetation where *C. oblonga* was present appeared not to have been burnt for at least ten to twenty years.

In addition to *S. microphyllum*, other rare endemic shrubs, *Acacia axillaris* and *Grevillea australis* var. *linearifolia*, were frequently encountered. Rare non



Plate 5.4a. St Pauls River. Remnant grassy *Eucalyptus ovata* riparian woodland (background, in front of hills). Cleared slopes above the river can be seen to the left.



Plate 5.4b. St Pauls River. *Spyridium microphyllum* plants approximately 0.5 m high at the edge of the road. Taller vegetation is regularly slashed for roadside maintenance (background).

endemics included *Callitris oblonga*, *Pomaderris phyllifolia* var. *ericoides* and *Pultenaea prostrata*. The taxon known as *Callitris oblonga* within Tasmania (*sensu* Curtis & Morris 1975) and as *Callitris* sp. aff. *oblonga* Apsley River (A. M. Gray 22495) elsewhere (Australian and New Zealand Environment and Conservation Council 1993) may be endemic to Tasmania and is considered as such for conservation purposes pending taxonomic treatment (Nadolny & Benson 1992).

### *Spyridium obcordatum*

A two dimensional solution was accepted for ordinations of quadrat data from the Hawley, Asbestos Range and both Dans Hill transects. NMDS attained a minimum stress of 0.100672 from all 10 random starts for the Hawley quadrats; 0.146890 from 4 starts for Asbestos quadrats; 0.1968504 from all 10 starts for the Dans Hill 1 quadrats and 0.130231 from all 10 starts for the Dans Hill 2 quadrats.

#### *Hawley site*

Analysis of dissimilarities distinguished quadrats with *S. obcordatum* as significantly different floristically from those without *S. obcordatum* ( $R = 0.16$ ,  $P < 0.05$ ; Fig. 5.10). In addition to *S. obcordatum*, three other rare taxa (*Pomaderris* aff. *apetala*, *Triglochin centrocarpum*, *Lepidosperma viscidum*) were recorded at this site. *Pomaderris* aff. *apetala* is an undescribed coastal form of *P. apetala* (N. Walsh, MEL, pers. comm.) and is confined to a small area in southern Gippsland near Wilsons Promontory and the north coast of Tasmania. It was observed near the transect. The latter two species are non endemics at the edge of their range in Tasmania, and both were present in quadrats with and without *S. obcordatum*.

Twenty quadrats were recorded in vegetation consisting of grassy *Allocasuarina verticillata* dominated woodland, open rock plate vegetation dominated by scattered low shrubs, sedges and ephemeral herbs, and in heathy *Eucalyptus amygdalina* woodland (Plate 5.5a). *Spyridium obcordatum* occurred in 6 quadrats, all located in *A. verticillata* woodland with a grassy ground layer consisting of *Poa rodwayi*, *Themeda triandra*, *Stipa mollis*, *S. pubinodis*, *Danthonia tenuior*, *D. penicillata*, *Lepidosperma viscidum* and a number of prostrate small shrubs and intertussock herbs (Plate 5.5b). Understorey species were sparse, represented by *Dodonaea viscosa*, *Allocasuarina littoralis* and *Hibbertia sericea*. Ground layer species other than *S. obcordatum* were typical of grassy vegetation on dolerite in Tasmania and included *Viola hederacea*, *Gonocarpus humilis*, *Bossiaea prostrata*, *Chaemiscilla corymbosa*, *Hypericum gramineum*, *Wahlenbergia* spp., *Gnaphalium collinum* and *Stackhousia monogyna*.

*Spyridium obcordatum* also occurred at the perimeter of dolerite rock plate vegetation with small annuals, grasses, *L. viscidum* and occasionally *Astroloma humifusum* and *Hibbertia sericea*. Species which were frequently recorded in this community were *Centrolepis strigosa*, *C. aristata*, *Daucus glochidiatus*, *Pelargonium australe*, *Crassula sieberiana*, *Centaureum erythraea*, *Stipa mollis* and *Danthonia tenuior*.





Plate 5.5a. Hawley. Open dolerite rock plate adjacent to grassy *Allocasuarina verticillata* woodland and *Eucalyptus amygdalina* woodland (background). *Spyridium obcordatum* occurs between at the perimeter of the rock plate.



Plate 5.5b. Hawley. *Spyridium obcordatum* habitat, where plants occur between exposed bedrock (foreground and right), with *Lepidosperma viscidum* (emergent) and *Astroloma humifusum*.

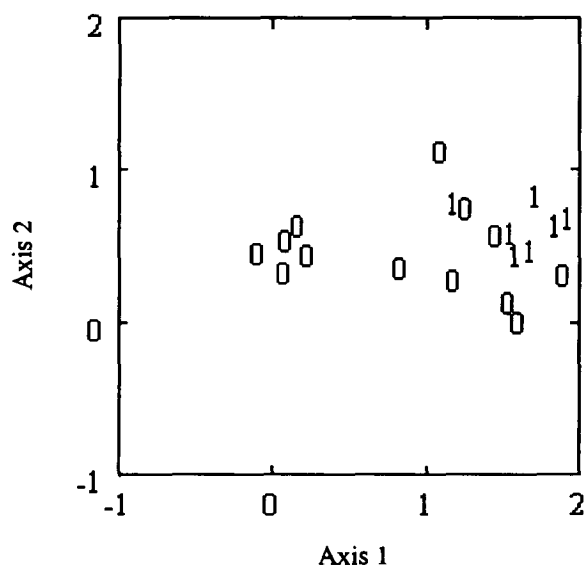


Figure 5.10. Hawley. The distribution of quadrats in the ordination space of the second NMDS, showing quadrats with *S. obcordatum* (1) and those without *S. obcordatum* (0).

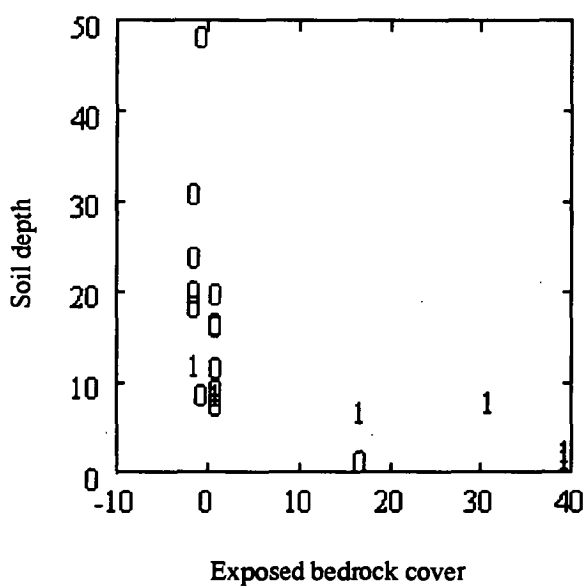


Figure 5.11a. Hawley. The distribution of quadrats according to exposed bedrock cover and soil depth, showing quadrats with *S. obcordatum* (1) and those without *S. obcordatum* (0).

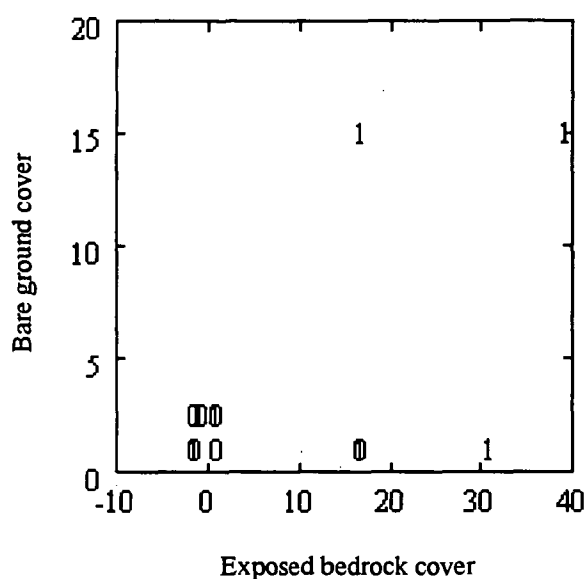


Figure 5.11b. Hawley. The distribution of quadrats according to exposed bedrock cover and bare ground cover, showing quadrats with *S. obcordatum* (1) and quadrats without *S. obcordatum* (0).

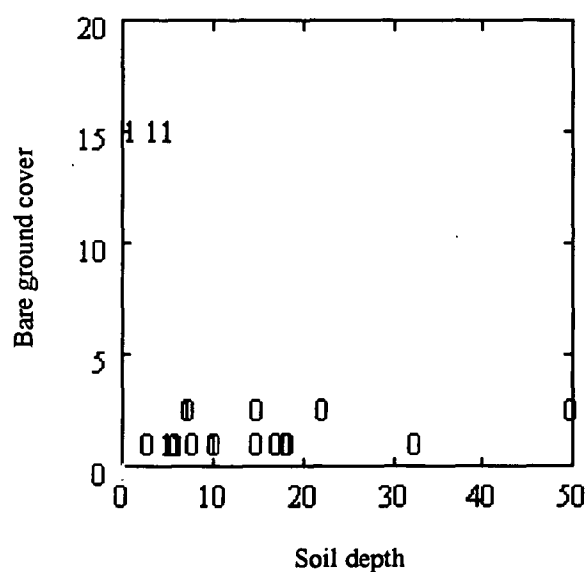


Figure 5.11c. Hawley. The distribution of quadrats according to soil depth and bare ground cover, showing quadrats with *S. obcordatum* (1) and those without *S. obcordatum* (0).

	<b>S.OBCORD?</b>	<b>pH</b>	<b>Average soil depth</b>	<b>Maximum soil depth</b>	<b>Minimum soil depth</b>	<b>Tree height</b>	<b>Tree cover</b>	<b>Tall shrub height</b>	<b>Tall shrub cover</b>
<b>pH</b>	-0.472(0.04)								
<b>Average soil depth</b>	-0.496(0.02)	0.189(0.45)							
<b>Maximum soil depth</b>	-0.489(0.02)	0.183(0.46)	0.932(0.00)						
<b>Minimum soil depth</b>	-0.486(0.03)	0.050(0.84)	0.864(0.00)	0.668(0.00)					
<b>Tree height</b>	-0.478(0.03)	0.219(0.33)	0.730(0.002)	0.569(0.009)	0.784(0.00)				
<b>Tree cover</b>	-0.472(0.03)	0.285(0.25)	0.660(0.005)	0.530(0.01)	0.702(0.00)	0.983(0.00)			
<b>Tall shrub height</b>	-0.041(0.91)	-0.046(0.84)	-0.157(0.52)	-0.069(0.80)	-0.160(0.51)	-0.213(0.36)	-0.244(0.34)		
<b>Tall shrub cover</b>	-0.121(0.63)	-0.019(0.93)	0.129(0.60)	0.166(0.48)	0.053(0.84)	0.038(0.91)	-0.015(0.95)	0.711(0.002)	
<b>Low shrub height</b>	-0.411(0.06)	0.453(0.06)	0.534(0.01)	0.446(0.03)	0.522(0.02)	0.676(0.001)	0.694(0.001)	-0.371(0.10)	-0.094(0.66)
<b>Low shrub cover</b>	-0.498(0.02)	0.258(0.30)	0.623(0.003)	0.439(0.05)	0.726(0.00)	0.930(0.00)	0.912(0.00)	-0.169(0.47)	0.113(0.62)
<b>Herb cover</b>	0.308(0.17)	-0.044(0.87)	-0.734(0.003)	-0.696(0.004)	-0.575(0.02)	-0.367(0.08)	-0.287(0.19)	-0.083(0.73)	-0.405(0.09)
<b>Grass cover</b>	0.256(0.24)	0.079(0.74)	-0.201(0.43)	-0.107(0.70)	-0.306(0.20)	-0.524(0.04)	-0.515(0.02)	0.160(0.47)	0.156(0.51)
<b>Graminoid cover</b>	-0.202(0.41)	0.304(0.20)	0.337(0.14)	0.282(0.21)	0.365(0.10)	0.077(0.76)	0.044(0.85)	0.007(0.98)	0.135(0.58)
<b>Fern cover</b>	-0.286(0.27)	0.526(0.02)	-0.129(0.53)	-0.141(0.55)	-0.104(0.68)	0.063(0.88)	0.133(0.55)	-0.277(0.27)	-0.332(0.14)
<b>Litter cover</b>	-0.338(0.13)	0.362(0.10)	0.095(0.70)	0.168(0.46)	-0.041(0.89)	0.004(0.99)	0.017(0.92)	0.490(0.02)	0.332(0.15)
<b>Surface rock cover</b>	0.526(0.01)	-0.179(0.44)	-0.542(0.02)	-0.501(0.03)	-0.529(0.03)	-0.553(0.003)	-0.549(0.01)	0.024(0.91)	-0.174(0.44)
<b>Bed rock cover</b>	0.669(0.001)	-0.398(0.08)	-0.553(0.02)	-0.541(0.02)	-0.451(0.03)	-0.424(0.04)	-0.417(0.04)	0.126(0.60)	-0.129(0.57)
<b>Bare ground cover</b>	0.562(0.03)	-0.534(0.009)	-0.355(0.12)	-0.349(0.13)	-0.275(0.23)	-0.260(0.39)	-0.265(0.32)	-0.347(0.11)	-0.288(0.14)
<b>Species richness</b>	0.414(0.07)	-0.370(0.11)	-0.016(0.96)	-0.105(0.67)	0.163(0.48)	0.124(0.57)	0.136(0.59)	-0.376(0.10)	-0.418(0.09)

Table 5.16. Correlations and 2-tail probabilities from 1000 random permutations between environmental variables at the Hawley site (degrees of freedom = 19).

	Low shrub height	Low shrub cover	Herb cover	Grass cover	Graminoid cover	Fern cover	Litter cover	Surface rock cover	Bed rock cover
Low shrub cover	0.635(0.005)								
Herb cover	-0.225(0.38)	-0.261(0.26)							
Grass cover	-0.396(0.08)	-0.409(0.08)	0.077(0.69)						
Graminoid cover	0.189(0.42)	0.150(0.53)	-0.180(0.51)	0.435(0.06)					
Fern cover	0.546(0.02)	0.041(0.86)	0.240(0.44)	-0.211(0.37)	0.148(0.53)				
Litter cover	-0.146(0.53)	0.042(0.87)	-0.044(0.86)	0.380(0.09)	0.406(0.08)	0.018(0.93)			
Surface rock cover	-0.145(0.55)	-0.532(0.03)	0.344(0.22)	-0.162(0.52)	-0.345(0.13)	0.040(0.90)	-0.436(0.06)		
Bed rock cover	-0.397(0.08)	-0.439(0.03)	0.251(0.24)	-0.052(0.81)	-0.411(0.07)	-0.043(0.87)	-0.553(0.01)	0.504(0.04)	
Bare ground cover	-0.124(0.56)	-0.306(0.15)	0.170(0.82)	-0.269(0.29)	-0.472(0.03)	-0.107(0.69)	-0.899(0.00)	0.591(0.03)	0.719(0.004)
Species richness	-0.141(0.56)	0.109(0.65)	0.212(0.35)	0.161(0.52)	0.286(0.23)	-0.264(0.24)	-0.171(0.47)	-0.161(0.49)	0.137(0.56)



Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	25.90	19			
pH	21.05	18	4.85	1	*
Average soil depth	17.51	18	8.39	1	**
Maximum soil depth	18.26	18	7.63	1	*
Minimum soil depth	17.47	18	8.43	1	**
Surface rock cover	19.57	18	6.33	1	*
Exposed bedrock cover	15.59	18	10.31	1	**
Bare ground cover	19.10	18	6.82	1	**
Tree height	19.41	18	6.49	1	*
Tree cover	19.41	18	6.49	1	*
Tall shrub height	25.86	18	0.03	1	ns
Tall shrub cover	25.59	18	0.30	1	ns
Low shrub height	21.97	18	3.93	1	*
Low shrub cover	17.46	18	8.44	1	**
Herb cover	23.04	18	2.86	1	ns
Grass cover	24.59	18	1.13	1	ns
Graminoid cover	25.05	18	0.85	1	ns
Fern cover	23.86	18	2.04	1	ns
Litter cover	23.66	18	2.24	1	ns
Species richness	22.11	18	3.79	1	ns

Table 5.17 Results of individual models for the Hawley site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ ; ns = not significant.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	25.90	19			
+ exposed bed rock cover	15.59	18	5.90	1	**
+ average soil depth	14.81	17	11.09	1	***
+ bare ground cover	13.44	16	12.46	1	***

Table 5.18. Final model for the Hawley site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ .

Estimate	se	Parameter
-1.57	2.57	constant
0.119	0.11	exposed bedrock cover
-0.100	0.13	average soil depth
0.63	1.10	bare ground cover

Table 5.19. Parameter estimates for the final model at the Hawley site. Se = standard error.

Quadrat no.	S.OBCORD?	Exposed bedrock cover	Average soil depth	Bare ground cover	Estimated predicted probability
1	1	4	7.6	1	0.82
2	1	3	6.6	1	0.51
3	0	3	1.2	1	0.64
4	0	2	7.4	1	0.20
5	0	2	19.6	1	0.07
6	1	2	8.6	2	0.36
7	1	4	1.6	3	1.00
8	1	4	2.4	3	1.00
9	1	3	6.6	3	1.00
10	0	2	9.2	1	0.17
11	0	2	16.2	1	0.09
12	0	2	11.6	1	0.14
13	0	0	19.8	1	0.05
14	0	0	18.4	1	0.06
15	0	0	23.6	2	0.09
16	0	0	30.8	1	0.02
17	1	0	11.8	1	0.11
18	0	2	16.4	2	0.21
19	0	1	8.6	2	0.32
20	0	1	48.0	2	0.01

Table 5.20. Estimated predicted probabilities of occurrence of *S. obcordatum* at the Hawley site, according to values for average soil depth (cm), exposed bedrock cover and bare ground cover (back transformed to their Braun Blanquet cover classes). Cover classes: 1 = <1%; 2 = 1-5%; 3 = 5-25%; 4 = 25-40%; 5 = 50-75%; 6 = >75%.

*Eucalyptus amygdalina* woodland was situated on deep, acidic sandy soils of Tertiary age. *Spyridium obcordatum* was absent from these quadrats. The understorey was tall scrub, consisting of *Exocarpos cupressiformis*, *Acacia verticillata* var. *verticillata*, *Banksia marginata* and *Melaleuca ericifolia*. The latter indicates a seasonal excess of moisture. A third stratum was dominated by *Lepidosperma ensiforme* and a number of shrubs, including *Pultenaea daphnoides* var. *obcordata*, *Leptospermum scoparium*, *Leptomeria drupacea*, *Epacris impressa* and *Leucopogon australis*. The ground layer was sparse, consisting of *Leptocarpus tenax*, *Viola hederacea*, *Gonocarpus tetragynus* and *Pteridium esculentum*.

The site did not appear to have been affected by recent fire or any other recent disturbances. Very little charcoal was observed in the quadrats. There were fewer than 100 *S. obcordatum* plants, most of which were large, having suffered little damage from rabbits or browsing animals. Ring counts of *S. obcordatum* and *Pultenaea daphnoides* in the adjacent *E. amygdalina* woodland community indicated that these components of the vegetation were 10 - 12 years old.

Soils were dark reddish brown sandy clay loams in the grassy woodland community, dark brown fine sandy loam where associated with plates, and grey sandy loams in *E. amygdalina* woodland.

*Spyridium obcordatum* was significantly positively correlated with cover of exposed bedrock, surface rock and bare ground and negatively correlated with pH, increasing soil depth, tree height, tree cover and low shrub cover (Table 5.16). The results show that *S. obcordatum* is associated with open vegetation on moderately shallow soils at the edge of rock plates. The inverse relationship between pH and *S. obcordatum* was unexpected, given its absence from sandy soils. This may be an artefact of a close relationship with exposed bedrock and more leached, shallow soils which exist patchily within a more neutral soil environment. This indicates confinement to a relatively narrow niche at this site.

Generalized linear modelling predicted that the realised niche of *S. obcordatum* at this site was defined by a combination of exposed bedrock cover, soil depth and bare ground (Tables 5.17 - 5.20; Fig. 5.11a -c).

#### *Asbestos Range site*

*Spyridium obcordatum* was recorded in 15 out of 26 quadrats located in elevated coastal heathland near Badger Head in the Asbestos Range National Park. These quadrats were in vegetation co - dominated by *Lasiopetalum baueri* and *Banksia marginata*. *Pomaderris oraria* ssp. *oraria* was also confined to this community (Plate 5.6a). *Pomaderris oraria* and *L. baueri* have a very narrow range in Tasmania, being restricted to a few locations on the north coast. *Pomaderris* aff. *apetala* was observed nearby. Sub - dominant taxa were *Leptospermum scoparium*, *Lepidosperma laterale*, *Hibbertia sericea* and *Allocasuarina monilifera*. Shrubs were generally between 0.3 m and 0.75 m high. Analysis of dissimilarities distinguished quadrats with *S. obcordatum* as significantly different floristically from those without *S. obcordatum* ( $R = 0.69$ ;  $P < 0.0001$ ; Fig. 5.12).



Plate 5.6a. Asbestos Range. *Lepidosperma baueri* - *Banksia marginata* coastal heathland at Badger Head. *Spyridium obcordatum* occurs in open patches between dominant shrubs.



Plate 5.6b. Asbestos Range. Coastal heathland dominated by *Leptospermum scoparium* and *Banksia marginata*, where *S. obcordatum* was absent.

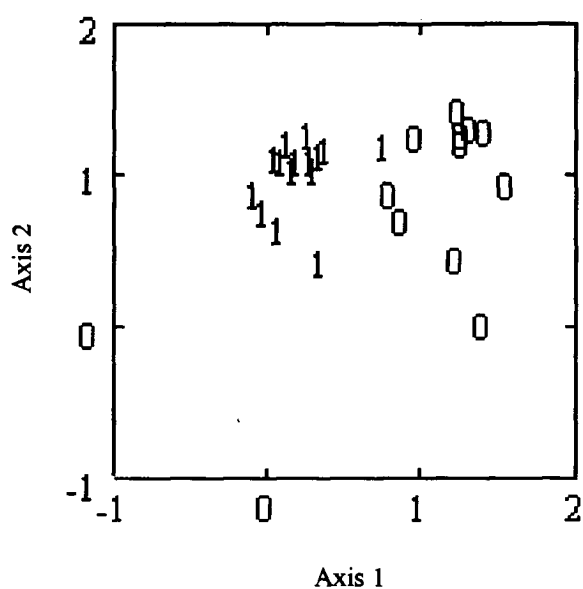


Figure 5.12. Asbestos Range. The distribution of quadrats in the ordination space of the second NMDS, showing quadrats with (1) and without (0) *S. obcordatum*.

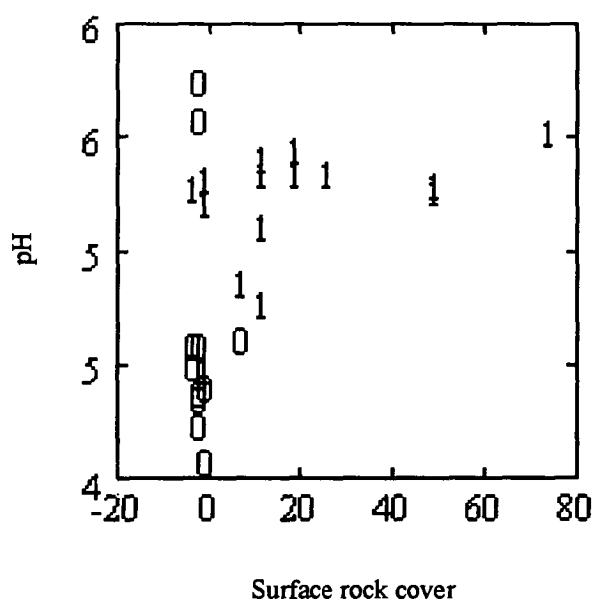


Figure 5.13. Asbestos Range. The distribution of quadrats according to surface rock cover and pH, showing quadrats with (1) and without (0) *S. obcordatum*.



	<b>S.OBCORD?</b>	<b>pH</b>	<b>Average soil depth</b>	<b>Maximum soil depth</b>	<b>Minimum soil depth</b>	<b>Tall shrub height</b>	<b>Tall shrub cover</b>	<b>Low shrub height</b>
<b>pH</b>	0.577(0.01)							
<b>Average soil depth</b>	0.043(0.85)	-0.216(0.27)						
<b>Maximum soil depth</b>	-0.234(0.38)	-0.281(0.17)	.8208(0.000)					
<b>Minimum soil depth</b>	0.224(0.25)	-0.090(0.67)	.8285(0.000)	0.456(0.00)				
<b>Tall shrub height</b>	0.171(0.66)	0.150(0.66)	-.2897(0.083)	-0.114(0.09)	-0.261(0.15)			
<b>Tall shrub cover</b>	0.171(0.83)	0.150(0.68)	-.2897(0.070)	-0.114(0.13)	-0.261(0.15)	1.000(0.005)		
<b>Low shrub height</b>	-0.426(0.02)	-0.392(0.05)	-.0447(0.815)	0.314(0.10)	-0.374(0.06)	0.357(0.02)	0.357(0.17)	
<b>Low shrub cover</b>	0.071(0.72)	-0.641(0.00)	.3293(0.092)	0.156(0.43)	0.394(0.05)	-0.235(0.12)	-0.235(0.13)	0.080(0.69)
<b>Herb cover</b>	0.113(0.56)	0.375(0.04)	.0076(0.969)	0.043(0.84)	-0.130(0.56)	-0.084(0.24)	-0.084(0.71)	-0.290(0.14)
<b>Grass cover</b>	0.012(0.83)	0.230(0.26)	-.5192(0.002)	-0.386(0.03)	-0.668(0.00)	0.216(0.005)	0.216(0.45)	0.357(0.07)
<b>Graminoid cover</b>	-0.576(0.001)	-0.346(0.07)	.0139(0.941)	0.124(0.59)	-0.129(0.55)	-0.211(0.31)	-0.211(0.32)	0.087(0.70)
<b>Fern cover</b>	-0.137(0.68)	-0.318(0.11)	.3733(0.065)	0.207(0.14)	0.479(0.003)	-0.076(0.36)	-0.076(0.28)	-0.148(0.45)
<b>Litter cover</b>	-0.067(0.74)	-0.525(0.004)	.2705(0.218)	0.265(0.22)	0.186(0.35)	-0.109(0.35)	-0.109(0.52)	0.326(0.12)
<b>Surface rock cover</b>	0.539(0.002)	0.470(0.01)	.3445(0.063)	0.113(0.63)	0.397(0.04)	-0.120(0.65)	-0.120(0.58)	-0.445(0.02)
<b>Bed rock cover</b>	0.247(0.37)	0.210(0.33)	-.7416(0.000)	-0.969(0.002)	-0.377(0.02)	-0.058(1.00)	-0.058(0.11)	-0.340(0.04)
<b>Bare ground cover</b>	0.451(0.02)	0.667(0.00)	.1391(0.538)	0.015(0.95)	0.112(0.58)	-0.064(0.59)	-0.064(0.74)	-0.378(0.04)
<b>Species richness</b>	0.677(0.00)	0.292(0.15)	-.2106(0.296)	-0.407(0.04)	-0.074(0.73)	0.244(0.21)	0.244(0.21)	-0.116(0.57)

Table 5.21. Correlations and 2-tail probabilities from 1000 random permutations between environmental variables at the Asbestos Range site (degrees of freedom =25).

	Low shrub cover	Herb cover	Grass cover	Graminoid cover	Fern cover	Litter cover	Surface rock cover	Bed rock cover	Bare ground cover
<b>Herb cover</b>	-0.416(0.04)								
<b>Grass cover</b>	-0.271(0.19)	0.222(0.39)							
<b>Graminoid cover</b>	-0.183(0.37)	-0.071(0.79)	-0.018(0.92)						
<b>Fern cover</b>	0.349(0.08)	-0.230(0.13)	-0.583(0.00)	0.218(0.26)					
<b>Litter cover</b>	0.572(0.004)	-0.211(0.27)	-0.155(0.44)	-0.126(0.56)	0.163(0.37)				
<b>Surface rock cover</b>	0.029(0.88)	0.330(0.08)	-0.137(0.52)	-0.455(0.02)	-0.056(0.75)	-0.213(0.230)			
<b>Bed rock cover</b>	-0.017(0.93)	-0.121(0.55)	0.312(0.06)	-0.129(0.62)	-0.182(0.25)	-0.202(0.36)	-0.068(0.81)		
<b>Bare ground cover</b>	-0.370(0.06)	0.546(0.003)	0.174(0.39)	-0.317(0.10)	-0.318(0.10)	-0.509(0.009)	0.610(0.001)	-0.031(0.92)	
<b>Species richness</b>	0.025(0.90)	-0.060(0.75)	0.266(0.20)	-0.073(0.73)	-0.132(0.50)	-0.040(0.86)	0.097(0.60)	0.390(0.05)	0.098(0.66)

Table 5.21 continued.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	35.43	25			
pH	25.92	24	9.51	1	**
Average soil depth	35.38	24	0.05	1	ns
Maximum soil depth	33.65	24	1.78	1	ns
Minimum soil depth	34.11	24	1.31	1	ns
Surface rock cover	20.10	24	15.32	1	***
Exposed bedrock cover	33.11	24	2.32	1	ns
Bare ground cover	29.41	24	6.02	1	*
Tall shrub height	34.30	24	1.13	1	ns
Tall shrub cover	34.30	24	1.13	1	ns
Low shrub height	30.56	24	4.97	1	*
Low shrub cover	35.30	24	0.13	1	ns
Herb cover	35.07	24	0.36	1	ns
Grass cover	35.42	24	0.004	1	ns
Graminoid cover	25.58	24	9.84	1	**
Fern cover	34.94	24	0.49	1	ns
Litter cover	35.31	24	0.12	1	ns
Species richness	18.29	24	17.14	1	***

Table 5.22. Results of individual models for the Asbestos Range site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ ; ns = not significant.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	35.43	24			
+ surface rock cover	20.10	23	15.33	1	***
+ pH	17.19	23	18.24	1	***

Table 5.23. Final model for the Asbestos Range site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ .



Estimate	se	Parameter
-11.07	6.27	constant
0.28	0.13	surface rock cover
1.99	1.25	pH

Table 5. 24. Parameter estimates for the final model at the Asbestos Range site.

Quadrat no.	S.OBCORD?	Surface rock cover	pH	Estimated predicted probability
1	1	2	5.2	0.48
2	1	2	5.31	0.54
3	1	0	5.27	0.36
4	0	0	4.49	0.11
5	0	0	4.58	0.12
6	1	3	5.4	0.97
7	1	3	5.33	1.00
8	1	3	5.43	1.00
9	1	3	4.85	0.79
10	1	3	5.1	0.95
11	1	4	5.33	1.00
12	1	4	5.25	1.00
13	1	5	5.52	1.00
14	1	4	5.28	1.00
15	1	3	5.33	0.97
16	1	3	4.76	0.91
17	1	2	4.47	0.18
18	0	2	4.4	0.16
19	0	3	4.6	0.70
20	0	1	4.34	0.10
21	0	2	4.07	0.09
22	0	1	4.23	0.08
23	0	1	4.37	0.11
24	0	1	4.58	0.15
25	0	1	5.57	0.57
26	0	1	5.73	0.64

Table 5.25. Estimated predicted probabilities of occurrence of *S. obcordatum* at the Asbestos Range site, according to values for surface rock cover (back transformed to their Braun Blanquet cover classes) and pH. Cover classes: 1 = <1%; 2 = 1-5%; 3 = 5-25%; 4 = 25-40%; 5 = 50-75%; 6 = >75%.

A small (four plants) population was also located at the edge of a walking track on an exposed hard pan within a gap in *Allocasuarina monilifera* - *Leptospermum scoparium* heathland. Surrounding heathland was situated on sandy soil. Soil supporting *S. obcordatum* was light grey, fine silty loam. *Spyridium obcordatum* was confined to patches of bare ground and gravel indicating that this area is also prone to erosion by strong on - shore winds.

Vegetation in quadrats where *S. obcordatum* was absent occurred in areas where locally deposited wind blown sands overlay sandy clay soils derived from Precambrian schists (Plate 5.6b). These quadrats were co - dominated by dense, wind pruned banks of *Leptospermum scoparium* and *B. marginata*, with emergent *Leptocarpus tenax* and *Lepidosperma concavum*. Other taxa typically associated with acidic sandy soils and heathland were also present including *Selaginella uliginosa*, *Melaleuca squarrosa*, *Patersonia fragilis* and *Lindsaea linearis*.

Growth rings indicated that the *S. obcordatum* population was 15 - 18 years old. Examination of *Banksia marginata* nodes also suggested a fire had occurred approximately 15 - 20 years prior to the survey. There was evidence of patch burning, with charcoal being recorded intermittently along the transect. Other disturbance included heavy browsing of *S. obcordatum* plants by native wildlife. Soils were dark grey sandy clay loam or greyish brown fine sandy loam in quadrats where *S. obcordatum* was present. Where it was absent, soils were very dark grey sandy loam or fine sandy loam.

*Spyridium obcordatum* was positively correlated with pH, surface rock and bare ground and negatively correlated with graminoid cover and low shrub height (Table 5.21). It occupied a niche defined by surface rock cover and pH (Tables 5.22 - 5.25; Fig. 5.13). Surface rock cover consisted of both quartz and schist pebbles present as lag deposits over eroded strips between shrubs, exposing less acidic clay soils. This is indicative of soil disturbance. *S. obcordatum* was absent from soils overlain by acidic sand which supported dense, species poor assemblages typical of coastal heathland.

#### *Dans Hill 1 site*

Quadrats with *S. obcordatum* were not significantly different floristically from those without *S. obcordatum* at this site, where all quadrats were on ultramafics ( $R = 0.09$ ;  $P < 0.2$ ). However, quadrats appeared well separated in the ordination space (Fig. 5.14). *Epacris virgata* was the only other restricted endemic present. Eighteen quadrats were recorded, with *S. obcordatum* present in eleven quadrats. Vegetation consisted of open forest dominated by *Allocasuarina littoralis* with emergent *Eucalyptus ovata*, *E. amygdalina* and *E. obliqua* (Plate 5.7a). The understorey was multilayered with the most frequent species being *A. littoralis*, *Banksia marginata*, *Acacia dealbata* and *Exocarpos strictus*. Shrubs, graminoids and grasses comprised the third stratum and ground layer. These were predominantly *Correa reflexa*, *Epacris virgata*, *E. impressa*, *Lomatia tinctoria*, *Lepidosperma ensiforme*, *Lomandra longifolia*, *Ehrharta distichophylla* and *Themeda triandra*. *Pteridium esculentum* was also well represented, as were a number of small herbs and shrubs such as



Plate 5.7a. Dans Hill 1. *Eucalyptus ovata* - *E. amygdalina* open forest on ultramafics. *Spyridium obcordatum* is associated with *Epacris virgata*, *Lepidosperma ensiforme*, *Lomandra longifolia*, *Ehrharta distichophylla* and *Themeda triandra*.



Plate 5.7b. Dans Hill 1. Vehicle track through open forest, where *S. obcordatum* is confined to *Lomandra longifolia* tussocks and between exposed boulders.

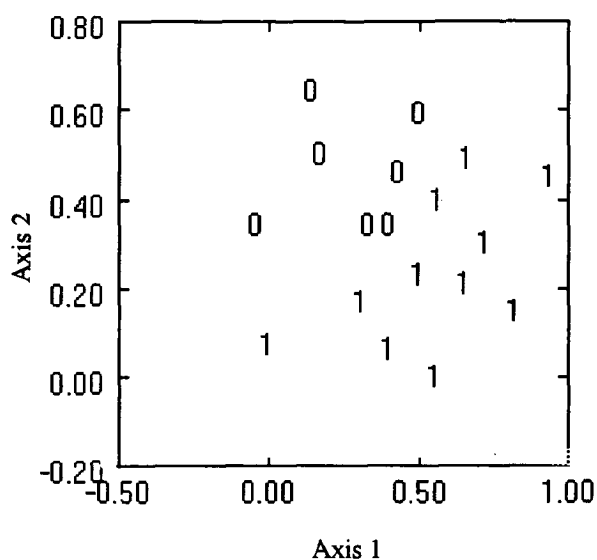


Figure 5.14. Dans Hill 1. The distribution of quadrats in the ordination space of the second NMDS, showing quadrats with (1) and without (0) *S. obcordatum*.

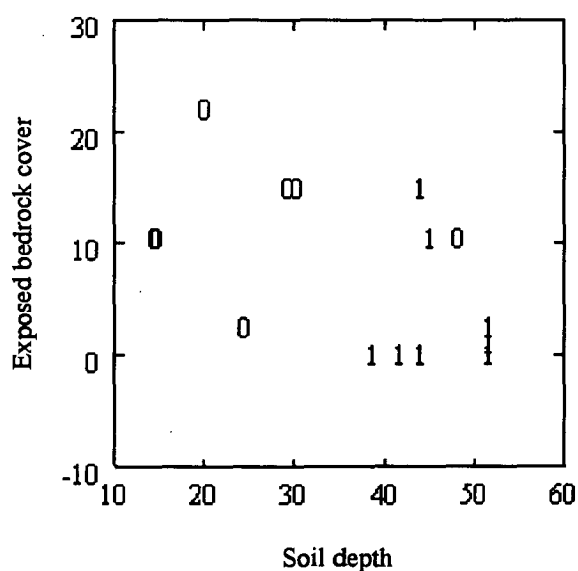


Figure 5.15. Dans Hill 1. The distribution of quadrats according to soil depth and exposed bedrock cover, showing quadrats with (1) and without (0) *S. obcordatum*.



Table 5.26. Correlations and 2-tail probabilities from 1000 random permutations between environmental variables at the Dans Hill 1 site (degrees of freedom = 17).

	pH	S.OBCORD?	pH	Average soil depth	Maximum soil depth	Minimum soil depth	Tree height	Tree cover	Tall shrub height	Tall shrub cover
Average soil depth	0.037(0.89)	0.790(0.00)	0.352(0.15)	0.174(0.50)	0.793(0.00)					
Maximum soil depth	0.555(0.03)	0.672(0.003)	0.421(0.08)	0.886(0.00)	0.535(0.04)					
Tree height	-0.297(0.23)	-0.086(0.71)	-0.148(0.57)	-0.134(0.60)	-0.139(0.63)	-0.098(0.71)				
Tree cover	-0.076(0.77)	-0.520(0.02)	-0.152(0.55)	-0.4669(0.06)	-0.232(0.38)	-0.443(0.06)	-0.144(0.56)			
Tall shrub height	-0.520(0.03)	-0.152(0.55)	-0.338(0.19)	-0.613(0.008)	-0.207(0.42)	0.543(0.02)	0.573(0.008)	-0.376(0.12)		
Tall shrub cover	-0.590(0.01)	-0.145(0.55)	0.266(0.21)	0.118(0.50)	-0.115(0.64)	-0.360(0.06)	-0.272(0.24)	-0.161(0.53)	0.766(0.00)	
Low shrub height	0.229(0.43)	0.361(0.21)	0.266(0.21)	0.095(0.81)	0.704(0.00)	-0.032(0.91)	-0.543(0.02)	0.198(0.43)	0.224(0.35)	-0.050(0.84)
Low shrub cover	0.250(0.32)	0.372(0.14)	0.413(0.08)	0.162(0.55)	0.352(0.15)	0.011(0.97)	-0.748(0.002)	-0.146(0.62)	-0.312(0.19)	
Grass cover	0.508(0.02)	0.530(0.03)	0.494(0.03)	0.128(0.61)	0.634(0.008)	0.352(0.16)	-0.381(0.11)	0.138(0.62)	0.146(0.62)	
Graminoid cover	0.111(0.68)	0.188(0.43)	0.128(0.61)	-0.011(0.94)	-0.418(0.06)	-0.092(0.83)	-0.045(0.87)	-0.173(0.52)	-0.138(0.55)	
Fern cover	-0.475(0.02)	0.119(0.65)	-0.417(0.07)	-0.160(0.44)	-0.457(0.05)	-0.415(0.09)	0.499(0.03)	-0.173(0.52)	-0.138(0.55)	
Litter cover	-0.251(0.36)	-0.599(0.01)	-0.513(0.02)	-0.305(0.29)	-0.643(0.003)	-0.415(0.09)	0.499(0.03)	-0.173(0.52)	-0.138(0.55)	
Surface rock cover	-0.241(0.43)	0.174(0.49)	-0.391(0.07)	-0.438(0.03)	-0.457(0.05)	0.353(0.17)	-0.153(0.59)	0.291(0.22)	-0.060(0.82)	
Bed rock cover	-0.670(0.004)	0.071(0.77)	-0.579(0.01)	-0.456(0.04)	-0.571(0.01)	0.370(0.15)	-0.243(0.33)	0.356(0.14)	0.252(0.330)	
Bare ground cover	0.253(0.39)	0.110(0.69)	0.154(0.62)	0.141(0.61)	-0.011(0.97)	0.173(0.81)	-0.296(0.23)	0.078(0.86)	-0.208(0.54)	
Species richness	0.047(0.85)	0.306(0.21)	-0.053(0.84)	-0.179(0.45)	0.174(0.49)	-0.029(0.91)	-0.588(0.008)	0.261(0.29)	0.089(0.75)	

	Low shrub height	Low shrub cover	Grass cover	Graminoid cover	Fern cover	Litter cover	Surface rock cover	Bed rock cover	Bare ground cover
Low shrub cover	0.562(0.00)								
Grass cover	0.359(0.06)	0.463(0.05)							
Graminoid cover	0.384(0.07)	0.435(0.07)	0.560(0.02)						
Fern cover	0.042(1.00)	-0.142(0.55)	-0.138(0.69)	-0.099(0.73)					
Litter cover	-0.339(0.12)	-0.625(0.003)	-0.661(0.002)	-0.585(0.01)	0.284(0.28)				
Surface rock cover	-0.159(0.18)	-0.283(0.22)	0.0724(0.74)	-0.109(0.69)	0.260(0.18)	-0.092(0.78)			
Bed rock cover	-0.240(0.29)	-0.367(0.13)	-0.132(0.59)	-0.128(0.61)	0.601(0.007)	0.251(0.32)	0.517(0.03)		
Bare ground	-1.00(0.31)	-0.156(0.46)	0.319(0.14)	-0.236(0.33)	0.037(0.90)	-0.179(0.53)	0.622(0.06)	0.231(0.39)	
Species richness	0.668(0.04)	0.414(0.08)	0.411(0.09)	0.532(0.03)	0.189(0.38)	-0.254(0.31)	0.022(0.92)	0.159(0.55)	-0.005(1.00)

Table 5.26 continued.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	24.06	17			
pH	24.03	16	0.03	1	ns
Average soil depth	9.78	16	14.28	1	***
Maximum soil depth	17.40	16	6.66	1	**
Minimum soil depth	13.54	16	10.52	1	**
Surface rock cover	23.03	16	1.03	1	ns
Exposed bedrock cover	14.92	16	9.14	1	**
Bare ground cover	20.73	16	3.33	1	ns
Tree height	22.41	16	1.65	1	ns
Tree cover	23.95	16	0.10	1	ns
Tall shrub height	18.58	16	5.48	1	*
Tall shrub cover	17.32	16	6.74	1	**
Low shrub height	19.17	16	4.88	1	*
Low shrub cover	22.84	16	1.22	1	ns
Herb cover	24.06	16	0.00	1	ns
Grass cover	18.83	16	5.23	1	*
Graminoid cover	23.83	16	0.23	1	ns
Fern cover	18.42	16	5.63	1	*
Litter cover	22.92	16	1.14	1	ns
Species richness	24.02	16	0.04	1	ns

Table 5.27. Results of individual models for the Dans Hill 1 site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ ; ns = not significant.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	24.06	17			
+ average soil depth	9.78	16	14.28	1	***
+ exposed bedrock cover	7.35	15	16.70	1	***

Table 5.28. Final model for the Dans Hill 1 site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ .

Estimate	se	Parameter
-7.76	5.57	constant
0.26	0.14	average soil depth
-0.22	0.16	exposed bedrock cover

Table 5.29. Parameter estimates for the final model at the Dans Hill 1 site. Se = standard error.

Quadrat no.	S.OBCORD?	Average soil depth	Exposed bedrock cover	Estimated predicted probability
1	1	37.0	0	0.850
2	1	40.0	0	0.920
3	1	42.4	0	0.960
4	1	50.0	0	0.990
5	1	50.0	0	0.990
6	1	50.0	1	0.990
7	1	50.0	1	0.990
8	1	50.0	2	0.990
9	1	50.0	1	0.990
10	1	42.4	3	0.460
11	1	43.4	3	0.740
12	0	46.4	3	0.860
13	0	26.0	2	0.160
14	0	16.2	3	0.003
15	0	31.8	3	0.050
16	0	21.6	3	0.001
17	0	16.0	3	0.003
18	0	30.8	3	0.040

Table 5.30. Estimated predicted probabilities of occurrence of *S. obcordatum* at the Dans Hill 1 site, according to values for soil depth (cm) and exposed bedrock cover (back transformed to their Braun Blanquet cover classes). Cover classes: 1 = <1%; 2 = 1-5%; 3 = 5-25%; 4 = 25-40%; 5 = 50-75%; 6 = >75%.



*Goodenia lanata*, *Viola hederacea*, *Helichrysum scorpioides*, *Bossiaea prostrata*, *Hibbertia riparia* and *Pimelea humilis*.

Inspection of the Dans Hill area revealed that *S. obcordatum* was absent from shaded, damp areas even when these had been disturbed in the past, although this may also be a consequence of inefficient seed dispersal or a spatially restricted seed bank, rather than intolerance to these conditions.

The site was highly disturbed from past asbestos mining activities and more recently, by vehicles, wood cutting and garbage dumping (Plate 5.7b). Fires have been lit frequently in the area and soil charcoal was recorded throughout the transect. Ring counts of *S. obcordatum* plants suggested the population was 10 -13 years old. Soils were reddish brown or dark brown gritty clay loams and fine sandy clays.

*S. obcordatum* was significantly positively correlated with average soil depth, maximum soil depth, minimum soil depth and grass cover. It was significantly negatively correlated with tall shrub height and cover, fern cover (*Pteridium esculentum*) and cover of exposed bedrock (Table 5.26). *Spyridium obcordatum* was present in vegetation on deeper, relatively less rocky soils within open vegetation.

Average soil depth and low cover of exposed bedrock also defined the qualitative realised niche for *S. obcordatum* (Tables 5.27 - 5.30; Fig. 5.15) at this site.

#### *Dans Hill 2 site*

Twenty quadrats were sampled at this site, with 14 containing *S. obcordatum*. The transect was placed over the boundary of Tertiary gravels and ultramafic rocks (Plate 5.8). Vegetation associated with the former was *Eucalyptus obliqua* forest with an open understorey of *Allocasuarina littoralis*. The ground layer was predominantly *Pteridium esculentum* and *Gahnia grandis*, a result of the frequent fires experienced by this community in the recent past. There were no rare or restricted taxa present, other than *Epacris virgata*, which was also absent from adjacent Tertiary gravels. Soils were light brownish grey gravelly, sandy clay loam. Analysis of dissimilarities distinguished quadrats with *S. obcordatum* as significantly different floristically from those without *S. obcordatum* ( $R = 0.78$ ,  $P < 0.0001$ ; Fig. 5.16).

Ultramafic substrates supported open forest dominated by *Eucalyptus ovata* and *E. amygdalina*, with an understorey consisting of *Allocasuarina littoralis*, *Banksia marginata* and *Pimelea nivea*. *Eucalyptus obliqua* was an occasional canopy co-dominant. A third stratum consisted of *Gahnia grandis*, *Lepidosperma elatius* var. *ensifforme*, *Epacris virgata* and *Hibbertia riparia*. *Spyridium obcordatum*, *Gonocarpus tetragynus*, *Bossiaea prostrata* and *Viola hederacea* comprised most of the ground layer vegetation. Soils in this community were gritty dark reddish brown loam.

Ring counts of *S. obcordatum*, *Pomaderris elliptica*, *Pimelea nivea* and *Allocasuarina littoralis* indicated that eight to ten years had elapsed since the last fire.



Plate 5.8. Dans Hill 2. The boundary of *Eucalyptus obliqua* forest on Tertiary gravels where *S. obcordatum* is absent (foreground) and *E. ovata* - *E. amygdalina* open forest on ultramafics (background).

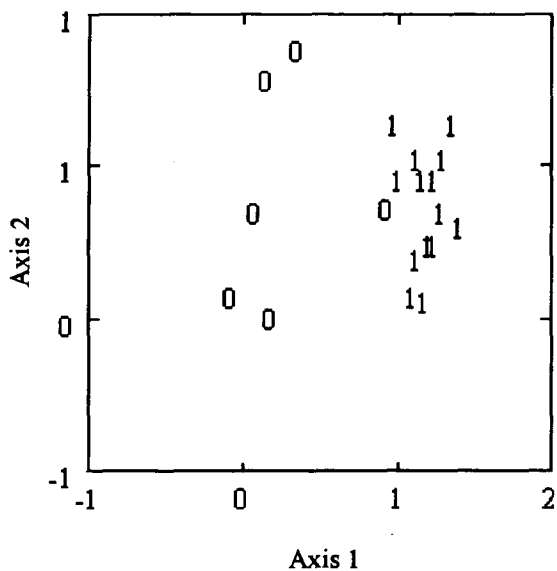


Figure 5.16. Dans Hill 2. The distribution of quadrats in the ordination space of the second NMDS, showing quadrats with (1) and without (0) *S. obcordatum*.

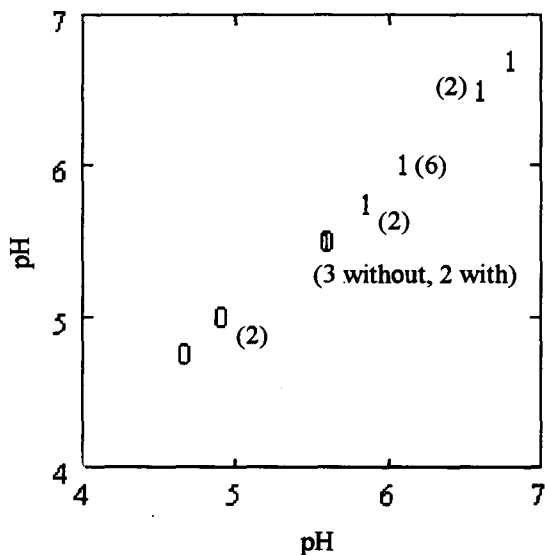


Figure 5.17. Dans Hill 2. The distribution of quadrats according to pH, showing quadrats with (1) and without (0) *S. obcordatum*. Numbers in brackets refer to overlapping points.

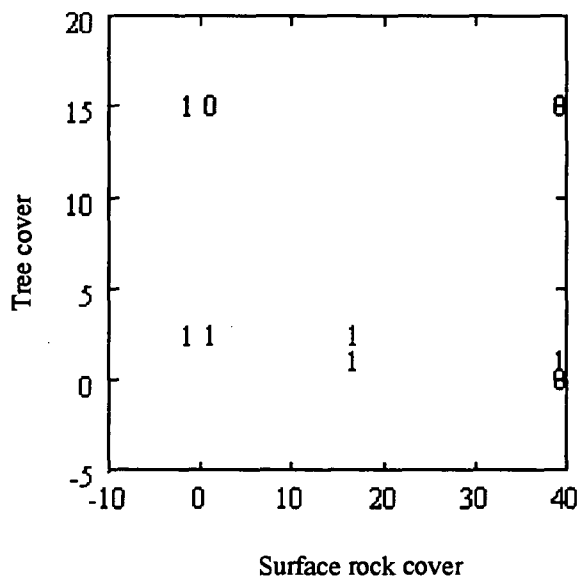


Figure 5.18. Dans Hill 2. The distribution of quadrats according to surface rock cover and tree cover, showing quadrats with (1) and without (0) *S. obcordatum*.

	<b>S.OBCORD?</b>	<b>pH</b>	<b>Average soil depth</b>	<b>Maximum soil depth</b>	<b>Minimum soil depth</b>	<b>Tree height</b>	<b>Tree cover</b>	<b>Tall shrub height</b>	<b>Tall shrub cover</b>
<b>pH</b>	0.730(0.00)								
<b>Average soil depth</b>	0.323(0.14)	0.089(0.68)							
<b>Maximum soil depth</b>	0.259(0.27)	0.023(0.94)	0.929(0.00)						
<b>Minimum soil depth</b>	0.479(0.03)	0.254(0.30)	0.888(0.00)	0.695(0.001)					
<b>Tree height</b>	-0.531(0.01)	-0.448(0.04)	-0.162(0.48)	-0.080(0.74)	-0.323(0.16)				
<b>Tree cover</b>	-0.530(0.01)	-0.473(0.03)	-0.437(0.06)	-0.372(0.10)	-0.516(0.03)	0.835(0.00)			
<b>Tall shrub height</b>	0.206(0.58)	0.076(0.81)	-0.128(0.60)	-0.174(0.49)	-0.063(0.82)	-0.037(0.89)	0.128(0.68)		
<b>Tall shrub cover</b>	0.150(0.78)	0.138(0.55)	0.172(0.46)	0.005(1.00)	0.343(0.16)	-0.337(0.30)	-0.252(0.71)	0.409(0.07)	--
<b>Low shrub height</b>	0.768(0.00)	0.703(0.00)	0.210(0.35)	0.222(0.34)	0.343(0.12)	-0.303(0.17)	-0.318(0.17)	0.236(0.35)	0.268(0.47)
<b>Low shrub cover</b>	0.482(0.01)	0.450(0.05)	0.148(0.53)	0.139(0.57)	0.250(0.30)	0.224(0.38)	0.075(0.78)	0.085(0.73)	-0.150(0.67)
<b>Herb cover</b>	-0.134(0.45)	-0.394(0.09)	0.420(0.07)	0.431(0.06)	0.225(0.33)	0.041(0.89)	-0.083(0.76)	-0.257(0.27)	-0.187(0.88)
<b>Grass cover</b>	0.155(0.51)	-0.025(0.92)	0.233(0.36)	0.127(0.60)	0.215(0.37)	-0.495(0.02)	-0.556(0.02)	-0.216(0.27)	-0.148(0.69)
<b>Graminoid cover</b>	0.610(0.007)	0.387(0.08)	-0.106(0.65)	0.025(0.92)	-0.152(0.55)	0.017(0.93)	0.075(0.77)	0.462(0.04)	-0.096(0.90)
<b>Fern cover</b>	0.157(0.66)	-0.020(0.92)	0.507(0.02)	0.408(0.06)	0.428(0.05)	-0.157(0.57)	-0.287(0.29)	-0.130(0.48)	-0.130(0.26)
<b>Litter cover</b>	-0.782(0.00)	-0.717(0.001)	-0.251(0.26)	-0.181(0.45)	-0.397(0.09)	0.641(0.005)	0.739(0.001)	-0.059(0.82)	-0.159(0.74)
<b>Surface rock cover</b>	-0.632(0.01)	-0.233(0.33)	-0.072(0.79)	-0.147(0.51)	-0.035(0.86)	0.024(0.90)	0.089(0.734)	-0.031(0.80)	0.311(0.29)
<b>Bed rock cover</b>	0.185(0.29)	0.193(0.28)	-0.016(0.96)	0.110(0.67)	-0.028(0.96)	-0.415(0.003)	-0.310(0.07)	-0.009(0.97)	0.1102(0.09)
<b>Bare ground cover</b>	0.200(0.48)	0.479(0.04)	0.133(0.59)	0.048(0.85)	0.288(0.22)	-0.598(0.001)	-0.498(0.001)	0.090(0.74)	0.438(0.07)
<b>Species richness</b>	0.670(0.001)	0.561(0.008)	0.097(0.70)	0.116(0.64)	0.138(0.57)	-0.048(0.86)	-0.101(0.69)	0.138(0.64)	-0.373(0.06)

Table 5.31. Correlations and 2-tail probabilities from 1000 random permutations between environmental variables at the Dans Hill 2 site (degrees of freedom =19).

	Low shrub height	Low shrub cover	Herb cover	Grass cover	Graminoid cover	Fern cover	Litter cover	Surface rock cover	Bed rock cover
<b>Low shrub cover</b>	0.646(0.00)								
<b>Herb cover</b>	-0.181(0.40)	-0.268(0.40)							
<b>Grass cover</b>	-0.358(0.12)	-0.424(0.04)	0.440(0.05)						
<b>Graminoid cover</b>	0.636(0.003)	0.572(0.01)	-0.222(0.34)	-0.306(0.18)					
<b>Fern cover</b>	-0.210(0.42)	-0.232(0.32)	0.481(0.009)	0.629(0.008)	-0.153(0.53)				
<b>Litter cover</b>	-0.601(0.006)	-0.212(0.37)	0.086(0.67)	-0.312(0.18)	-0.274(0.26)	-0.097(0.77)			
<b>Surface rock cover</b>	-0.363(0.11)	-0.398(0.06)	0.065(0.72)	-0.149(0.52)	-0.643(0.004)	-0.229(0.37)	0.387(0.097)		
<b>Bed rock cover</b>	0.329(0.09)	-0.163(0.57)	-0.230(0.54)	-0.182(0.44)	0.188(0.49)	-0.160(0.12)	-0.291(0.256)	-0.0630(1.00)	
<b>Bare ground cover</b>	0.338(0.15)	-0.023(0.92)	-0.264(0.36)	-0.110(0.74)	-0.207(0.40)	-0.237(0.17)	-0.347(0.108)	0.4503(0.02)	0.221(0.12)
<b>Species richness</b>	0.629(0.003)	0.561(0.006)	-0.037(0.88)	-0.019(0.95)	0.626(0.001)	0.071(0.77)	-0.479(0.040)	-0.6477(0.001)	0.163(0.61)
<b>Bare ground cover</b>									
<b>Species richness</b>	-0.108(0.67)								

Table 5.31 continued.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	25.44	19			
pH	NC	18		1	
Average soil depth	21.97	18	2.47	1	ns
Maximum soil depth	22.97	18	1.47	1	ns
Minimum soil depth	18.92	18	5.52	1	*
Surface rock cover	16.27	18	8.17	1	**
Exposed bedrock cover	NC	18	-	1	-
Bare ground cover	23.36	18	1.07	1	ns
Tree height	15.44	18	9.00	1	**
Tree cover	18.36	18	6.07	1	*
Tall shrub height	22.92	18	1.52	1	ns
Tall shrub cover	23.70	18	0.74	1	ns
Low shrub height	8.480	18	15.95	1	***
Low shrub cover	NC	18	-	1	-
Herb cover	24.08	18	0.34	1	ns
Grass cover	23.92	18	0.52	1	ns
Graminoid cover	13.36	18	11.08	1	***
Fern cover	23.85	18	0.59	1	ns
Litter cover	10.59	18	13.85	1	***
Species richness	13.28	18	11.15	1	***

Table 5.32. Results of individual models for the Dans Hill 2 site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ ; ns = not significant.; NC = no convergence.

Model	Deviance	df	$\Delta$ Deviance	df	Significance
Constant	24.44	19			
+ surface rock cover	16.27	18	8.17	1	**
+ tree cover	8.60	17	15.84	1	***

Table 5.33 Final model for the Dans Hill 2 site. Deviance = scaled deviance; df = degrees of freedom; significance: \* =  $0.05 > p > 0.01$ ; \*\* =  $0.01 > p > 0.001$ ; \*\*\* =  $p < 0.001$ .

Estimate	se	Parameter
9.20	8.58	constant
-0.55	0.56	surface rock cover
-0.21	0.22	tree cover

Table 5.34. Parameter estimates for the final model at the Dans Hill 2 site. Se = standard error.

Quadrat no.	S.OBCORD?	Surface rock cover	Tree cover	Estimated predicted probability
1	0	3	4	0.001
2	0	3	4	0.001
3	0	0	4	0.810
4	0	3	4	0.001
5	0	3	4	0.001
6	0	3	3	0.610
7	1	3	0	1.000
8	1	3	0	1.000
9	1	3	3	0.999
10	1	3	0	1.000
11	1	1	4	0.717
12	1	1	4	0.717
13	1	3	3	0.991
14	1	1	3	0.996
15	1	1	3	0.996
16	1	1	4	0.717
17	1	1	3	0.996
18	1	3	0	0.723
19	1	3	0	0.723
20	1	3	0	1.000

Table 5.35. Estimated predicted probabilities of occurrence of *S. obcordatum* at the Dans Hill 2 site, according to values for surface rock cover and tree cover (back transformed to their Braun Blanquet cover classes). Cover classes: 1 = <1%; 2 = 1-5%; 3 = 5-25%; 4 = 25-40%; 5 = 50-75%; 6 = >75%.

The site has experienced frequent fires in the past (G. Stewart, Forestry Tasmania, pers. comm.). Quadrats situated on ultramafics had also been mined.

*S. obcordatum* was significantly positively correlated with pH, minimum soil depth, low shrub height and cover, graminoid cover and species richness. It was significantly negatively correlated with tree height and cover, litter cover and surface rock cover (Table 5.31). *Spyridium obcordatum* was strongly associated with ultramafics. It was absent from *Eucalyptus obliqua* forest on acidic, gravelly soils.

No model was attained for this site owing to problems with convergence related to the size of the data set. Quadrats with and without *S. obcordatum* were almost perfectly separated on the basis of pH (Fig. 5.17). Combinations of nearly all other significant individual models failed to converge. However, the combined variables surface rock and tree cover adequately predicted that *S. obcordatum* was likely to be absent from forest on gravelly soils (Tables 5.32 - 5.35; Fig. 5.18).

#### *Greens Beach site*

Inspection of this site revealed that prior to clearing for housing development, the vegetation consisted of *Allocasuarina verticillata* coastal woodland, with *Eucalyptus amygdalina* present as an occasional small tree (Plate 5.9a & b). The understorey was made up of low shrubs and graminoids such as *Calytrix tetragona*, *Hibbertia sericea*, *Correa reflexa*, *Lomandra longifolia* and *Diplarrena moraea*. The ground was open but with a diverse array of small sedges and herbs. The most common were *Drosera peltata*, *Wahlenbergia gracilentia*, *Angianthus preissianus*, *Hydrocotyle callicarpa*, *Poranthera microphylla*, *Crassula sieberana*, *Stylidium perpusillum*, *Centrolepis aristata* and *C. strigosa*. Grasses were represented by a sparse cover of *Danthonia setacea* and *Vulpia bromoides*. *Spyridium obcordatum* was most abundant on rocky slopes with a northerly aspect but was also found in open areas having a southwesterly aspect. The site is exposed to onshore winds. The vegetation at this site was very similar to the Hawley site. In addition to *S. obcordatum*, there were a number of rare or threatened species present at the site. None of these were Tasmanian endemics. They included *A. preissianus*, *H. callicarpa*, *Stylidium perpusillum*, *S. inundatum*, *Mitrasacme paradoxa*, *Ajuga australis*, *Lepidosperma viscidum* and *Hypoxis vaginata* var. *brevistigma*.

## Discussion

### *Spyridium microphyllum*

The three sites where *S. microphyllum* occurs are sufficiently floristically and environmentally different from each other to imply a lack of habitat specificity. This argues against a requirement for a unique habitat. At the Douglas - Apsley, the floristic composition of quadrats with and without *S. microphyllum* was broadly similar. However, vegetation containing *Spyridium microphyllum* was floristically distinct from adjacent plant communities at two sites (Thumbs and Swan River),





Plate 5.9a. Greens Beach. Disturbed *Allocasuarina verticillata* coastal woodland on dolerite, recently cleared for housing. *Spyridium obcordatum* grows in this artificially created low open - shrubland with *Calytrix tetragona* and a number of graminoids and small herbs.



Plate 5.9b. Greens Beach. Low open - shrubland, resulting from disturbance, with undisturbed coastal woodland in the background. *Spyridium obcordatum* occurs in both communities.

suggesting that populations are phytosociologically restricted and thus environmentally restricted. All populations are reproductively mature and plants are healthy. Some seedlings were observed in areas where spot fires had occurred but in general showed no sign of invasion into undisturbed adjacent vegetation.

At all three sites, *S. microphyllum* is a component of treeless vegetation. Treeless environments are not rare within the present climatic range of *S. microphyllum*. There are extensive stretches of river valleys where *S. microphyllum* is absent that are closely similar in their physical features to the Swan and St Pauls Rivers (Kirkpatrick *et al.* 1980; Askey - Doran 1993). Some of these, including the Prosser and Apsley Rivers, also support a number of rare endemic taxa.

Exposed rocky dolerite ridges and slopes and rock plates with surrounding soils too shallow to support trees are also extremely common in eastern Tasmania but extensive searches within the Douglas - Apsley and Thumbs region failed to reveal additional populations of *S. microphyllum*. Its disjunct distribution at the Thumbs, the spatially restricted nature of the population and the apparent availability of suitable habitat there, strongly suggests that it has survived by chance at this site. The area is known for its high numbers of species disjunctions and is recognised as having biogeographic significance (Coates 1993). A diverse terrain supports a wide range of species and vegetation assemblages, including relict patches of rainforest. However, disjunct taxa other than *S. microphyllum* which are also associated with dry sclerophyll vegetation, occur apparently at random on dry, rocky sites, suggesting that their local distribution is influenced by stochastic processes relating to random establishment and extinction events, as well as an ability to withstand drought.

*Spyridium microphyllum* populations can also develop over relatively large areas. At the Douglas - Apsley, a mosaic of low shrubland and tall shrubland covers approximately 0.3 square kilometres. At the Swan River, *S. microphyllum* populations occur discontinuously for approximately 20 kilometres. Populations are regenerating and can extend their ranges, given appropriate disturbance regimes and environments suitable for the development of low open - shrubland. Thus, the results are more readily interpretable in terms of interspecific competition from adjacent forest taxa, or by a combination of factors relating to local environmental conditions, including disturbance.

An apparent ability to tolerate droughty soils and an apparent inability to survive in shaded environments or compete for underground resources is a common attribute of all three *S. microphyllum* populations.

At the Douglas - Apsley, there were no direct environmental correlates which explained its preference for low shrubland. Tall shrubland, which contained a few depauperate *S. microphyllum* plants, was confined to areas having deeper soils. This implies *S. microphyllum* is excluded from the most favourable sites from competition.

At the Thumbs, *S. microphyllum* is clearly associated with shallow soils and with areas free of surface rock. However, it was absent from the most shallow soils and rock plate surface. It is likely that it is confined to shrubland associated with the perimeter of rock plates by competition from forest vegetation confined to deeper

soils. Deep rooted, faster growing tall shrubs on boulder slopes (surface rock) overlying damp, deeper soils may also compete with *S. microphyllum*. Its restriction between the perimeter of rock plates and forest, or between rock plates and tall shrubland on boulder slopes, suggests that it is confined to a spatially narrow niche by taxa competing for light and root space. Post - fire regeneration from resprouting shrubs, graminoids and grasses in adjacent communities may also exceed the ability of *S. microphyllum* seedlings to compete for resources. The site demonstrates probable niche partitioning where competing vegetation associations grow in close proximity but where a range of habitats are potentially available.

At the Swan River, *S. microphyllum* generally occupies the most marginal sites between riparian scrub and forest, although its habitat is less clearly defined than at the Thumbs. *Spyridium microphyllum* populations along the Swan River are excluded from moist sites by dense riparian shrubland dominated by *Melaleuca pustulata* and *Acacia mucronata*, and are confined to infrequent open gaps on rocky shallow soils. The results also showed that it fails to occupy sites which are potentially available on the basis of soil depth and rockiness alone and that tree cover was an important determinant of *S. microphyllum* habitat. Above the river, it is generally excluded from deeper soils and is uncommon at the margins of forest vegetation.

The relatively poor solutions arrived at by the niche prediction method at two sites indicates that the distribution of *S. microphyllum* may be related to a broader range of ecological factors. At the Douglas - Apsley site, shrub dominated vegetation is maintained by fire, but a consideration of the interaction between fire history and soil depth may more fully explain its existence. *Spyridium microphyllum* is not confined to shallow soils at this site, suggesting that it has a potentially wider range, at least until co - existing species such as *Leptospermum grandiflorum* and *Hakea megadenia* attain greater heights and impose a lethal amount of shade. Provided that there is a suitable frequency of disturbance, shrubby patches will probably persist.

Low open - shrubland may also be more susceptible to fire than closed - scrub. Clayton -Greene & Wimbush (1988) reported that rare *Acacia* closed - scrub communities burn only in response to high intensity fires and that the failure of low intensity fires to burn this type of vegetation is probably a result of its dense closed canopy, open understorey and litter having low flammability. Higher moisture levels within closed - scrub may also offer protection from fires. At the Douglas - Apsley, hot fires have burnt up north facing slopes and through forest on deeper soils than those at the sample site. A ridge crest, just above the *S. microphyllum* community, provides protection from low intensity fires. Whereas the impact of high intensity fires may also decrease as a result of topography and soil moisture, low open - shrubland will still be burnt, but tall closed - scrub is less likely to do so. However, although tall scrub and low shrubland are fire protected to some extent, both are likely to experience patch burns from time to time.

Disturbance is relatively frequent along the Swan River. Vegetation experiences low level flooding at the river's edge, and infrequent major flooding up to seven metres above the average height of the river. Further disturbance in the form of slope erosion takes place on a more continuous but less catastrophic scale. Natural fires



occur infrequently, although burning by landowners attempting to control the spread of gorse (*Ulex europaeus*) affects indigenous vegetation. Fires and floods may be crucial in maintaining open shrubby vegetation.

Similarly at the Thumbs, disturbance may be crucial in maintaining low shrubland. Charcoal was recorded in most quadrats where *S. microphyllum* was present. However, low litter cover and a high incidence of bare ground mean that the overall likelihood of fire in open shrubland is lower than in forest vegetation. Populations have been periodically burnt, but probably experience some degree of protection from low intensity fires. Consequently, populations experience a balance between protection from frequent fires but also rely on fire for regeneration.

### *Conclusions*

The survival of populations of *S. microphyllum* in eastern and southeastern Tasmania can be attributed to site specific histories rather than confinement to a rare habitat. These almost certainly involve interactions between local environmental factors and disturbance. At two sites, competitive forest vegetation is excluded from *S. microphyllum* dominated shrubland communities by shallow soils. At a third site, *S. microphyllum* was excluded from deeper soils. All three sites experience various levels of disturbance but these appear to differ from that experienced by adjacent vegetation.

### *Spyridium obcordatum*

The four sites supporting *S. obcordatum* were floristically, physiognomically and environmentally diverse. At three sites *Spyridium obcordatum* was associated with vegetation that was compositionally distinct from adjacent communities.

Extensive searches of the West Tamar region failed to locate any further *S. obcordatum* populations, although similar habitat containing the associated *Lepidosperma viscidum* occurred in the area. At Hawley, except for the presence of *S. obcordatum*, the environment is typical of open grassy vegetation in Tasmania on dolerite. This habitat is well known for its high numbers of rare or threatened species in other parts of the State (Kirkpatrick *et al.* 1988), but could not be classified as a rare habitat.

At Asbestos Range, it was absent from other areas of identical coastal heath containing *Lasiopetalum baueri* and/or *Pomaderris oraria*. A late nineteenth century herbarium record for West Head was not confirmed although suitable habitat existed at this site (open coastal woodland/shrubland on dolerite, similar to that at Greens Beach). Furthermore, *S. obcordatum* has no geological preference. Dans Hill was the only site on ultramafics in the area. However, *S. obcordatum* is not an edaphic endemic and the vegetation of the site is extremely common in eastern Tasmania. Consequently, it is unlikely that *S. obcordatum* is restricted to a unique habitat.

Competitive exclusion, as well as local environmental specificity, might be restricting further expansion of populations. At Hawley, *S. obcordatum* occupies a relatively narrow niche. This small population is restricted to areas close to exposed bedrock with shallow soils relatively free of litter. Confinement to a narrow niche might result from competitive exclusion by more widespread or aggressive taxa that are common in grassy vegetation in Tasmania, and which occupy deeper, moister soils. Edaphic factors such as relatively clay rich, non - acidic soils, also influence the distribution of the population at Asbestos Range. At this site *S. obcordatum* is confined to microsites in coastal heathland, free of competition from dense vegetation on acidic soils.

Its association with low bedrock cover and deeper soils at Dans Hill is at odds with its niche at Hawley and at Asbestos Range. However, it was also observed growing on rocky sites, particularly in abandoned quarries or in gullies. *Spyridium obcordatum* also occupies a narrow niche at this site, with plants confined to areas where soil depth is substantial but still shallow enough to exclude mature trees. There was no significant floristic difference between quadrats containing *S. obcordatum* and those where it was absent in the transect located entirely on ultramafic soils. However, it was almost always associated with *Epacris virgata*, suggesting that the regenerative and growth requirements of the two narrow endemics may be similar. *Epacris virgata* is widespread at Dans Hill and is distributed on both ultramafics and laterites.

The distribution of *Spyridium obcordatum* showed a strong environmental preference for ultramafic soils over gravels. Ong (1992) demonstrated that the ultramafic soils at Dans Hill are more fertile and likely to be more favourable for plant growth than gravel, laterite or limestone soils also found within the immediate area. This pattern is unlike ultramafic soils elsewhere (Ong 1992; Brooks 1987). *Spyridium obcordatum* may be restricted by soil fertility at this site. Another possibility is preadaptation for serpentine tolerance (Kruckeberg, 1987), specific to the Dans Hill population.

In Australia and elsewhere, ultramafic soils are generally considered to have high magnesium, nickel, iron, cobalt and chromium levels (Wild & Bradshaw 1977; Kruckeberg 1986, 1987; Brooks 1987; Batianoff *et al.* 1990; Gibson *et al.* 1992). At Dans Hill, ultramafic soils are higher in phosphorus and lower in nitrogen and magnesium levels than recorded in the literature for their counterparts elsewhere (Ong 1992). However, it seems more likely that the extensive population of *S. obcordatum* on ultramafic soils is due to a requirement for an open habitat. In this respect it is probably similar to *S. gunnii* populations on ultramafics in western Tasmania.

The abundance of *S. obcordatum* varied between sites, but it was most prolific at Dans Hill. Disturbance history includes mining, with the *S. obcordatum* population most abundant in areas that have been heavily mechanically disturbed. The recent fire history of the site may also have been advantageous, by allowing ample light availability and reducing competition from taller shrub species. Low cover and low height of tall shrubs, in this case *Allocasuarina littoralis* and young eucalypts, support this notion. Fire further advantages *S. obcordatum*, by stimulating

regeneration from seed in response to heat and probably by stimulating resprouting. Furthermore, the deep, moist ultramafic soils are favourable for seedling establishment. However, prior to the initiation of this regime, it may have been restricted to a relatively narrow area, in a similar way to the Asbestos and Hawley populations on shallow, rocky soils in undisturbed areas.

The edaphic characteristics of the quartzite/serpentinite quadrats recorded in the Dans Hill 2 transect are analogous to the Asbestos Range transect. At both sites, *S. obcordatum* is confined to less acidic and more clay rich soils. Populations are maintained by disturbance, albeit at different scales. Furthermore, ultramafics which support open vegetation formations often allow high levels of light penetration (Kruckeberg 1987).

At Asbestos Range *Spyridium obcordatum* is confined to a narrow ecological niche whose edaphic relationships are also maintained by disturbance. At this site, the results indicated that this is linked to more or less ongoing disturbance from prevailing northwesterly salt laden winds, which expose clay soils where vegetation has been removed by low intensity patch fires. Taller vegetation consisting of *Eucalyptus amygdalina* and *Allocasuarina verticillata* is confined to gullies, suggesting there has been a shift away from forest towards heath. The history of these heaths is not known although they are likely to be associated with fire, sea level rise and salt spray, as has been demonstrated in other heaths in northern Tasmania from around 6,500 years BP (Thomas 1992). Thus, *S. obcordatum* may be restricted to micro sites related to interactions between topographic and edaphic characteristics, and maintained by disturbance over long periods of time.

There was no evidence of any recent fires or other forms of disturbance at the Hawley site, although fires would be expected to occur periodically in both grassy and heathy woodland. The Greens Beach site had recently been disturbed by bulldozer scraping and *S. obcordatum* seedlings, as well as resprouting adults which had been mechanically damaged were observed. Both sites were consisted of *Allocasuarina verticillata* coastal woodland, where *S. obcordatum* was associated with outcropping dolerite bedrock. The Hawley population is small, and although individual plants were robust and reproductively active, regeneration was not apparent. It would seem that fire may be vital to population maintenance at this site, by reducing competition from grasses and as a stimulus for seed germination.

### Conclusions

Combinations of locally specific environmental conditions, rather than a unique habitat appears to offer a feasible explanation for rarity in *S. obcordatum*. At all three sites, populations appears to be restricted by competition. The data show that it is favoured at sites which are periodically, or even continuously disturbed.

Regeneration, establishment and maintenance of populations rely on a high level of light availability and a non acidic, relatively clay rich soil environment. The ability to thrive on both shallow and deep soils argues against confinement to a rare habitat, as does its association with grassy vegetation on dolerite soils, one of the most common environments in eastern Tasmania. A rare habitat type such as ultramafic rock

appears to favour *S. obcordatum*. However, it was absent from lateritic ironstone soils, which support denser vegetation but are compositionally similar to plant assemblages on adjacent ultramafics (Ong 1992; Gibson *et al.* 1992).

## CHAPTER 6

### PHYTOCHOROLOGY OF PLANT COMMUNITIES DOMINATED BY *SPYRIDUM MICROPHYLLUM* AND *SPYRIDUM OBCORDATUM*

#### Introduction

This chapter examines whether the phytochorology of taxa comprising vegetation containing *S. microphyllum* and *S. obcordatum* is different from that of taxa in adjacent areas where they are absent.

The association between species' distributions and ecology is important, since these relationships are used as a basis for biogeographic interpretations, from both past and present perspectives (Cowling 1983; Lausi & Nimis 1991). A function of phytochorological analyses is to relate the patterns of distribution to the ecological requirements of taxa and to determine whether differences in distribution reflect ecological differences (Nimis & Bolognini 1990). Phytochorological analyses can also be used to test hypotheses concerning the biogeographic status of vegetation, by comparing the distributions of co-occurring taxa at a given site, and by identifying the relationships between widespread, narrow and intermediate taxa.

The quantitative analysis of intrageneric phytogeographic patterns has been applied to taxa in Australia and overseas (for example Clayton & Hepper 1973; Hopper & Maslin 1978; Gill *et al.* 1985; Hnatiuk & Maslin 1988; Friesen *et al.* 1993).

However, the quantitative analysis of the biogeographic composition of vegetation associations has been largely overlooked in Australia. The studies that do exist are mainly broad regional analyses (for example Hooker 1860; Burbidge 1960; Nelson 1981; Kirkpatrick & Brown 1984b). An exception is work by Bridgewater (1976) who analysed distributional data for six angiosperm families in Victoria, using quantitative methods to generate hypotheses regarding the origins of floras. He identified the Rhamnaceae as a predominantly western group, most closely associated with the Little Desert, Grampians and Melbourne regions as defined by grids of 1° latitude by 1.5° longitude. However, ongoing research into the taxonomy and systematics of *Pomaderris* may reveal an eastern element within the family (N. Walsh & F. Coates, National Herbarium of Victoria, in prep.).

Phytochorological aspects of vegetation have also received some attention in the northern hemisphere, Brazil, West Africa and in South Africa (Werger 1978; Cowling 1983; Nelson *et al.* 1990; Nimis & Bolognini 1990; Palmer 1990; Lausi & Nimis 1991; Bolognini & Nimis 1993; Nimis & Bolognini 1993). Elsewhere, when direct evidence is unavailable, ecologists and biogeographers have mainly relied on historical studies to interpret contemporary patterns of plant distributions and have drawn conclusions about the present day distribution of taxa from patterns evident in the pollen or macrofossil record (for example Martin 1989; Kershaw *et al.* 1991; Macphail *et al.* 1993). This may not always be appropriate because palaeoenvironments do not necessarily mirror extant conditions and plant communities of the past are certain to have been vastly different to those of today, regardless of dominant genera or their contemporary distribution (Thomas 1992;



Macphail *et al.* 1993). Furthermore, diversity both within and between assemblages of taxa in response to environmental diversity and complexity can be difficult to interpret from the fossil record, especially where rare plants or relictual plant communities exist.

## Methods

### *Site selection and vegetation survey*

Floristic data were obtained during the phytosociological survey. Methods of data acquisition are outlined in the preceding chapter.

To briefly recapitulate, the sites were of varying vegetation types.

1. *S. microphyllum* (Douglas - Apsley): low shrubland and tall closed - scrub dominated almost entirely by Tasmanian endemics on dolerite.
2. *S. microphyllum* (Thumbs): populations were confined to low shrubland at the perimeter of rock plates within dry sclerophyll forest on dolerite.
3. *S. microphyllum* (Swan River): riparian low open shrubland and scrub adjacent to grassy dry sclerophyll forest on dolerite.
4. *S. obcordatum* (Hawley): grassy open woodland on dolerite adjacent to heathy woodland on infertile sandy soils.
5. *S. obcordatum* (Asbestos Range): coastal heath on Precambrian schists overlain by wind blown sands.
6. *S. obcordatum* (Dans Hill 1): dry sclerophyll forest on ultramafics.
7. *S. obcordatum* (Dans Hill 2): dry sclerophyll forest on ultramafics adjacent to forest on Tertiary gravels.

### *Distributional data acquisition*

Australia wide distributional data for all taxa recorded during the phytosociological survey were collected from a number of sources. Tasmanian records were extracted from Brown *et al.* (1983); Kirkpatrick & Backhouse (1985); Kirkpatrick (1986a); Kirkpatrick & Wells (1987); Kirkpatrick *et al.* (1991); Morris & Curtis (1994) and personal observations. Data for Victorian occurrences were extracted from the Department of Conservation and Natural Resources data base. Distributions of taxa in New South Wales were taken from Harden (1990, 1991, 1992, 1993). South Australian distributions were extracted from Jessop & Toelken (1986a - d). Hnatiuk (1990) was consulted for the distributions of taxa in Western Australia, the Northern Territory and Queensland. Exotic species and

taxa identified to genus only were excluded from the analysis. Information for some taxa was confused, with disagreement regarding their distributions, or ongoing taxonomic revision confounding the available published information. Examples include *Epacris virgata*, *Euchiton gymnocephalus* and *Callitris oblonga*. Final decisions were based on published distribution and discussions with reliable sources. Taxonomic nomenclature follows Kirkpatrick *et al.* (1991) for Tasmania; Ross (1993) for Victoria; Harden (1990, 1991, 1992, 1993) for New South Wales, and Hnatiuk (1990) for South Australia, Western Australia, Queensland and the Northern Territory.

Biogeographic provinces recognised by State and Territory herbaria were used. These are published by Orchard (1988) and modified by the Tasmanian Forestry Commission for Tasmanian regions (Williams 1989); Conn (1993) for Victorian regions and Hnatiuk (1990) for New South Wales, South Australia, Queensland, Western Australia and the Northern Territory. The absence of any Australia wide biogeographic classificatory system that takes into account natural regions was a major obstacle and the results represent a compromise between biogeographic veracity and the data available. This is also recognised as problematic by Ladiges *et al.* (1983), Briggs & Leigh (1988), Hnatiuk (1990) Beard (1981, 1985), Barlow (1984, 1985) and Conn (1993). Burbidge (1960) designated four principal floristic zones for Australia. However, these were too broad for the present study. Barlow (1985) also produced a botanical regions map for Australia, consisting of 33 "natural regions" subdivided into 1 degree grid cells. This document has not gained wide acceptance by biogeographers and was not appropriate for the present study (see below).

Previous phytochorological studies have used distributional data (latitude and longitude), extracted from herbarium records and/or floristic surveys, organized as presence or absence of a species in a predetermined set of grid squares (Bridgewater 1976). In Europe, extensive phytosociological data in addition to herbarium records have made possible the analysis of large data sets covering large geographic areas (for example Bolognini & Nimis 1993). These studies have analysed matrices of unit areas (Operational Geographic Units abbreviated to OGUs) by species. OGUs are unit areas derived from the superimposing of a grid over a geographic map, with the presence or absence of a species scored for each cell (Nimis & Bolognini 1990; Lausi & Nimis 1991; Bolognini & Nimis 1993). This technique relies on relatively precise distributional information, depending on the size of the OGU but its main advantage is that it allows quantitative comparisons between areas, thereby minimising some of the problems of using unit areas discussed by Clayton & Hepper (1973). These include the problem of unequally sized units having different chances of containing different numbers of species, the effect of bias of botanical collection to particular areas and the preconceived or subjective restriction of placing species within ecological boundaries which might be questionable or without sound foundation. This approach was beyond the scope of the present study, requiring travel to herbaria Australia - wide and demanding an extensive period of time to obtain data. Even where these data are available through electronic data bases, there is not sufficient personnel available in herbaria to oversee the supply of information in this quantity.

This study is restricted by these limitations and alternative methods of data analysis were used to satisfy statistical assumptions.

### *Numerical analyses*

Each taxon in the data set was given a number or set of numbers representing its regional occurrence across Australia. This produced a matrix of species by regions, analogous to a typical phytosociological data set consisting of quadrats and floristic data, only in this case taxa were "quadrats" and regions were "species" scored in binary form.

The data were classified using the flexible agglomerative hierarchical clustering procedure recommended by Lance & Williams (1967) to produce groups of species with similar regional distributions. Flexibility refers to the ability to produce clusters which vary in definition according to the degree of alteration to the  $\beta$  parameter. A strong cluster was required to minimize the creation of "...non-conformist groups' whose members have little in common beyond the fact that they are rather unlike everything else, including each other" (Lance & Williams 1967: p. 377). Beta was set at -2.5, although -0.1 may be adequate (Belbin *et al.* in press). This does not alter the underlying data structure but serves to minimize chaining (Lance & Williams 1966, 1967; Belbin & McDonald 1993). The Bray - Curtis coefficient was used to compute compositional dissimilarities between all sample pairs.

The data were also subjected to a second, non - hierarchical clustering method for comparison. Non - metric multidimensional scaling (NMDS) was carried out, again using the Bray - Curtis coefficient. The scores derived from a three dimensional solution (stress = 0.106281, achieved from all 10 starts) were then classified using the K-means partitioned (non - hierarchical) clustering method. K-means proceeds by selecting a "seed" sample for each cluster, the number of which is specified at the outset. The seed is separated as much as possible from the centre of all the samples which are subsequently assigned to the nearest seed. Each sample is then assigned to a different cluster, eventually producing groups whose between group sum of squares is greater than within group sum of squares. K-means uses Euclidean distance as a measure of dissimilarity (Wilkinson *et al.* 1992). Each derived group (phytochorion) represented the overall distribution of a species and was used to identify its biogeographic affinities.

### *Mapping*

For each phytochorion identified by the clustering procedure, the proportion of taxa which occurred in each biogeographic province was calculated as a compound average. A map of Australia was produced for each phytochorion which showed the concentration of species across Australia according to region. Proportions were represented by a grey scale corresponding in shading to degree of concentration of taxa, ranging from black (100% representation) to white (0% representation).

### *Comparison of group composition*

Proportions of species in each phytochorion were compared between quadrats with and without *Spyridium* using Student's t - test following arcsin transformations of the data. Where *Spyridium* was present, it was excluded from calculations.

### *Computer programs*

DECODA (Minchin 1991) was used to store, sort and edit raw data files, to compute dissimilarity matrices and compound averages and to execute non - metric multidimensional scaling. Hierarchical clustering was achieved using the WPGMA (Weighted Pair Group using ArithMetic Averaging) option in PATN (Belbin 1987), which also provides group memberships and a dendogram. K-means clustering was carried out using SYSTAT Version 5.03 (Systat Inc. 1993), as were transformations and t - tests. Maps were produced using the Viridans (1992) and CorelDraw! 3.0 (Corel Corporation 1992) software packages.

## **Results**

### *Numerical analyses - phytochoria*

The hierarchical clustering method produced the better classification over the K-means non - hierarchical method for both sets of *Spyridium* data. Groups were more clearly defined and there were no single species clusters. A number of group sizes were specified for the latter method, which resulted in the splitting of individual groups into smaller but biogeographically meaningless clusters. The results of the non - hierarchical method are not considered further.

The distribution of taxa frequently implied that European land clearance is likely to explain the absence of species from certain regions. Particularly outstanding in this regard were the Victorian Volcanic Plain and Gippsland Highlands regions. Lack of botanical exploration and taxonomic inconsistencies were also apparent when comparing the distribution of taxa across State boundaries. The absence of a national map of biogeographic provinces also limits the interpretation of species distributions. However, generalisations can be made with a degree of confidence based on the percentage occurrence of taxa in each State biogeographic region.

The following section describes the phytochorological groups derived from the classification of taxa associated with *S. microphyllum* and *S. obcordatum*.

### *Spyridium microphyllum*

A total of 167 taxa recorded during the phytosociological survey were used for the analysis, including 28 Tasmanian endemic species and 2 endemic varieties, approximately half of the endemic flora which occur in the region (Appendix D.1). The proportion of endemics in pooled quadrats was 18 per cent, which is substantially higher than the regional level of endemism of 11 per cent. Fourteen chorological groups were identified from the classification of taxa and regional distributions, representing taxa which ranged from narrow Tasmanian endemics to those which are widespread throughout Australia. This number of groups was accepted because some subtle, but important distributions were masked when small groups were amalgamated. Consequently, some are closely related. The first division in the classification occurred between widespread taxa and Tasmanian endemics, near endemics or taxa with a discontinuous distribution in eastern Australia and Tasmania (Appendix E.1). Groups were subsequently identified depending on their breadth of distribution Australia wide.

The percentage occurrence of each group in each biogeographic province is tabulated in Appendix E.2.

#### *Group 1*

These taxa are all rare and are predominantly narrow endemics restricted to the Central East Coast of Tasmania. The range of *Hakea megadenia* extends to Flinders Island while two others occur on the Tasman Peninsula or near Hobart (*Spyridium obovatum* var. *velutinum*; *Gahnia rodwayi*).

*Stenanthemum pimeleoides* also occurs in the Midlands region, although its main centre of abundance is the Central East Coast, and is best placed in group 1, rather than with groups 2 or 3. The group includes some species (*Lasiopetalum micranthum*, *Pultenaea selaginoides*) which have extremely narrow distributions even within the region, as well as one species with a disjunct distribution (*Deyeuxia apsleyensis*) similar to that of *S.*

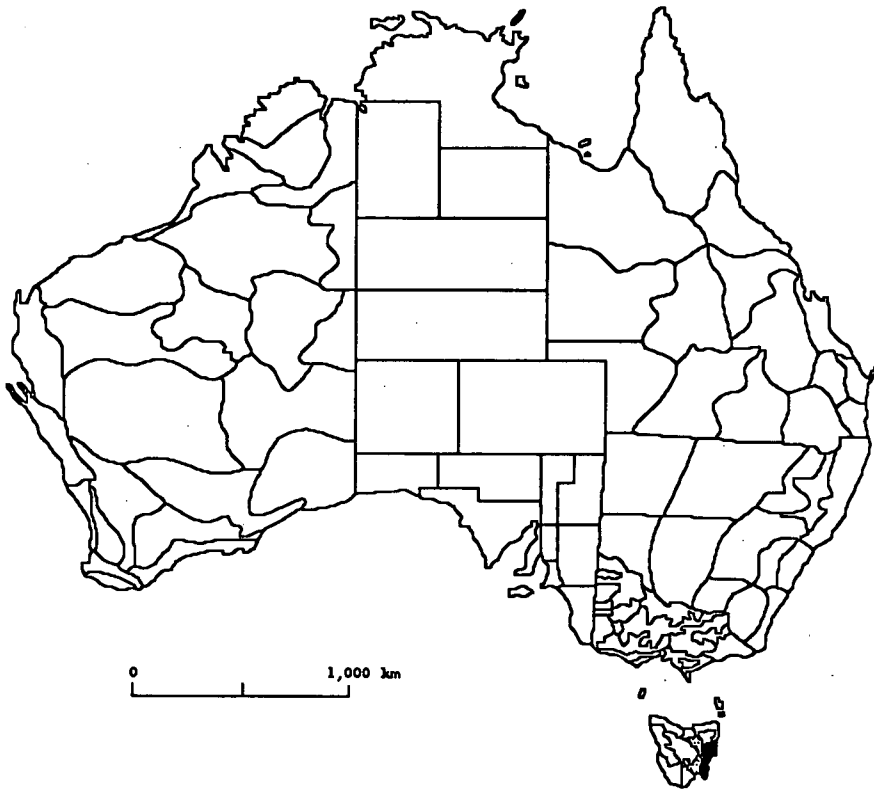
*microphyllum*. All are confined to dry sclerophyll vegetation and are associated with both herbaceous and woody understoreys on dolerite, granite and less frequently, sandstone (Fig. 6.1a).

#### *Group 2*

Taxa in this small group are endemics common in central eastern and southeastern Tasmania, with some extending to the Midlands, Central Plateau and/or Southwest regions, but are absent from the northeast of the State. Some have been recorded from the Furneaux group in Bass Strait. All except *Spyridium obovatum* var. *obovatum* are associated with grassy dry sclerophyll forest and all are strongly associated with dolerite (Fig. 6.1b).

**Figure 6.1a. Group 1 distribution (*S. microphyllum*).**

**Figure 6.1b. Group 2 distribution (*S. microphyllum*).**



### Group 3

The majority of species in this group are widespread Tasmanian endemics. They tend to be associated with forested, rocky (mainly dolerite) environments and occasionally river banks. Some prefer cool, moist sites (*Callistemon viridiflorus*, *Veronica formosa*, *Bedfordia salicina*, *Cyathodes glauca*). The distribution of the single non - endemic in this group (*Pomaderris pilifera*) includes the Furneaux Islands and Victoria, where it occurs in East Gippsland and the Eastern Highlands, mainly on dry, rocky slopes (N. Walsh, pers. comm.), in common with its preferred habitat in Tasmania. It is widespread in Tasmania but is most frequent in the southeast (Fig. 6.1c).

### Group 4

This small group is strongly associated with the Great Dividing Range in eastern Australia. Species are distributed along the New South Wales Tablelands to eastern Victoria and Tasmania but are absent from alpine areas. These were *Tetratheca pilosa*, *Bulbine glauca* and *Poa hookeri* (Fig. 6.1d).

### Group 5

This very small group consists of two species, *Callitris rhomboidea* and *Phyllanthus australis* whose distributions coincide in eastern Tasmania, as well as in part of the mediterranean belt of Victoria and South Australia, including Kangaroo Island (Fig. 6.1e). *C. rhomboidea* is the more widespread of the two, with *P. australis* absent from New South Wales and eastern Victoria. Disjunct distributions and species with discontinuous ranges are not uncommon in the genus *Callitris* (Harris & Kirkpatrick 1991; Bowman & Harris 1993). The group is absent from the northeast of Tasmania, although *C. rhomboidea* is found on Flinders, Cape Barren and Clarke Islands in Bass Strait and has no specific habitat preference (Harris & Kirkpatrick 1991).

### Group 6

Taxa in group 6 include species mostly restricted to the Otways, Midlands, Gippsland Plain and Eastern Highlands in Victoria, southern New South Wales and throughout Tasmania. Minor occurrences are in southern regions with a disjunction in the distribution of *Melaleuca gibbosa* on either side of the Nullabor Plain. Similar disjunctions have been observed in a number of



Figure 6.1c. Group 3 distribution (*S. microphyllum*).

Figure 6.1d. Group 4 distribution (*S. microphyllum*).

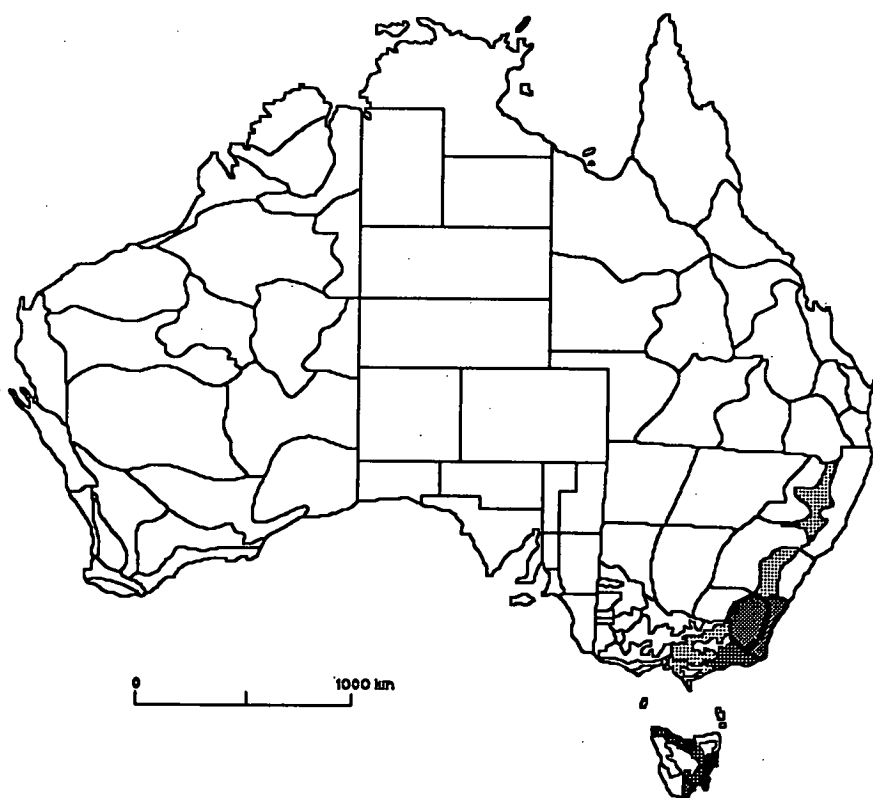
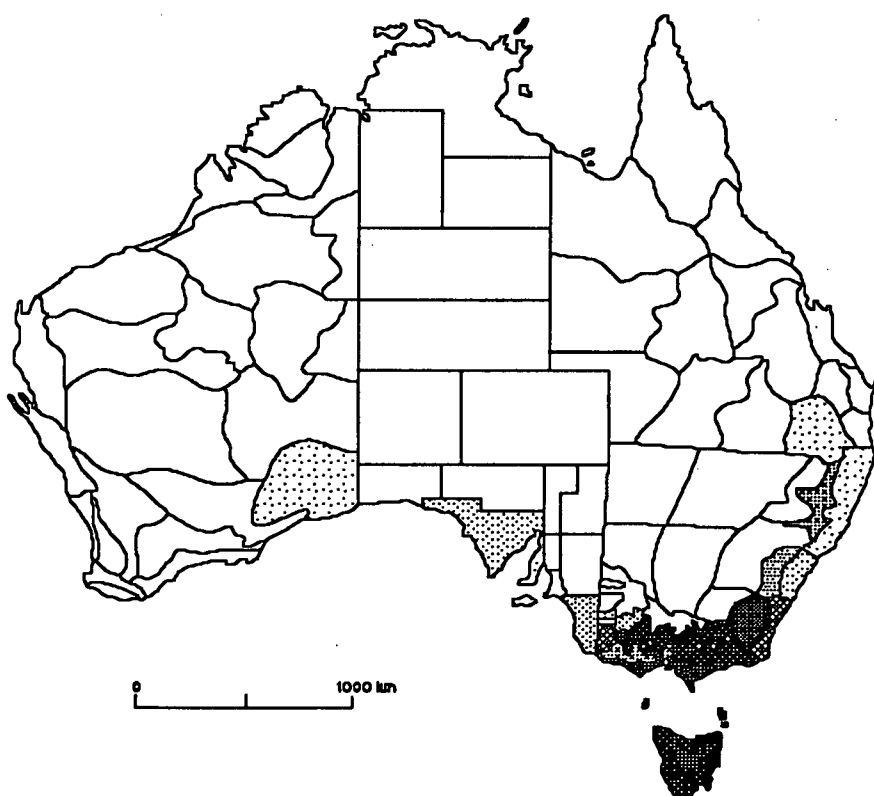
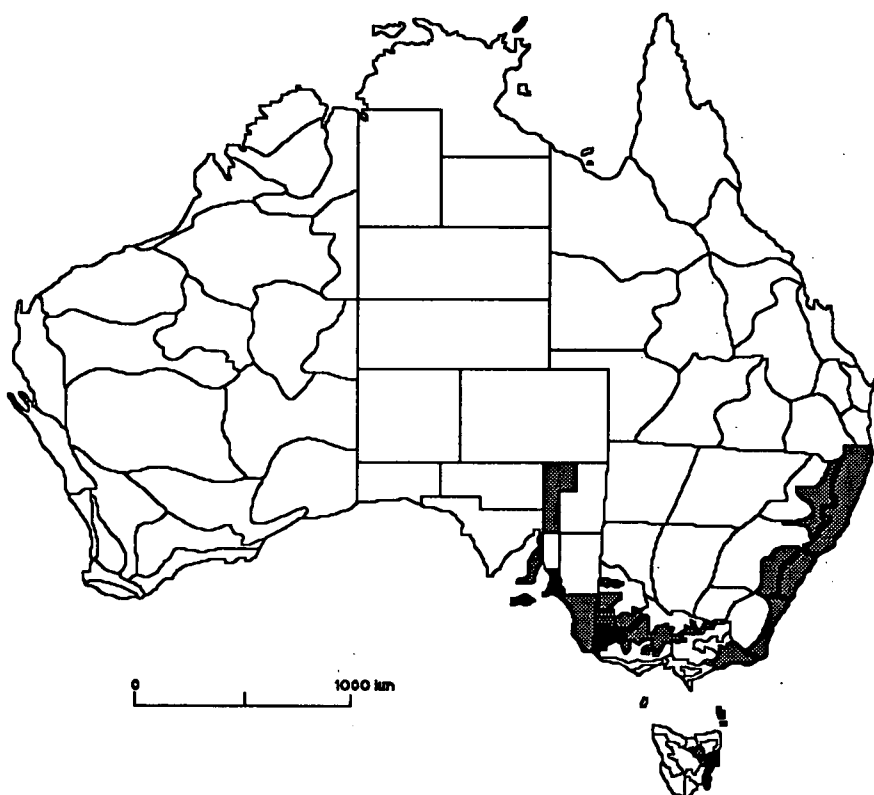


Figure 6.1e. Group 5 distribution (*S. microphyllum*).

Figure 6.1f. Group 6 distribution (*S. microphyllum*).



other taxa between these regions, including *Spyridium* and were discussed in chapter 4. However, in general, this group contains taxa which occur on cool or elevated sites in dry sclerophyll forest and in some wet sclerophyll communities, damp, heathy woodland or along rivers. In Tasmania they are common elements of dry sclerophyll forest or riparian vegetation, particularly in the east. Most have no geological preference (Fig. 6.1f).

#### Group 7

The distribution of this small group is highly fragmented as a result of the presence of *Brachyscome tenuiscapa*, which occurs in the Darling Downs region in southeastern Queensland, to the New South Wales Northern Tablelands, South Coast and Victorian Snowfields. It is uncommon on predominantly basalt soils in alpine or subalpine areas (N. Walsh pers. comm.). The remainder of species are distributed over similarly cool sites and are absent from the northeast lowlands, central west and Midlands in Tasmania. Two of the 3 taxa were endemic varieties of widespread species (*Grevillea australis* var. *linearifolia* and *Poa labillardieri* var. *acris*). The group's stronghold is the Central East Coast and the Central Plateau regions (Fig. 6.1g).

#### Group 8

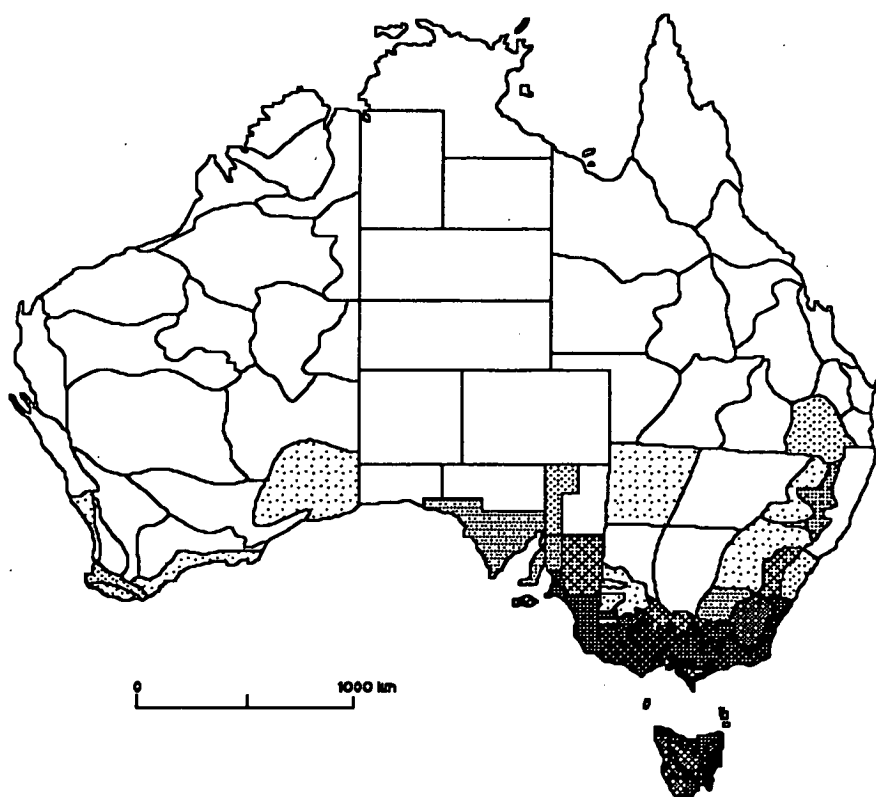
This group is similar to group 6, only with a stronger southern component. Species are best represented in Victoria and in southeastern South Australia, central and eastern Tasmania. All are components of forest or coastal heathy woodland and occasionally heath or mallee. There are also minor occurrences in southwestern Western Australia consisting of three species whose distributions are disjunct between eastern and western States (*Stipa flavescens*, *Danthonia penicillata* and *Craspedia glauca*). In Tasmania, most taxa in this group occupy dry, moderately rocky habitats within dry sclerophyll forest and tend to be associated with predominantly grassy understoreys. It is a widespread group but is most concentrated in the southeast and Midlands in Tasmania (Fig. 6.1h).

#### Group 9

This group is closely related to groups 6 and 8 but has a strong east coast component. The Coast and Tablelands of New South Wales, the Eastern Highlands and East Gippsland of Victoria contain 75% -100% of group members. Half of all group members occur in southeastern Queensland. In Tasmania, the group's stronghold is in the east, southeast and Midlands. However, western and central regions are also well represented (Fig. 6.1i). Species are a component of riparian, wet forest, heathland and elevated rocky woodland associations, or occur in the understoreys of heathy dry sclerophyll vegetation. *Beyeria viscosa* and *Callistemon pallidus* are

Figure 6.1g. Group 7 distribution (*S. microphyllum*).

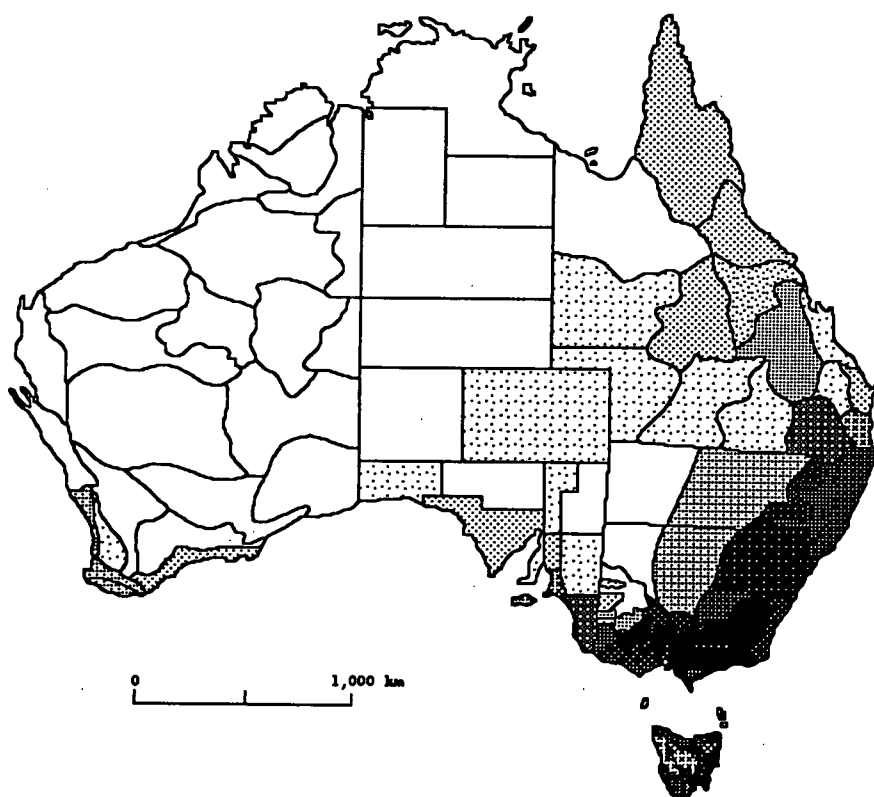
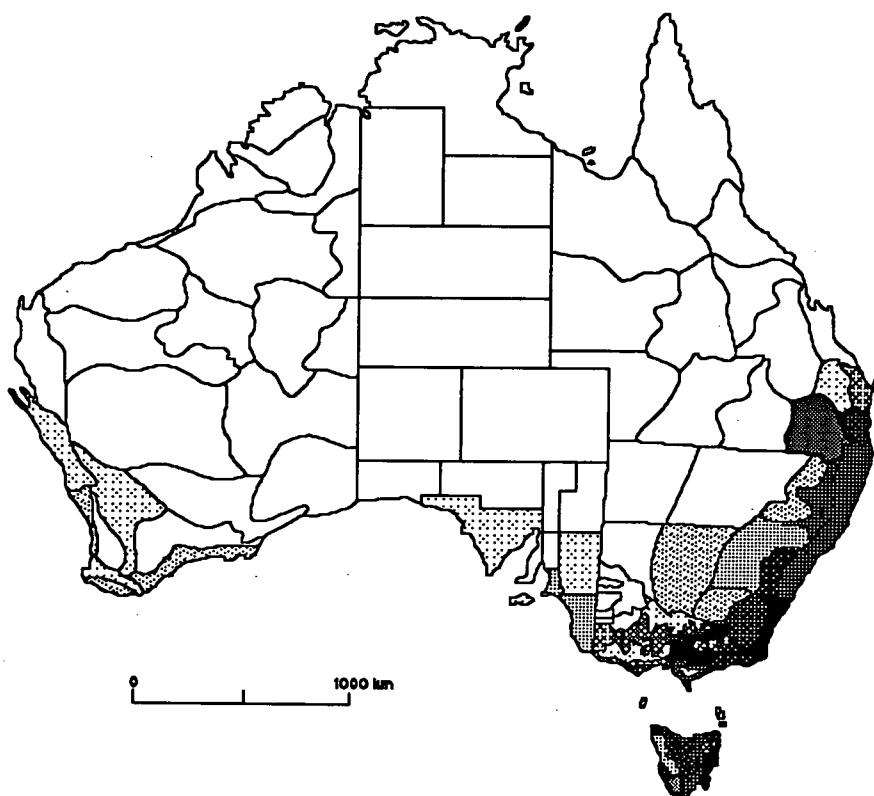
Figure 6.1h. Group 8 distribution (*S. microphyllum*).



**Figure 6.1i. Group 9 distribution (*S. microphyllum*).**

**Figure 6.1j. Group 10 distribution (*S. microphyllum*).**





common in Tasmania but rare in parts of mainland Australia (Gullan *et al.* 1990; Keith & Ashby 1992).

#### *Group 10*

This group is distributed throughout a great deal of eastern Australia, extending to southwestern Western Australia and the eastern tropics. Its stronghold is in the southeastern temperate zone and although widespread throughout Tasmania, is better represented in elevated areas throughout the Great Dividing Range. It consists of species common to dry sclerophyll forests of southeast Australia, such as Box- Ironbark or Box - Stringybark vegetation and dry sites in Tasmania. Most taxa are widespread. However, *Callistemon sieberi* is rare in Tasmania and is confined to the Central East Coast along the St Pauls, Apsley and Swan Rivers. The remainder of species are typical components of the understoreys of grassy forest (Fig. 6.1j).

#### *Group 11*

Taxa common throughout southern and southeastern Australia comprise group 11. Its distribution is more strongly linked to mainland Australia and eastern Tasmania, including the Furneaux Islands. It includes species whose distributions extend into a predominantly dry but wide range of habitats, including Box - Ironbark forests, semi - arid, arid, subtropical and tropical environments. Species include *Dodonaea viscosa* and *Allocasuarina verticillata*, both known to tolerate drought prone conditions (Fig. 6.1k).

#### *Group 12*

This group is extremely wide ranging in eastern Australia but is best represented along the southern and eastern seaboard and throughout eastern Tasmania. It is closely related to group 10 but extends further north and is also widespread throughout the eastern tropical zone. Many taxa are drought resistant and commonly found in heaths or rocky environments in Tasmania and in damp vegetation communities which may be ecotonal between woodland and riparian associations (Fig. 6.1l).

#### *Group 13*

Group 13 is unique insofar as the distribution of taxa is strongly associated with southern Australia from west to east, including regions in the arid and semi - arid zones. In Tasmania, it occurs in the north and east, but is absent from the Bass Strait Islands. Two species are rare in Tasmania (*Teucrium corymbosum* and *Millotia tenuifolia*) and are erratically distributed on mainland Australia, predominantly in seasonally inundated sites (N. Walsh pers. comm.). All species in the group, except for *T. corymbosum* occur

Figure 6.1k. Group 11 distribution (*S. microphyllum*).

Figure 6.1l. Group 12 distribution (*S. microphyllum*).

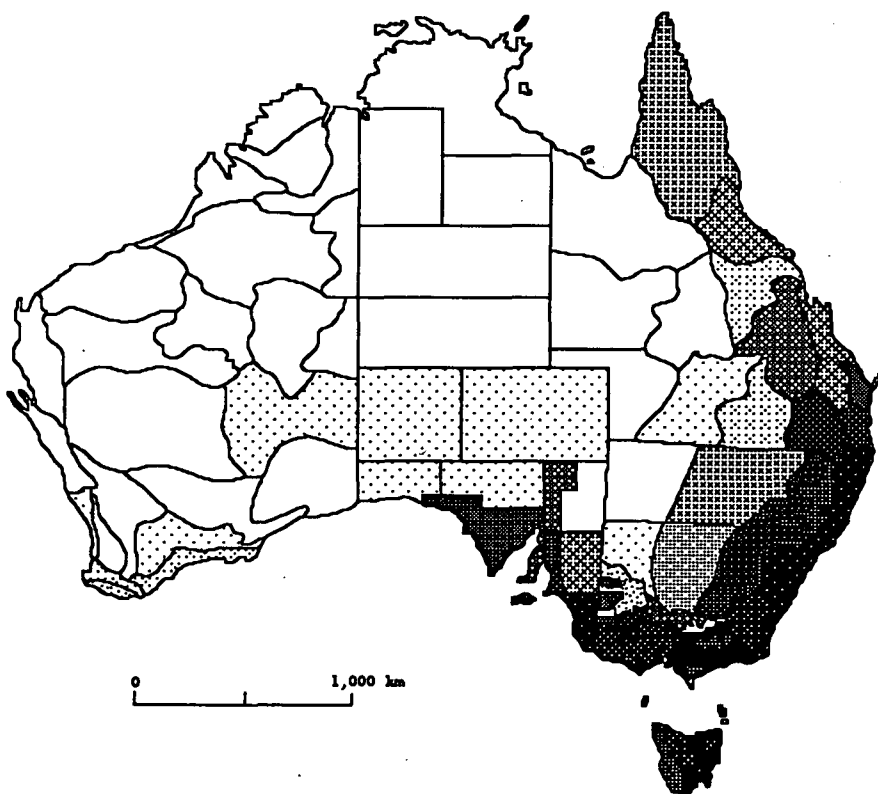
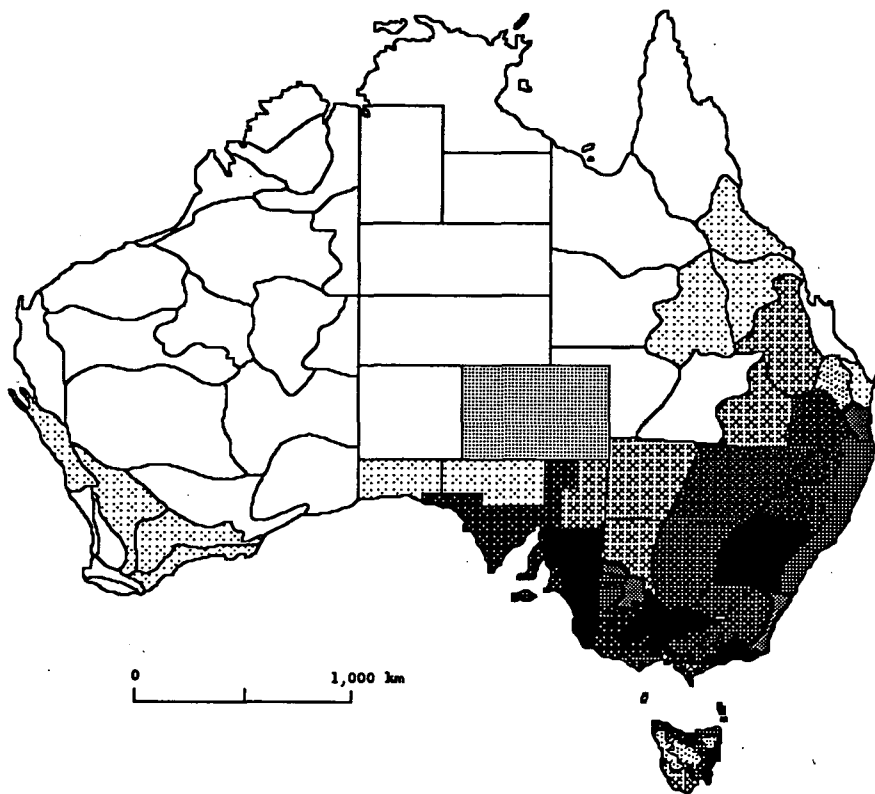
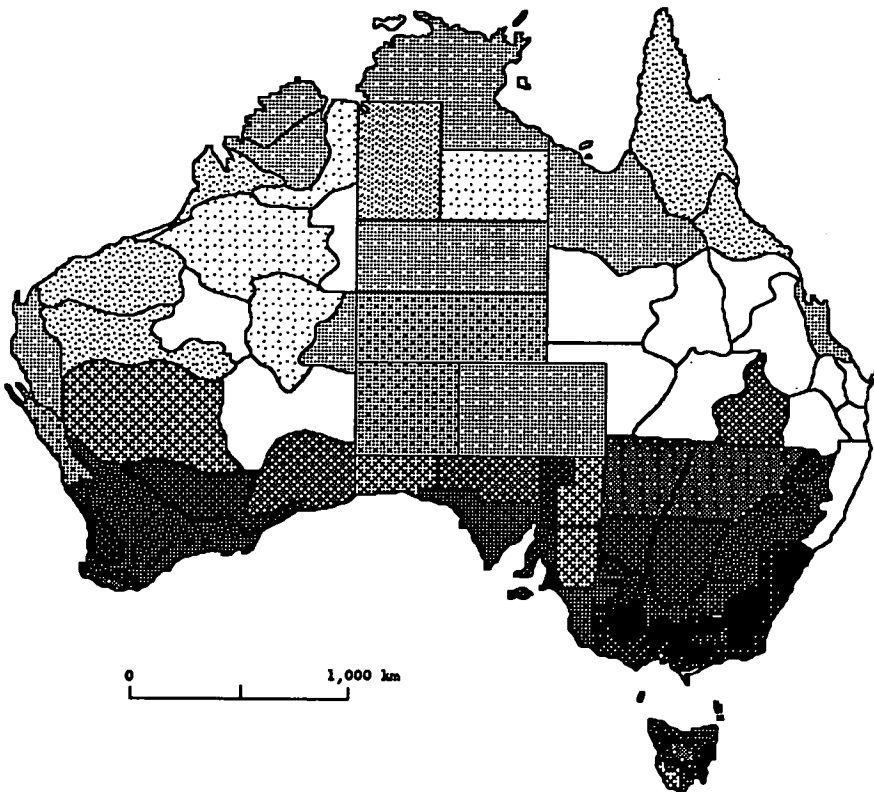
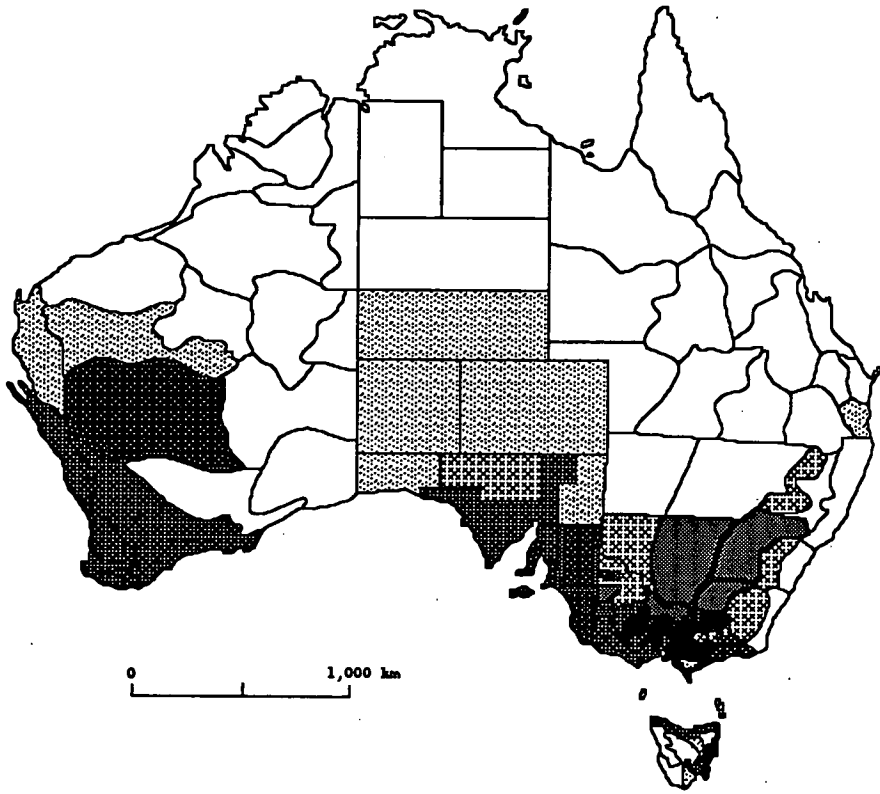


Figure 6.1m. Group 13 distribution (*S. microphyllum*).

Figure 6.1n. Group 14 distribution (*S. microphyllum*).



relatively widely in Western Australia and in central Australia. In Tasmania the group is distributed within a range of habitats but is confined to the lowland north and east of the State (Fig. 6.1m).

#### *Group 14*

These taxa are widespread throughout Australia including the tropics. Typical species are *Themeda triandra*, *Cheilanthes austrotenuifolia*, *Poranthera microphylla*, *Pelargonium australe* and *Comesperma volubile*. They occupy a wide range of environments but are most concentrated in southern regions and in the lowland central, northern and eastern regions of Tasmania (Fig. 6.1n).

#### *Spyridium obcordatum*

There were 9 species endemic to Tasmania (6%) out of a total of 141 taxa recorded during the phytosociological survey (Appendix D.2). Regionally this represents 14% of the endemic flora found in the region. Ten species groups were selected from the classification (Appendix E.3). The first division split endemics and near endemics from more widespread groups. Subsequent divisions separated southern, narrowly southeastern and broadly southeastern groups. The group consisting of narrow endemics was the only cluster which contained less than nine taxa. Some larger groups, such as groups 3 and 4, are closely related.

The percentage occurrence of each group in each region is tabulated in Appendix E.4.

#### *Group 1*

This group is widespread in southeastern, southern and western Australia in coastal heath and heathy woodland but is less well represented in Tasmania. Taxa are common in dry, grassy open forest or coastal woodland in the lowlands of the north and east, and poorly represented in the highlands and west. They are frequently associated with rocky ground. Species include *Allocasuarina verticillata*, *Stipa mollis*, *Cheilanthes austrotenuifolia* and *Astroloma humifusum* (Fig. 6.2a).

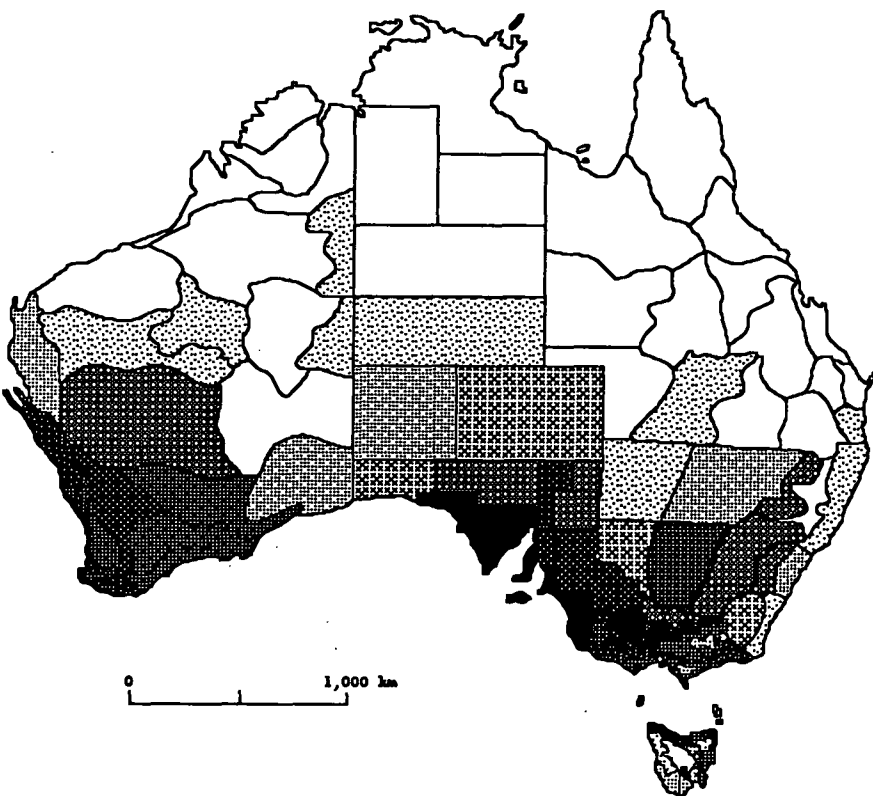
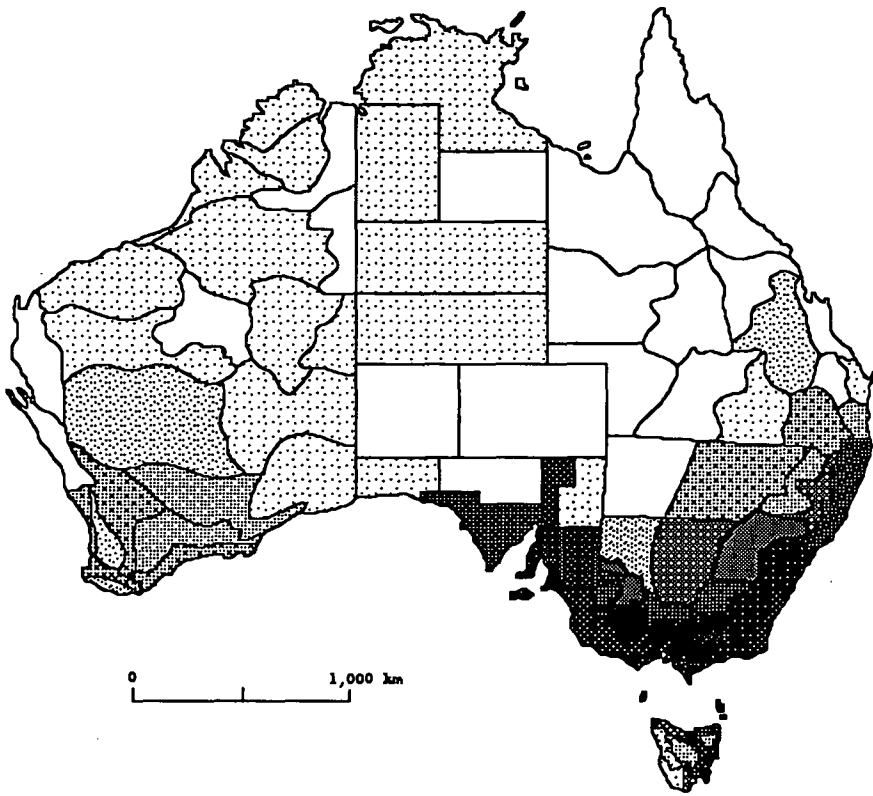
#### *Group 2*

Taxa in this group are strongly associated with southern and southwestern Australia and are only sparsely represented in Tasmania other than in the central north and central east coast regions. Elsewhere, the group is best represented in the mediterranean belt of southern Australia. It consists of a mixture of species, including three which are rare in Tasmania: *Triglochin centrocarpum*, *Lasiopetalum baueri* and *Lepidosperma viscidum*. Others,

Figure 6.2a. Group 1 distribution (*S. obcordatum*).

Figure 6.2b. Group 2 distribution (*S. obcordatum*).





such as *Oxalis perennans* and *Thysanotus patersonii*, are common components of grassy dry sclerophyll forest (Fig. 6.2b).

### Group 3

Southeastern and eastern Australia is the stronghold for Group 3, particularly throughout the Tablelands of New South Wales, the foothills of eastern Victoria in heathy open forest, and in southeastern Queensland. It is widespread in Tasmania, with taxa concentrated in the eastern lowlands. Most taxa are common components of shrubby or grassy dry sclerophyll forest. Some species, such as *Acacia dealbata*, *Allocasuarina littoralis*, *Pultenaea daphnoides*, *Billardiera scandens* and *Exocarpos strictus*, have achieved an extensive distribution along the Great Dividing Range. Group 3 contains species whose distributions are disjunct between eastern and western Australia (Fig. 6.2c).

### Group 4

This group is closely related to the previous group but is also strongly represented in southern and eastern Australia in regions including the Eyre and Yorke Peninsulas, Kangaroo Island and the southeast of South Australia. It extends to arid, semi - arid, subtropical and tropical areas. Taxa which are particularly widespread in Tasmania include *Lepidosperma laterale*, *Schoenus apogon*, *Gonocarpus tetragynus* and *Correa reflexa*. A number of vegetation types, including dry sclerophyll forest and heathland and in Victoria in dry rocky Box -Peppermint or Stringybark open forest and woodland (N. Walsh pers. comm.), include these taxa. A disjunction between eastern and western Australia occurs in this group, with taxa absent from the Nullarbor Plain (Fig. 6.2d).

### Group 5

Concentrations of taxa in this group occur in central Victoria and eastern Tasmania, with some extending to the west, east and semi - arid regions. They are notably absent from regions adjoining the Great Australian Bight. The group is relatively large (21 members) but is reasonably discrete in its distribution. It contains species which are common in shrubby or grassy southeastern forest associations on fertile soils, as well as heathy, lowland forest and woodland on sandy soils. It includes widespread taxa such as *Eucalyptus obliqua*, *Pimelea humilis* and *Platylobium triangulare* (Fig. 6.2e).

Figure 6.2c. Group 3 distribution (*S. obcordatum*).

Figure 6.2d. Group 4 distribution (*S. obcordatum*).

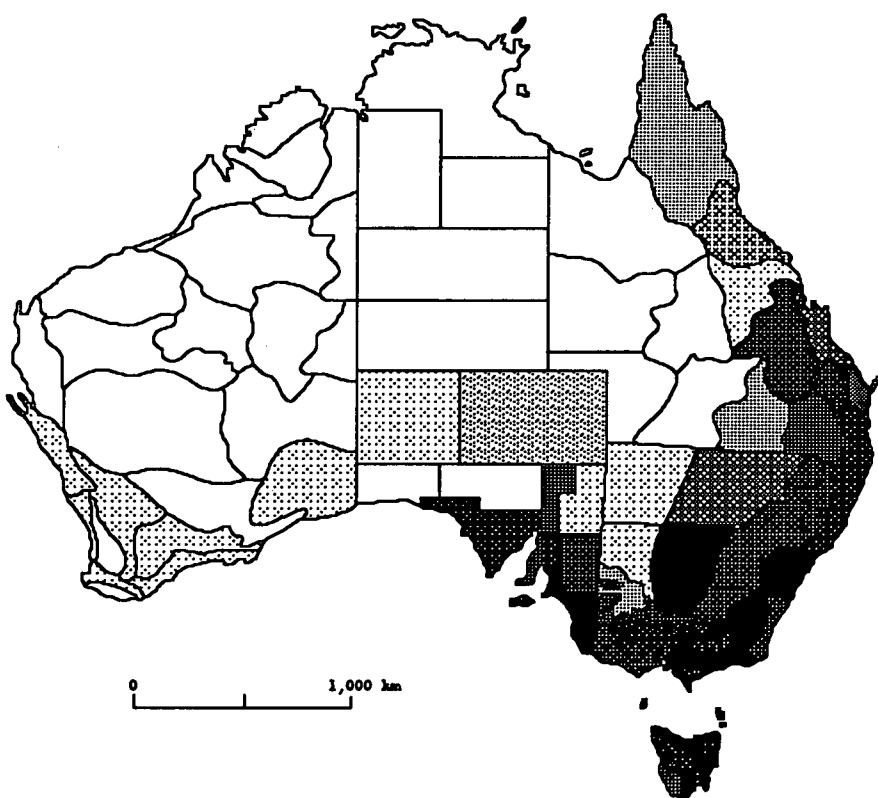
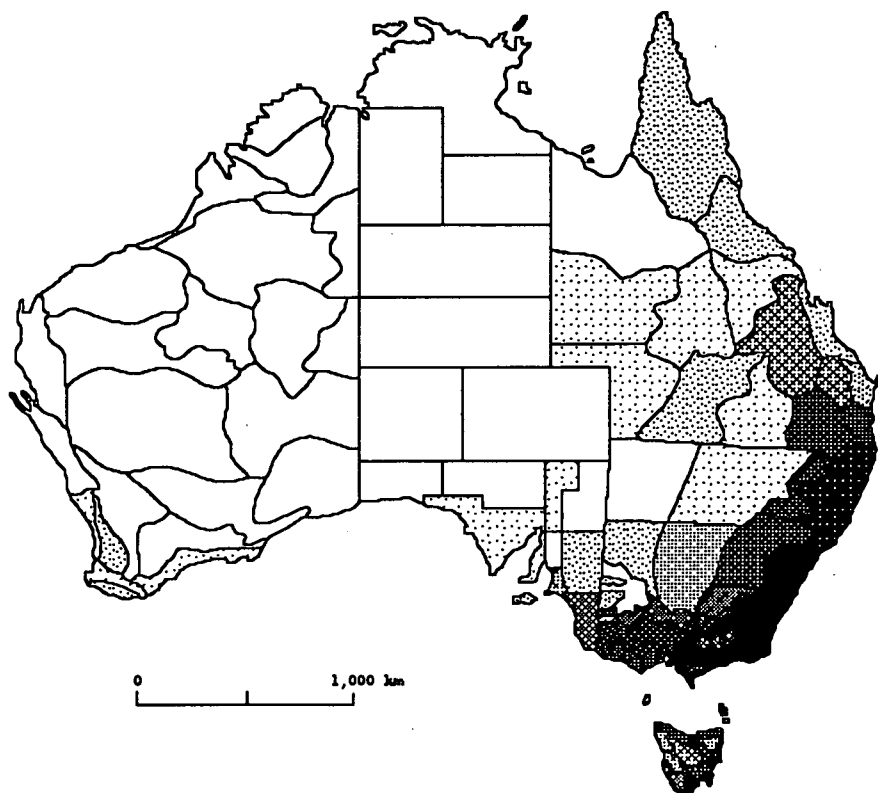
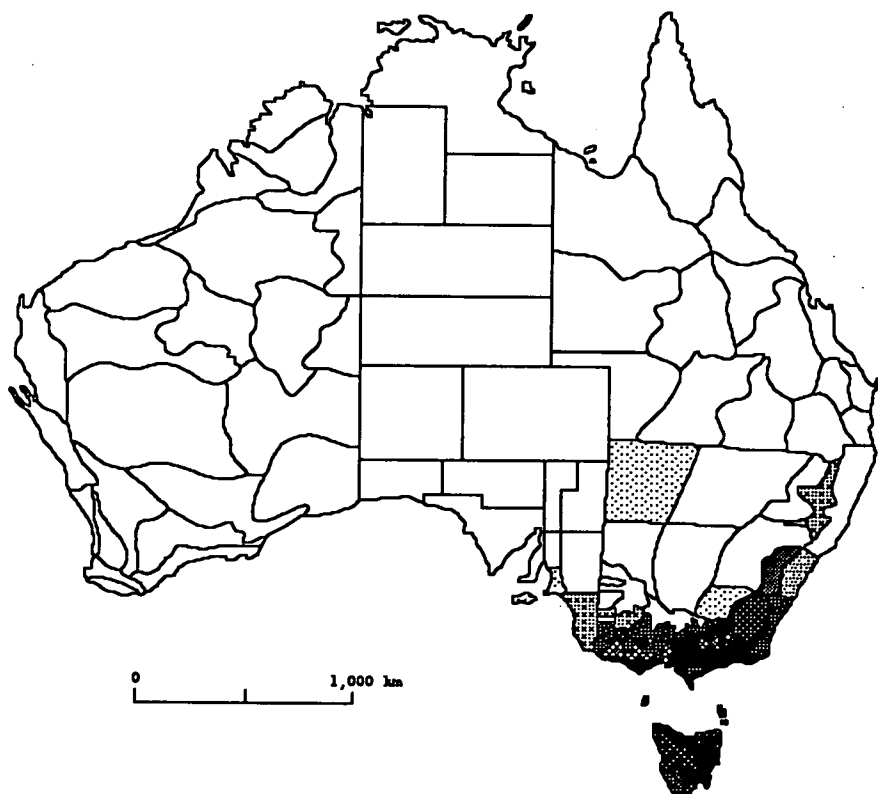
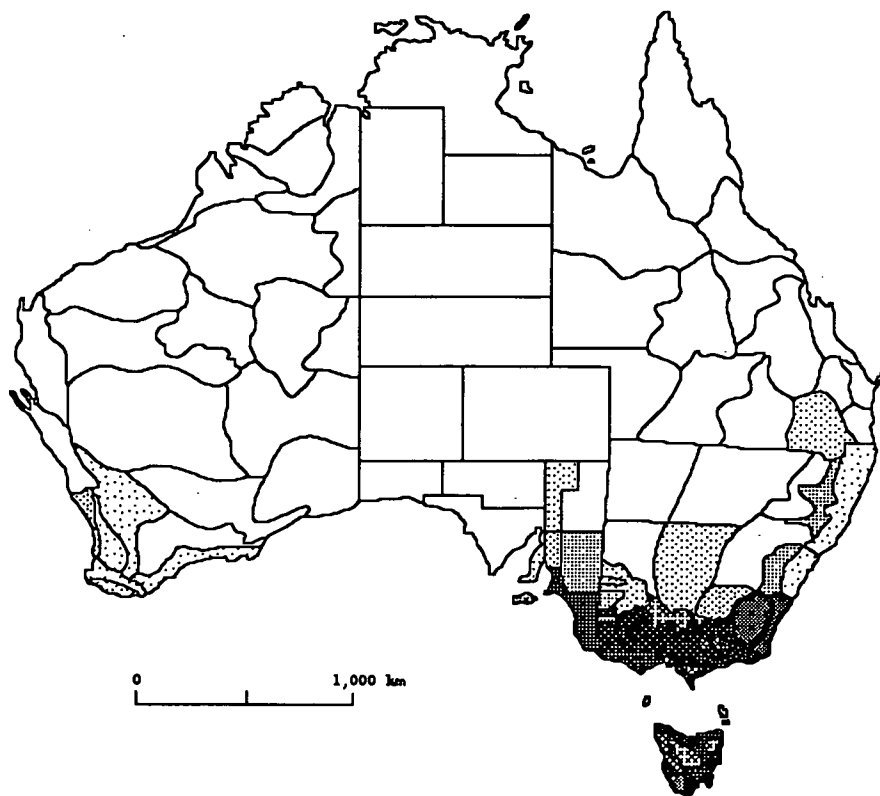


Figure 6.2e. Group 5 distribution (*S. obcordatum*).

Figure 6.2f. Group 6 distribution (*S. obcordatum*).



### Group 6

Group 6 is closely related to group 5 but is concentrated in the Otway range, eastern Victoria and in northern and eastern Tasmania. With the exception of Tasmanian endemics, these taxa are highly restricted in their distribution. One outlying record (*Danthonia penicillata* - northern far western plains of NSW) may be a misidentification as it also appeared as an outlier in the *S. microphyllum* analysis (group 8). Taxa faithful to the core regions are *Goodenia lanata*, *Eucalyptus ovata* and *Lepidosperma ensiforme*. Group 6 species are common components of dry sclerophyll forest or heath in moderately fertile damp open forest (Fig. 6.2f).

### Group 7

This group is distributed throughout a number of regions, but is most strongly associated with the southeast and east coast of mainland Australia and with the north and east coast regions of Tasmania. It typically consists of a number of heath species as well as species frequently recorded from coastal environments. The former include *Dillwynia glaberrima*, *Acacia myrtifolia*, *Selaginella uliginosa*, *Patersonia fragilis*, *Lepidosperma filiforme*, and *Leucopogon australis*. The latter include *Samolus repens*, *Lobelia alata*, *Melaleuca ericifolia* and *Acacia sophorae* (Fig. 6.2g).

### Group 8

Group 8 is widespread throughout Australia. It includes *Themeda triandra*, *Stackhousia monogyna*, *Daucus glochidiatus*, *Hypericum gramineum* and *Poranthera microphylla*. Many show no habitat specificity and occur in a wide variety of vegetation types. However, most prefer structurally open associations. The group is concentrated in southeast Australia and eastern Tasmania, where taxa are usually associated with grassy dry sclerophyll forest or open, rocky environments (Fig. 6.2h).

### Group 9

This group consists of Tasmanian endemics as well as three non - endemics, *Pomaderris pilifera*, *Gahnia grandis* and *Tetratheca pilosa*. The stronghold for the group is the southeast and central north of the State. Although *Eucalyptus amygdalina* and *Hibbertia hirsuta* are confined to the eastern half of the State, others are widespread. All are common in heathy, shrubby or grassy dry sclerophyll forest or occasionally in heath or scrub (Fig. 6.2i).

Figure 6.2g. Group 7 distribution (*S. obcordatum*).

Figure 6.2h. Group 8 distribution (*S. obcordatum*).



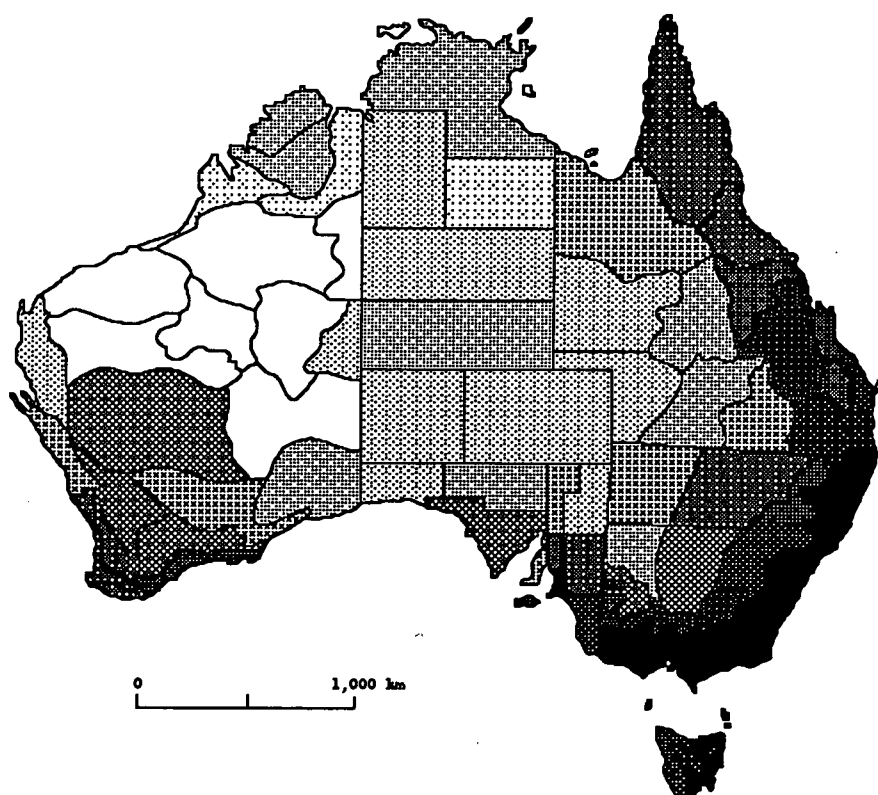
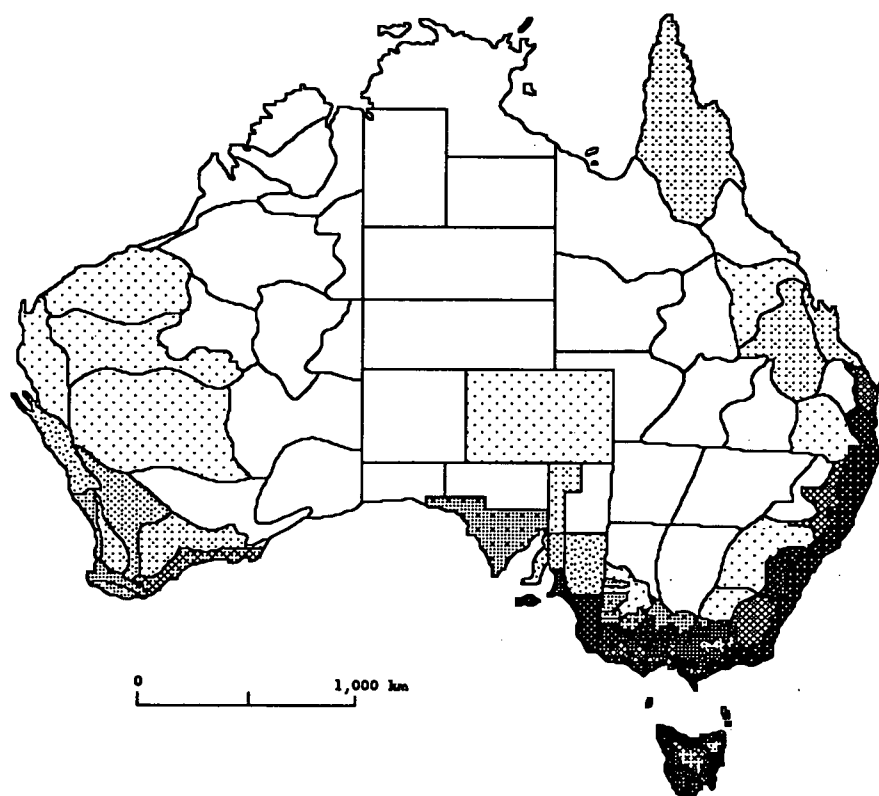
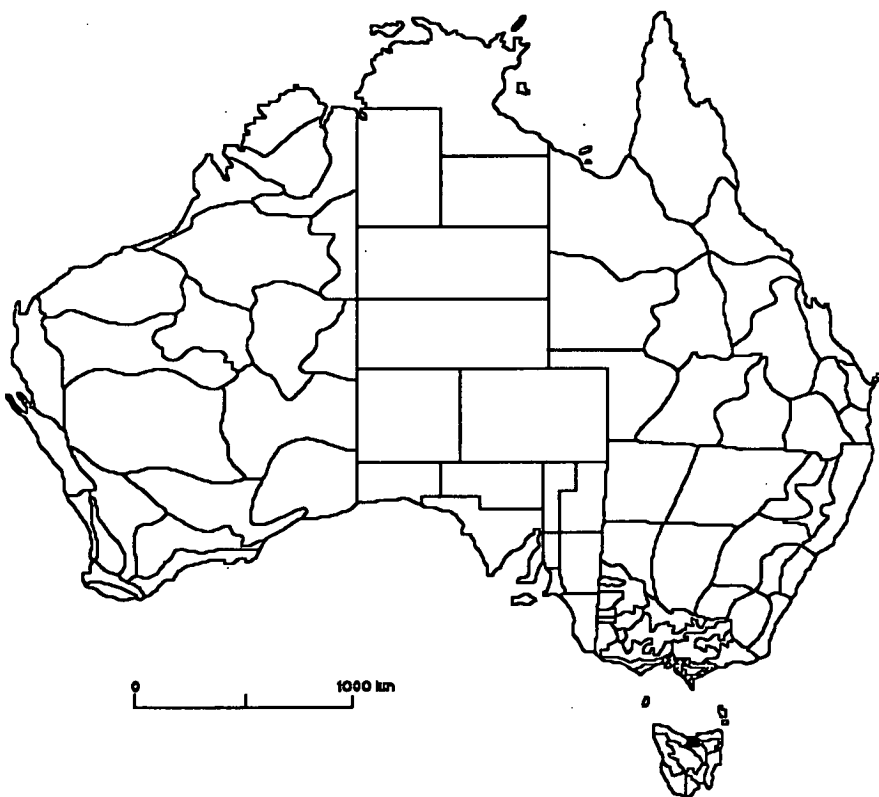
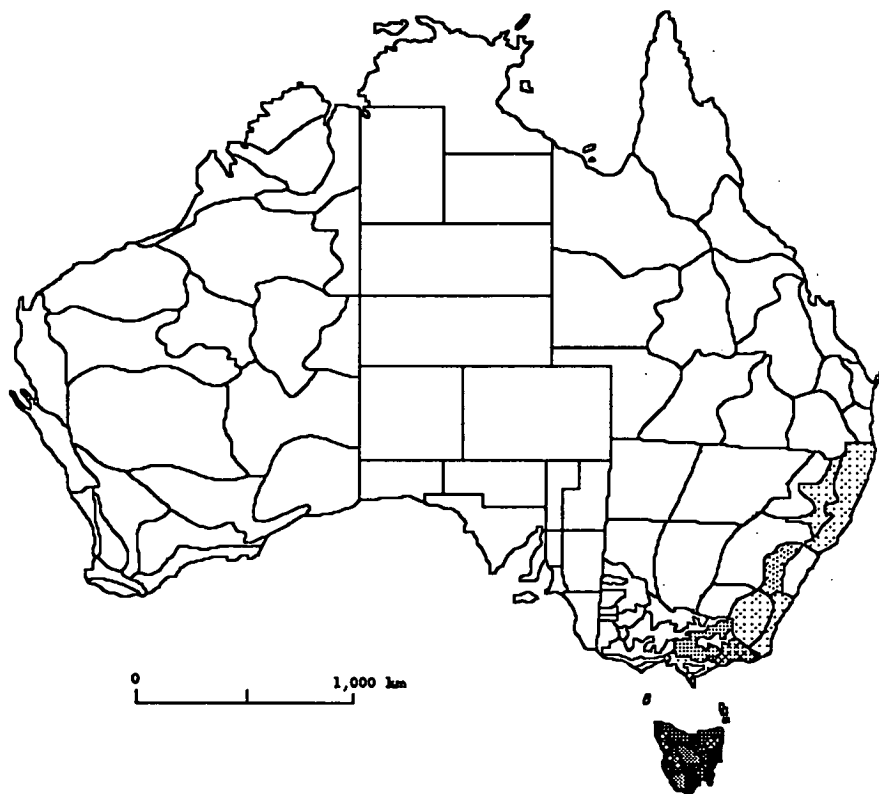


Figure 6.2i. Group 9 distribution (*S. obcordatum*).

Figure 6.2j. Group 10 distribution (*S. obcordatum*).



### Group 10

This small group consists of three species. Two of these, *Spyridium obcordatum* and *Epacris virgata* are restricted to the central north coast. *Pomaderris oraria* ssp. *oraria* has very limited distribution on the north coast of Tasmania and coastal South Gippsland in Victoria. It has not been recorded from the Furneaux Islands but may occur there (Fig. 6.2j).

### **Comparison between *S. microphyllum* groups (SM) and *S. obcordatum* groups (SO) and assessment of the effectiveness of the classification**

The clustering technique produced a number of clear distribution patterns which illustrate the range of geographic elements contained within regional floras. Groups produced from the analyses of separate data sets were broadly similar but with some exceptions. The groups comprising Tasmanian endemics or near endemics (SO: group 10; SM: groups 1, 2, 3) were unique to each data set. There were no SO equivalents of SM groups 5 and 7 which were both very small groups having a relatively uncohesive distribution. SM group 9 and SO group 7 were broadly similar but not an entirely close match, with the latter containing a strong coastal element not apparent in SM 9.

The groups can be roughly divided into six categories:

1. Tasmanian endemics or near endemics (SM groups 1, 2, 3; SO groups 9, 10).
2. Restricted or disjunct eastern taxa (SM groups 4, 7).
3. Predominantly southern taxa (SM groups 6, 8; SO groups 5, 6).
4. Predominantly eastern with minor extensions to the temperate southwest (SM groups 9, 10; SO groups 3, 4, 7).
5. Predominantly south to southwestern taxa, subhumid taxa or semi - arid taxa associated with mediterranean -type regions (SM group 5, 13; SO groups 1, 2).
6. Widespread species (SM groups 11, 12, 14; SO group 8).

Eastern, western and widespread floral elements were also identified by Bridgewater (1976) in the flora of Victoria and he categorised the six largest families represented in Victoria into 12 groups. He found that elements in the Victorian flora, including southwestern affiliates, were common to Tasmania. However, species which extended their range as far as Queensland were commonly only found in the East Gippsland element.

The *S. obcordatum* analysis resulted in a higher number of groups with representatives in southwestern Australia, with all but three groups extending to Western Australian regions. Tasmanian endemics and restricted or disjunct eastern

Australian taxa were relatively poorly represented at *S. obcordatum* sites. However, taxa with disjunct distributions between northern Tasmania and southern mainland Australia were apparent. These and other taxa associated with coastal or semi - arid environments were well represented. By comparison, *S. microphyllum* groups were generally more strongly associated with eastern Australia, in particular the Great Dividing Range. Some groups contained taxa with disjunct or otherwise fragmented distributions and their allocation to small groups was retained because they represent interesting biogeographic patterns which would have been overlooked had they been included in larger groups. Tasmanian endemics were better represented at *S. microphyllum* sites, with the analysis identifying three phytochoria containing such taxa. *Spyridium microphyllum* sites lacked a coastal phytochorion.

### *Comparisons between quadrats with and without Spyridium*

In the analysis below, groups whose representation differed significantly between quadrats with and without *Spyridium* are listed in parentheses after the site name.

#### *Spyridium microphyllum*

##### *Douglas - Apsley site (group 1)*

Most taxa at the site were eastern and southeastern narrow Tasmanian endemics or near narrow endemics (groups 1 & 2). Taxa associated with cool, moist sites in southeastern Australia, especially the Victorian Eastern Highlands and East Gippsland and Tasmania, also accounted for a relatively large proportion of the flora (group 6). Group 12 was also well represented, and contained widespread ruderals. Quadrats were deficient in widespread Tasmanian endemics (group 3); south to southwestern Australian flora (groups 8 & 13); taxa with a restricted distribution in southeastern Australia (groups 4 & 7) and groups containing taxa widespread in southeastern Australia (groups 10 & 11).

Narrow endemics (group 1) were significantly better represented in quadrats with *S. microphyllum* (Table 6.1), whereas groups 5 and 9 were completely confined to these quadrats. The former consisted of *Callitris rhomboidea* and *Phyllanthus australis* and are associated with mediterranean climates and aseasonal subhumid climates. However, group 5 was poorly represented overall and too few data existed for statistical analyses. Group 9 is strongly associated with the Great Dividing Range and was represented at this site by two widespread heath species (*Baeckea ramosissima* and *Sphaerolobium vimineum*).

PHYTOCHORION	S.MICRO?	n	Mean	SD	T	DF	P
GROUP 1	1	19	12.80	3.0	2.10	23	0.05
	0	6	10.00	2.5			
GROUP 2	1	19	5.05	2.0	-0.64	23	0.50
	0	6	5.50	1.2			
GROUP 5	1	19	0.32	1.0	ID	23	ID
	0	6	0.00	0.0			
GROUP 6	1	19	5.20	3.7	1.3	23	0.21
	0	6	3.00	3.3			
GROUP 9	1	19	2.10	2.0	ID	23	ID
	0	6	0.00	0.0			
GROUP 12	1	19	3.60	2.6	1.38	23	0.18
	0	6	2.50	3.5			
GROUP 14	1	19	0.37	0.5	-0.55	23	0.59
	0	6	0.50	0.6			

Table 6.1. Douglas - Apsley. Comparisons between the chorological composition of quadrats with and without *S. microphyllum* using Student's t-test between arcsin transformed pairs. Means are back transformed to percentages.

*Thumbs site (groups 1, 2, 3, 6, 9, 11, 13, 14)*

Group 5 was the only group unrepresented at the Thumbs. However, neither narrow nor widespread Tasmanian endemics were well represented at this site. Rather, taxa broadly distributed throughout Tasmania but concentrated mainly in cool regions in Victoria (group 6) and widespread southeastern Australian taxa (group 12), characterised the flora.

Quadrats where *S. microphyllum* was present did not contain significantly higher proportions of narrow endemics. Narrow endemics, at this site consisted of two taxa associated with open shrubland (*S. microphyllum* and *Ozothamnus lycopodioides*) and two found in open forest (*Cyathodes divaricata* and *Deyeuxia apsleyensis*). The bias arose by excluding *S. microphyllum* from the analysis.

Quadrats with *S. microphyllum* had significantly higher proportions of endemics confined to southeastern Tasmanian (group 2) as well as widespread Australian taxa (group 11 & 14), taxa concentrated in temperate or mediterranean regions in southern and southwestern Australia (group 13) and taxa concentrated in elevated rocky sites in eastern Australia, including southeast Queensland (group 9). Quadrats where *S. microphyllum* was absent were significantly higher in group 3 and 6 taxa which consisted of widespread Tasmanian endemics and taxa mainly concentrated in cool and moist habitat or elevated areas in southern Australia (Table 6.2).

*Swan River site (groups 1, 3, 7, 8, 9, 11, 14)*

Group 6 taxa were well represented overall, as were taxa confined to the closely related group 8. Widespread southeastern Australian taxa were also strongly represented (groups 10, 11 & 12). Tasmanian endemics associated with cool, damp sites were surprisingly sparse (group 3), given the proximity of quadrats to the river's edge.

Quadrats containing *S. microphyllum* were significantly higher in group 1 taxa (narrow endemics) and endemic group 7 taxa. Group 9 taxa (eastern Australia) also occurred in significantly higher proportion in quadrats with *S. microphyllum*, thus suggesting an association with disjunct species and species confined to cool sites along the Great Divide. However, there was very little data for groups 7 & 9. Widespread taxa (groups 11 & 14) were affiliated with quadrats where *S. microphyllum* was absent, as were group 8 taxa which are common in heathy forests and coastal woodland mainly throughout Victoria and lowland grassy forests in Tasmania; and with group 3 taxa which were widespread Tasmanian endemics (Table 6.3).

PHYTOCHORION	S.MICRO?	n	Mean	SD	T	DF	P
GROUP 1	1	23	1.17	0.4	1.90	38	0.06
	0	17	1.71	0.8			
GROUP 2	1	23	2.70	1.0	-3.00	38	0.005
	0	17	1.77	1.3			
GROUP 3	1	23	0.17	0.4	5.50	38	0.00
	0	17	1.06	0.8			
GROUP 4	1	23	0.10	0.3	0.31	38	0.76
	0	17	0.12	0.3			
GROUP 6	1	23	2.10	2.1	5.10	38	0.00
	0	17	6.00	1.8			
GROUP 7	1	23	0.00	0.0	ID	38	ID
	0	17	0.10	0.2			
GROUP 8	1	23	2.04	1.4	-0.63	38	0.53
	0	17	2.10	1.6			
GROUP 9	1	23	2.70	1.1	-3.12	38	0.003
	0	17	1.60	1.3			
GROUP 10	1	23	3.00	1.8	0.50	38	0.63
	0	17	3.10	1.4			
GROUP 11	1	23	0.61	0.7	-2.17	38	0.04
	0	17	0.18	0.4			
GROUP 12	1	23	4.61	2.1	-0.24	38	0.81
	0	17	4.53	1.9			
GROUP 13	1	23	0.35	0.5	-2.24	38	0.03
	0	17	0.10	0.2			
GROUP 14	1	23	1.40	1.5	-2.00	38	0.05
	0	17	0.60	0.62			

Table 6.2. Thumbs. Comparisons between the chorological composition of quadrats with and without *S. microphyllum* using Student's t-test between arcsin transformed pairs. Means are back transformed to percentages.



PHYTOCHORION	S.MICRO?	n	Mean	SD	T	DF	P
GROUP 1	1	22	2.40	1.1	-3.00	36	0.005
	0	16	1.40	0.9			
GROUP 2	1	22	1.40	1.0	-1.10	36	0.30
	0	16	1.14	1.0			
GROUP 3	1	22	0.13	0.3	1.84	36	0.07
	0	16	0.50	0.6			
GROUP 4	1	22	0.20	0.4	-0.04	36	1.00
	0	16	0.18	0.4			
GROUP 5	1	22	0.31	0.6	-0.02	36	1.00
	0	16	0.27	0.5			
GROUP 6	1	22	2.50	1.5	0.18	36	0.86
	0	16	2.60	1.4			
GROUP 7	1	22	0.31	0.5	-2.33	36	0.03
	0	16	0.05	0.2			
GROUP 8	1	22	1.63	0.7	2.00	36	0.07
	0	16	2.50	1.2			
GROUP 9	1	22	0.63	0.6	-2.80	36	0.009
	0	16	0.27	0.6			
GROUP 10	1	22	1.44	1.0	0.56	36	0.58
	0	16	1.50	0.9			
GROUP 11	1	22	0.31	4.9	3.54	36	0.001
	0	16	1.36	1.1			
GROUP 12	1	22	0.60	1.6	1.14	36	0.30
	0	16	5.90	2.4			
GROUP 13	1	22	0.25	0.5	-0.16	36	0.88
	0	16	0.23	0.4			
GROUP 14	1	22	2.81	1.5	2.60	36	0.02
	0	16	4.10	1.7			

Table 6.3. Swan River. Comparisons between the chorological composition of quadrats with and without *S. microphyllum* using Student's t-test between arcsin transformed pairs. Means are back transformed to percentages.

## *Spyridium obcordatum*

### *Hawley site (groups 1 & 2)*

Vegetation was dominated by taxa widespread across all of southern Australia (group 1). Pan - continental taxa (group 8), coastal heath taxa (group 7) and taxa concentrated in heathy dry sclerophyll forest in Victoria and Tasmania (group 5) were also prominent. *Spyridium obcordatum* was the only narrow endemic present and there were insufficient data for statistical analyses between group 10 and other phytochoria.

Quadrats containing *S. obcordatum* contained significantly higher proportions of taxa belonging to groups 1 and 2, whose regional distributions are concentrated in lowland southern and southwestern Australia in heathy vegetation, mediterranean - type heaths and shrublands or grassy dry sclerophyll forest (Table 6.4). These groups are generally poorly represented in Tasmania and are mainly associated with rocky ground or coastal habitats. Quadrats where *S. obcordatum* was absent were significantly higher in Tasmanian endemics (group 9), or near endemics, both of which are widespread throughout the State in dry sclerophyll forest and in eastern Victoria and New South Wales (Table 6.4).

### *Asbestos Range site (groups 1, 4, 7, 9)*

Coastal heath species (group 7) were most strongly represented overall, followed by species associated with heathy or shrubby dry sclerophyll forests concentrated in Victoria and Tasmania on both fertile and sandy soils (group 5). The two group 10 taxa (narrow or near narrow endemics), *Spyridium obcordatum* and *Pomaderris oraria* ssp. *oraria*, always occurred together making statistical analysis impossible as only the latter remained when *S. obcordatum* was removed to fulfil methodological criteria. Taxa from other groups were more or less evenly distributed throughout quadrats, although greater diversity was associated with quadrats containing *S. obcordatum*.

Quadrats with *S. obcordatum* were significantly higher in groups 1, 4 and 9, which at this site consisted mainly of taxa associated with coastal woodland or grassy forest on fertile soils (Table 6.5). The association between *S. obcordatum* and group 9 contrasts with the results from Hawley. However, the species vary substantially between the two sites. At Asbestos Range species are associated with heathland, or heathy or grassy woodland, whereas at Hawley they comprised shrubby forest species. *Allocasuarina monilifera* has very strong Bassian connections, being endemic to northern and eastern Tasmania including the Bass Strait Islands (Wilson & Johnson 1989). *Lasiopetalum baueri*, the sole representative of group 2 at this site, occurred exclusively with *S. obcordatum*. Quadrats without *S. obcordatum* were higher in taxa associated with coastal heath or coastal woodland and dry coastal vegetation throughout southern, southeastern and southwestern Australia on acid, sandy infertile soils (group 7).

PHYTOCHORION	S.OBCORD?	n	Mean	SD	T	DF	P
GROUP 1	1	7	9.00	1.6	2.23	19	0.04
	0	13	5.10	3.1			
GROUP 2	1	7	3.60	0.5	2.63	19	0.02
	0	13	1.54	1.6			
GROUP 3	1	7	2.00	0.6	-0.08	19	0.94
	0	13	2.70	1.3			
GROUP 4	1	7	3.00	0.8	0.90	19	0.40
	0	13	3.20	1.2			
GROUP 5	1	7	2.43	1.7	-1.10	19	0.30
	0	13	3.50	1.7			
GROUP 6	1	7	1.14	1.2	-1.61	19	0.12
	0	13	2.10	1.4			
GROUP 7	1	7	1.30	1.0	-0.62	19	0.54
	0	13	2.20	1.5			
GROUP 8	1	7	2.90	1.8	0.72	19	0.58
	0	13	1.62	1.1			
GROUP 9	1	7	0.60	0.5	-1.60	19	0.13
	0	13	1.92	1.5			
GROUP 10	1	7	0.00	0.0	ID	19	ID
	0	13	0.00	0.0			

Table 6.4. Hawley. Comparisons between the chorological composition of quadrats with and without *S. obcordatum* using Student's t-test between arcsin transformed pairs. Means are back transformed to percentages.

PHYTOCHORION	S.OBCORD?	n	Mean	SD	T	DF	P
GROUP 1	1	15	4.2	1.5	2.84	24	0.009
	0	11	2.46	1.2			
GROUP 2	1	15	2.00	0.0	ID	24	ID
	0	11	0.00	0.0			
GROUP 3	1	15	1.10	1.5	0.19	24	0.90
	0	11	1.00	1.6			
GROUP 4	1	15	7.80	1.2	8.90	24	0.00
	0	11	3.46	1.0			
GROUP 5	1	15	3.50	1.9	0.39	24	0.70
	0	11	3.30	1.4			
GROUP 6	1	15	3.40	1.6	-1.24	24	0.23
	0	11	4.30	1.5			
GROUP 7	1	15	6.90	1.7	-3.90	24	0.001
	0	11	10.00	2.7			
GROUP 8	1	15	0.27	0.7	ID	24	ID
	0	11	0.00	0.0			
GROUP 9	1	15	3.10	1.4	2.64	24	0.01
	0	11	1.64	1.1			
GROUP 10	1	15	0.30	0.7	ID	24	ID
	0	11	0.00	0.0			

Table 6.5. Asbestos Range. Comparisons between the chorological composition of quadrats with and without *S. obcordatum* using Student's t-test between arcsin transformed pairs. Means are back transformed to percentages.

*Dans Hill 1 site, ultramafics only (group 1)*

Chorological groups containing flora which are either widespread throughout southeastern Australia and restricted regionally, were best represented at this site (groups 4, 5 & 6). Pan - continental taxa were also prevalent (group 8).

*Spyridium obcordatum* and the other regional endemic, *Epacris virgata* always occurred together, but there were too little data for statistical testing.

There was a significantly higher proportion of group 1 species where *S. obcordatum* was absent (Table 6.6), which contrasts with the results from Hawley and Asbestos Range.

*Dans Hill 2 site, quartzite and ultramafics (groups 4, 7, 9)*

Species distributed throughout southern and southwestern Australia (group 2) were absent from this site, otherwise groups were more or less evenly distributed throughout quadrats, with the exception of the two narrow endemics (*S. obcordatum* and *Epacris virgata*), which always occurred together.

Widespread heathy taxa (group 7) were associated with quadrats where *S. obcordatum* was present (Table 6.7). However, species from this group are suited to a wide range of vegetation types. Groups 4 and 9 also occurred in significantly higher proportions in quadrats where *S. obcordatum* was present (Table 6.7). Group 4 consisted of taxa widespread in southeastern Australia which are common in a number of dry sclerophyll vegetation associations. Group 9 contained widespread Tasmanian endemics. Group 10 contained only *E. virgata* when *S. obcordatum* was excluded. However, the two nearly always occurred together.

## Discussion

### *Biogeographic patterns at Spyridium sites*

#### *Spyridium microphyllum*

At the Douglas - Apsley site, *Spyridium microphyllum* and other narrow endemics were associated with higher proportions of species closely associated with elevated areas of the eastern Great Dividing Range and with taxa with disjunct distributions in southeastern Australia (chorological groups 5 and 9). In addition to *S. microphyllum*, this site harbours a number of narrow endemics and endemics confined to eastern Tasmania. The most widespread groups (2 and 14) consisted mainly of taxa from dry and often rocky environments.

PHYTOCHORION	S.OBCORD?	n	Mean	SD	T	DF	P
GROUP 1	1	11	2.91	1.0	-4.2	16	0.001
	0	7	6.00	2.0			
GROUP 2	1	11	0.00	0.0	ID	16	ID
	0	7	0.30	0.8			
GROUP 3	1	11	3.50	2.6	-0.6	16	0.56
	0	7	3.60	1.8			
GROUP 4	1	11	7.00	1.7	-0.47	16	0.64
	0	7	7.43	2.6			
GROUP 5	1	11	4.30	2.2	-0.98	16	0.34
	0	7	5.71	2.4			
GROUP 6	1	11	7.60	2.3	-0.54	16	0.60
	0	7	8.14	1.6			
GROUP 7	1	11	3.20	1.6	0.33	16	0.75
	0	7	3.14	1.1			
GROUP 8	1	11	5.64	2.9	1.10	16	0.30
	0	7	3.90	1.7			
GROUP 9	1	11	1.82	1.4	-1.73	16	0.10
	0	7	2.9	1.1			
GROUP 10	1	11	1.64	0.8	ID	16	ID
	0	7	0.00	0.0			

Table 6.6. Dans Hill 1. Comparisons between the chorological composition of quadrats with and without *S. obcordatum* using Student's t-test between arcsin transformed pairs. Means are back transformed to percentages.

PHYTOCHORION	S.OBCORD?	n	Mean	SD	T	DF	P
GROUP 1	1	14	2.30	1.3	1.90	18	0.08
	0	6	3.80	1.8			
GROUP 2	1	14	0.00	0.0	ID	18	ID
	0	6	0.00	0.0			
GROUP 3	1	14	2.90	1.3	1.90	18	0.07
	0	6	4.00	1.3			
GROUP 4	1	14	7.40	1.2	-4.44	18	0.00
	0	6	4.50	1.8			
GROUP 5	1	14	3.80	2.6	1.48	18	0.20
	0	6	5.20	1.3			
GROUP 6	1	14	5.40	1.8	-1.40	18	0.20
	0	6	4.30	1.5			
GROUP 7	1	14	5.64	1.8	-3.03	18	0.007
	0	6	3.30	1.0			
GROUP 8	1	14	4.20	2.5	0.08	18	0.94
	0	6	5.20	1.8			
GROUP 9	1	14	7.40	1.1	-5.50	18	0.00
	0	6	4.20	1.6			
GROUP 10	1	14	1.70	0.7	ID	18	ID
	0	6	0.00	0.0			

Table 6.7. Dans Hill 2. Comparisons between the chorological composition of quadrats with and without *S. obcordatum* using Student's t-test between arcsin transformed pairs. Means are back transformed to percentages.

Widespread Tasmanian endemics were completely absent from the Douglas - Apsley. However, dry sclerophyll forest dominated by the common eastern Tasmanian endemic *Eucalyptus amygdalina* occurs nearby on the other side of the ridge. This forest has a northeasterly aspect, implying ample light levels for open shrubland. It has a multi layered understorey of tall shrubs and a rocky ground layer with a number of widespread endemics and non - endemics. Typical species are *Allocasuarina littoralis*, *Leptospermum grandiflorum*, *Callitris rhomboidea*, *Banksia marginata*, *Cyathodes divaricata*, *Lomatia tinctoria*, *Lomandra longifolia* and *Hibbertia riparia*. It is likely that both the tall shrub and low open shrubland are restricted to areas where exposed bedrock and shallow soils replace dolerite boulder fields.

*Spyridium microphyllum* was not exclusively associated with other narrow endemics at the Thumbs. It occurred with Tasmanian endemics confined to central and eastern regions, taxa strongly associated with the Great Dividing Range in eastern Australia and taxa associated with mediterranean - type regions. The Thumbs is disjunct from the other two *S. microphyllum* sites, although broadly similar grassy forest dominated by *Eucalyptus pulchella* occurs at, or in close proximity to all three. There are other narrow endemics which are associated with grassy forest in the region which were absent at the study site (for example *Olearia lanceolata*, *Cyphanthera tasmanica*, *Odixia angusta*). Narrow endemics at this site, other than *S. microphyllum* and *Ozothamnus lycopodioides*, are components of forest and are likely to have different ecological and biogeographical affinities than narrow endemics concentrated in shrubland in the Douglas - Apsley and Swan River areas. *Spyridium microphyllum* was not associated with forest taxa and may be refugial at this site.

Vegetation containing *S. microphyllum* at the Swan River include taxa which are a mixture of both narrow endemics and endemics with a restricted range in Tasmania. Taxa which are narrowly concentrated in cooler regions in southern Australia and closely associated with the Great Dividing Range, or taxa with disjunct distributions, also occurred with *S. microphyllum* at this site. Quadrats from which *S. microphyllum* was absent were made up predominantly of widespread Tasmanian endemics or taxa widespread throughout southern and southeastern Australia.

The results are consistent between the two central east coast sites, but differ from the Thumbs to the southeast. This is compatible with current perceptions of past environmental conditions and biogeographic history of the region. Southeastern Tasmania is thought to have been a major refugium for eucalypts during Pleistocene glacials (Ladiges *et al.* 1983; Kirkpatrick & Brown 1984b; Potts & Jackson 1986). The considerable topographic diversity of the Thumbs and surrounding area, and the equally diverse complement of vegetation and flora which comprises a mosaic of rainforest, wet and dry sclerophyll forest and shrubland in varying proportions supports this notion (Coates 1993). At present, there is a high number of dry sclerophyll vegetation associations, some of which include taxa well outside their centres of abundance in alpine and sub - alpine areas (Coates 1993). Narrow endemics in the Asteraceae and Epacridaceae are



significantly represented or even dominant in the understoreys of these communities, and have no contemporary analogue outside the immediate region (Coates 1993). This is a likely consequence of isolation and subsequent speciation in a geographically confined space.

The *S. microphyllum* site at the Thumbs was well above the treeline during the arid late Last Glacial Maximum and is likely to have supported drought tolerant taxa which were not refugial at that time but were excluded from more mesic sites by eucalypt dominated vegetation.

The high concentration of narrow endemics in the drier central east coast has been attributed to present day precipitation levels approximating those at the height of the late Last Glacial Maximum in eastern Tasmania (Kirkpatrick & Brown 1984a). These have allowed the perpetuation of flora which comprised the dominant vegetation type at that time. Consequently, concentrations of narrow endemics in the area are thought to signify an interglacial refugium (Kirkpatrick & Brown 1984a). If this were true, co - occurring disjunct taxa concentrated elsewhere in semi - arid or dry, cool and rocky environments are also likely to be refugial in this area by virtue of having similar physiological requirements.

#### *Spyridium obcordatum*

At Hawley, shallow, rocky soils and structurally open vegetation containing *S. obcordatum* support drought tolerant taxa, including ephemeral herbs and shrubs belonging to predominantly southern to southwestern Australian mainland phytochoria (groups 1 and 2). Widespread Tasmanian endemic species are excluded from these sites, as are taxa associated with forests elsewhere in southern and eastern Australia. This suggests that species patterning at this site is determined by site specific factors which enable taxa to survive at the edge of their range.

At Asbestos Range, biogeographic and floristic patterns also suggest that the site provides refuge for restricted taxa. *Spyridium obcordatum* has a strong relationship with some widespread Tasmanian endemics, taxa restricted to regions of southeastern mainland Australia and disjunct taxa. Group 7 species are probably excluded by soil pH at this site, which probably reflects the general affiliation of this widely ranging group with heathland elsewhere in southern, southwestern and eastern Australia.

Results from Dans Hill 1 conflicted with those from Hawley and Asbestos Range. *Spyridium obcordatum* co - occurred with another narrow endemic (*Epacris virgata*), indicating that similar environmental controls may determine the distribution of the two narrow endemics. However, taxa concentrated in southern and southwestern Australia were associated with quadrats where *S. obcordatum* was absent. It is likely that the biogeographic composition of the flora at this site is complicated by a history of soil disturbance, the removal of bedrock and vegetation cover. It seems as though the ongoing occupation of narrow endemics at the site is dependent on disturbance. In the absence of disturbance, it is likely

that *S. obcordatum* would be confined to areas currently occupied by widespread taxa. The disruption of biogeographic patterns has often been observed in Australia, with the most obvious example being the invasion of exotic taxa as a result of soil or canopy disturbance, grazing or nutrient enrichment creating open conditions within indigenous vegetation (Hobbs & Hopkins 1990). It is suggested that in this case, conditions created as a result of disturbance may allow taxa at the edge of their range to survive by creating open conditions suitable for seedling establishment.

At Dans Hill 2, *S. obcordatum* is associated with a biogeographically diverse range of taxa including those widely distributed throughout southeastern and southern Australia, as well as with widespread Tasmanian endemics. However, there is a stronger link with the eastern Australian flora and a weaker relationship with the southwestern Australian flora than was observed at Hawley or Asbestos Range. The results suggest that soil disturbance has also strongly influenced biogeographic patterns at this site, by creating deeper soils having higher moisture levels than would previously have existed.

The differences between the biogeographic composition of the vegetation at Hawley and Asbestos Range and that of Dans Hill suggest differing site histories. The former two sites suggest there are stronger connections with southern and southwestern mainland Australian flora. The closer proximity of these two sites to the present coastline and the presence of rare non - endemic taxa, indicate that they may contain relictual elements of a Bassian Plain flora. However, the forested sites at Dans Hill may have a similar history to the Thumbs site. It is part of the steeply dissected Dazzler and Asbestos Ranges, which also harbour relict rainforest, wet forest and an array of unusual dry sclerophyll communities (Duncan & Brown 1985; Williams 1989; Neyland 1992). This may also have been a refugial site where forest vegetation retreated from cold arid conditions resulting from increased continentality with the drying of Bass Strait during the late Pleistocene. Open, rocky sites at Dans Hill, as well as the numerous dolerite knolls within the West Tamar region, may have supported low open vegetation, including *S. obcordatum* and associated flora, more or less continuously linked to the edge of the Bassian Plain, but excluded from more mesic areas. These are now relictual but have been favoured by soil disturbance at Dans Hill.

### *Origins and patterns of floristic invasions*

The phytochorological analysis identified some biogeographic patterns which might explain the current distribution of flora at *S. microphyllum* and *S. obcordatum* sites. These patterns support widely held perceptions of past vegetation migrations. Similar patterns were also revealed by Bridgewater's (1976) analysis of part of the Victorian flora.

The continental distributions of phytochorological groups suggests two major migratory pathways across the Bassian Plain during times of lowered sea levels throughout the Quaternary. Migrations in the southeastern Australian region are thought to have been facilitated during the late Last Glacial Maximum, when sea

levels fell by up to 200 metres, exposing the Bassian Plain (Nelson 1981, Tyler 1985).

The Great Dividing Range has clearly provided an important migratory pathway throughout eastern and southeastern Australia (Burbidge 1960; Barlow 1981). Similarly, an exchange of floras almost certainly took place between Tasmania and the east coast of the continent, via the eastern Bass Strait Islands, as might be expected (Burbidge 1960; Bridgewater 1976; Barlow 1981).

However, conditions at this time, which saw the formation of longitudinal dune systems between northeast Tasmania and Kangaroo Island (Bowler 1978; 1982; Sprigg 1979; Bowden 1983), suggest the Bassian Plain represented a barrier to migration, rather than providing a pathway for movement simply because there was the exposure of a new land surface. The possible expansion and migration of flora over these glacial deserts during the late Last Glacial between Tasmania and regions to the north west, such as the Lofty Ranges and Kangaroo Island in South Australia is problematic. If there was any migration it is more feasible that plants would migrate toward warmer conditions, unless rainfall exerted a primary control over direction of movement.

Burning by Aboriginal people may also have aided species migrations. Geomorphic processes including erosion or aeolian activity might have opened up new habitats for colonisation of species previously unknown to the region. However, it is unlikely that taxa would be able to migrate readily through established vegetation communities at the height of the Last Glacial, in the absence of disturbance or the creation of habitat by some other means. Continuous disruption to plant communities by abiotic forces is expressed in the migration and establishment of individual taxa which respond differently to change, unlike communities, which do not respond as units (Davis 1986). However, there is much evidence for broadscale phytosociological change as a result of disturbance by people, usually associated with agricultural activities (Stuwe & Parsons 1977; Williams & Ashton 1983; Hobbs & Hopkins 1990).

The ability of species to overcome ecological and geographic barriers to dispersal may have been affected during earlier periods of low sea level at approximately 37,000 BP or even earlier at 55,000 BP. If either of these earlier periods also facilitated the arrival of people in Tasmania, new habitats are almost certainly to have been created through increased burning.

Warm sea currents which extended to southeastern Australia allowed the survival of rainforest in eastern Tasmania and Victoria throughout the Last Glacial maximum (Burbidge 1960; Thomas & Kirkpatrick 1995). The exchange of flora along the east coast of Australia is most likely to have persisted under these conditions (Burbidge 1960; Thomas 1992; Thomas & Kirkpatrick 1995), in spite of greatly increased aridity in rainshadow areas to the west and on the Bassian Plain (Bowden 1983; Bowler 1982). Alternatively, migrations may have occurred at the beginning of the Holocene when increasing temperatures and precipitation allowed taxa to migrate from glacial refugia in eastern Victoria, prior to the flooding of Bass Strait (Cullen 1992).

A second pathway between Tasmania and areas to the northwest, via the Flinders and Lofty Ranges, Kangaroo Island and King Island may have facilitated further exchanges (Bridgewater 1976). Both pathways indicate that the vegetation must have been well enough suited to the prevailing late Pleistocene climate in order to allow processes of reproduction and dispersal. Conversely, these distributions date to the long distant past or have resulted from long distance dispersal.

## CHAPTER 7

### ECOLOGICAL AND BIOGEOGRAPHICAL CORRELATES OF RARITY IN *SPYRIDIMUM MICROPHYLLUM* AND *SPYRIDIMUM OBCORDATUM*

#### Introduction

This chapter synthesises the evidence presented in the previous chapters. It assesses the ecological and biogeographical data in the preceding chapters and seeks to determine which approach best explains rarity in *S. microphyllum* and *S. obcordatum*.

#### Ecological causes of rarity

##### *Herbivory and phenology*

*Spyridium microphyllum* is an obligate seed regenerator which is not significantly affected by herbivory but which has phenological attributes that may render populations vulnerable to depletion.

Delayed fruit development exposes the annual seed output of populations to environmental threats throughout the year. This characteristic prevails in other *Spyridium* taxa, as well as in *Cryptandra* and *Stenanthemum*. For example, *Spyridium eriocephalum* and *S. vexilliferum* are both widespread in southeastern Australia and are well known from fire prone sclerophyllous environments such as heath, shrubland and woodland and are obligate seed regenerators. The distributions of both taxa include disjunct populations, suggesting local extinctions could have occurred within formerly continuous ranges. For example, the only known Tasmanian population of *S. eriocephalum* has been significantly reduced by fire. It presently consists of a few young plants, the majority of which have not reached reproductive maturity. Regeneration has occurred in the past. The seed bank may be dangerously close to depletion because plants have been repeatedly burnt within the last 20 years, therefore destroying developing seed as well as immature plants.

There is no evidence at present that extant *S. microphyllum* populations have experienced high levels of fire frequency. Unsuccessful searches for one population along the Apsley River at a site which had been recently burnt and which may have been frequently burnt in the past, suggests that fire has eliminated *S. microphyllum* in this area. *Spyridium microphyllum* does not attain reproductive maturity for at least three years. If a fire occurs at virtually any time in the first year after flowering, it will be at least another four years until the seed bank is replenished. Even then, seed production in young plants which have few branches is much lower than in more mature individuals.

Conversely, delayed fruit development may be advantageous. In fynbos vegetation in South Africa, seed maturation that is delayed until summer allows a plant a

longer time to seize nutrients in environments where moisture is available during the summer months (Keeley 1992b). *Spyridium microphyllum* populations occupy the driest of any Tasmanian *Spyridium* sites, although they receive rain in every month of the year. Delayed fruit maturation may allow plants to allocate nutrients over a longer period of time so that the development of photosynthetic organs is maximised. Shoot elongation occurs from September to April, but new leaves are produced throughout the year. Vegetative growth during more than one season has been observed elsewhere where there is sufficient available moisture and relatively high winter temperatures (Le Roux *et al.* 1989; Orshan *et al.* 1989). Conservative use of resources also enables plants to avoid competition by virtue of slow growth (Grime 1979) and is an adaptation to conditions where resources may be limiting, such as on shallow, rocky soils. Therefore, the phenological attributes of *S. microphyllum* may have ecological implications.

Summer flowering may also advantage *S. microphyllum* over co - existing species, the majority of which flower in spring, and are thus under more pressure to compete for pollinators. *Spyridium microphyllum* is advantaged by possessing conspicuous floral leaves which are likely to act as strong attractors to pollinators. Summer seed release, when ant activity is maximised (Hughes & Westoby 1990) may also advantage *S. microphyllum* and facilitate rapid storage of seed in the soil.

Thus, phenological characteristics are unlikely to explain rarity in *S. microphyllum*. However, populations may have been reduced by past and present European land management practices.

*Spyridium obcordatum* is a likely post - fire resprouting species which is vulnerable to predation by herbivores. It will resprout after mechanical damage. There is no direct evidence that *S. obcordatum* can resprout following fire, as no sites were burnt during the time the project was undertaken. Experimental burning of a rare species was decided against for ethical and methodological reasons. Inspection of plants at Dans Hill which were known to have been burnt a few years previously, indicated that they had resprouted. Furthermore, the area has experienced multiple fires in close succession in the past few decades (G. Stewart, Forestry Tasmania, pers. comm.), yet *S. obcordatum* is still abundant at this site.

Herbivory significantly affected *S. obcordatum* growth in summer. Recovery occurred during the following spring and development of reproductive organs was not significantly reduced at Dans Hill. Seed was collected at Dans Hill and Hawley but was scarce at Asbestos Range where plants had been heavily grazed. This suggested that concentrations of native animals confined to a fenced national park surrounded by farmland was more likely to affect *S. obcordatum* populations than introduced herbivores of a comparable size. The vegetation at Asbestos Range was coastal heathland containing few grasses or other herbaceous taxa, whereas these were well represented in the understorey at both Dans Hill and Hawley. The ground layer of undisturbed vegetation at Greens Beach was also grassy. Consequently, associated species may influence the degree to which *S. obcordatum* experiences grazing damage. Native animals have been observed to affect seed production in one other rare endemic Rhamnaceae species, *Stenanthemum*

*pimeleoides*, where it occurs in a national park dominated by sclerophyllous vegetation in eastern Tasmania (pers. obs.).

The present grazing regime is an indirect consequence of land clearance and is unlikely to signify a cause of rarity in *S. obcordatum*, although it may partially contribute to the current scarcity of populations. Ironically, the single reserved *S. obcordatum* population at Asbestos Range may be threatened under current management practices. Herbarium records indicate that there was only one *S. obcordatum* population (at West Head) which was not re - located during the project. This site consists of coastal shrubland and open *Allocasuarina* woodland also in the Asbestos Range National Park. The ground layer is open and rocky, consisting mainly of prostrate woody species. The possibility exists that *S. obcordatum* has been eliminated from this site by grazing, probably combined with a fire protection policy that has not enabled regeneration of the population from soil stored seed. However, even in the absence of adult plants, the population still may exist as soil stored seed and if so, might reappear given the appropriate fire regime. Alternatively, *S. obcordatum* was not detected at this site. Suitable habitat exists and it is possible that any surviving populations were overlooked.

Life history events in *S. obcordatum* are comparable to both restricted and widespread taxa in the Rhamnaceae, and to a high number of taxa widespread in Tasmania. *Spyridium obcordatum* lacks conspicuous floral leaves but successfully competes for pollinators, producing abundant seed where not affected by herbivory. Thus, phenological attributes of *S. obcordatum* are highly unlikely to explain rarity.

Timing of seed maturation and floral morphology suggest the two species evolved under different climate regimes. However, neither phenological pattern is confined to Tasmanian taxa. These patterns may indirectly provide evidence for rarity as a consequence of biogeographic history.

Seasonal patterns of growth and reproductive activity are generally considered to be adaptations to the availability of resources, in particular moisture availability (Mooney & Kummerow 1981). Specht & Rayson (1957) and Specht (1981) maintain that shoot growth during summer in semi - arid mallee vegetation is a result of moisture made available by occasional summer rainfall, as well as moisture conserved in the soil from winter and spring falls. This is in contrast to a typical mediterranean - type pattern of spring growth. If this were true, life history traits observed in *S. microphyllum* suggest its origins may lie with a different section of the biota to *S. obcordatum*. *Spyridium microphyllum* sites, which experience a more aseasonal precipitation pattern and are relatively warm year round, may experience environmental conditions which signify refugia. *Spyridium obcordatum* showed life history traits typical of many widespread taxa, suggesting it may be better adapted to a more seasonal climate. Thus, phenological characteristics of the two species may provide a basis for the hypothesis that *S. microphyllum* is relictual, whereas *S. obcordatum* is more recently diverged but has been unable to become widespread.

### *Germination and seed bank ecology*

The results of germination trials and observations made during the phytosociological survey supported the hypothesis that *S. microphyllum* and *S. obcordatum* will regenerate by seed following fire and are unlikely to be rare because of poor seed viability or lack of stimulus for germination. Inappropriate levels of stimuli will prevent germination of *S. obcordatum* seed from Hawley and to a lesser extent, *S. microphyllum* seed from the Swan River, relative to other populations. Temperature and time combinations which stimulated germination were within the ranges recorded for taxa elsewhere. There was little evidence in support of the hypothesis that narrow endemics necessarily have a narrow germination niche relative to more widespread congeners or related taxa, although the Hawley population had significantly less germination success. Germination of seed from the Hawley population was also affected by incubation temperature, as were some more widespread Tasmanian *Spyridium* species. However, other populations of the two narrow endemics were unaffected.

Germination response to heating trials differed between populations of the same species from different sites, suggesting genecological variation within each species, possibly because of long periods of isolation in varying environments having different fire histories. Repeated trials over a number of seasons are needed to examine this possibility. Differences in response to stimuli are unlikely to be a consequence of low genetic diversity resulting from small population size, because both narrow and wide germination responses were apparent in populations having the least individuals. Conversely, one of the largest and most extensive populations had much less germination success than the smallest and least extensive.

Highest germination of *S. microphyllum* seed was recorded for a forested site (Thumbs), followed by open shrubland situated on a ridgetop (Douglas - Apsley). The overall low litter levels associated with these populations affords a degree of fire protection relative to surrounding vegetation and may not burn as frequently. However, fire has been influential in the maintenance of low open shrubland at the Douglas - Apsley site.

The Swan River population had the least germination success overall. Fires tend to be relatively uncommon in riparian vegetation in Tasmania and it is known to harbour rare Tasmanian endemics and non - endemics, some of which may be fire sensitive (Askey - Doran 1993). This population extends intermittently along the river for a number of kilometres. Soil disturbance caused by periodic flooding of both the Swan and St Pauls Rivers may be more effective than fire in stimulating regeneration at these sites, as well as providing open, light conditions for seedling growth. The relationship between disturbance and regeneration in the maintenance of species and ecosystems is widely recognised (Grubb 1977; Keeley 1987; Grime 1989; Keddy *et al.* 1989; Chesson 1986; Chambers *et al.* 1990). In environments where perturbations are unpredictable and intermittent, a species is likely to be successful if it has developed a life history strategy which overcomes environmental variability (Ellner 1987). Fires have been deliberately lit in the



recent past and probably throughout the last 180 years since European occupation of the area.

No seed was available from the Asbestos Range site, so comparisons between populations were limited in the case of *S. obcordatum*. However at Hawley, the most isolated population having fewest plants, and a strong association with shallow soils and exposed bedrock, seeds responded to a more narrow range of heat treatments than the Dans Hill population, situated in open forest.

The ability of *S. microphyllum* (all populations) and *S. obcordatum* (Dans Hill) to germinate under a range of incubation temperatures may partially explain rarity in the two species because seedlings are more vulnerable to desiccation due to unpredictable moisture availability.

Seedling mortality within gaps created after disturbance may allow invasion by more widespread taxa. The phytosociological and phytochorological analyses suggested that except at Dans Hill, these are mainly likely to be Tasmanian endemics with restricted distributions or taxa with relictual or disjunct distributions confined to shallow soils. It was not determined whether these have the appropriate colonising abilities to fit this role. At Dans Hill, soils are deeper and drought stress is less likely to occur. Similar environmental conditions to Hawley and Greens Beach are likely to have prevailed prior to disturbance of the site by mining. Depletion of the population may only be temporary, until further disturbance stimulates establishment of another generation. This is an unconvincing explanation for rarity unless this pattern was repeated until the soil seed bank was depleted, or in the case of *S. obcordatum*, until plants were killed. Furthermore, the putative strategy of avoidance of drought stress was not supported by results using seed of *Pomaderris* species. These are particularly common in Tasmania, despite being obligate seeders which showed high germination percentages at the higher incubation temperature.

Loss of soil stored seed may be a cause of rarity in the two species. Seed burial experiments showed that the soil seed bank of both species was likely to be depleted by predation by micro - organisms or by decay, possibly as a result of fungal activity. The amount of *S. microphyllum* seed lost from the soil through attrition or predation is within the ranges reported in other studies, whereas loss of *S. obcordatum* seed is comparatively low (Hodgkinson *et al.* 1980; Auld 1983; Crist & Friese 1993). Predation by vertebrates or macro - invertebrates was not tested during the project and may further deplete the soil seed bank of both species. It offers an unlikely explanation for rarity in either species because all populations except *S. obcordatum* at Asbestos Range produce abundant seed each year, thus facilitating annual restocking of the seed bank. Again, *S. microphyllum* is likely to be more at risk if fire free intervals are less than four years apart and the soil seed bank is depleted, provided fires are hot enough to stimulate germination. Poor dispersal ability and the death of individuals after fire means that *S. microphyllum* populations would be unlikely to re - establish in the absence of a nearby seed source. Although it is a relatively long lived shrub (at least up to 45 years and still reproductively active) and able to regenerate at a low level without a specific germination cue, the stimulation of germination by heat may be a crucial

factor in producing large numbers of seedlings. This level of regeneration is likely to sustain a population over time by allowing large scale seedling recruitment, which offsets partial losses resulting from frequent fires. Eventually the process results in the accumulation of soil stored seed. Large seed banks are also an investment against possible adverse conditions, such as a number of fires within a short space of time.

Other studies have shown that soil stored seeds are concentrated in the upper 5 cm of the soil, but are also incorporated deeper into the soil profile (Hodgkinson *et al.* 1980; Auld 1986a). The spatial distribution of seeds in the soil indicates that a single rare event such as two fires in close succession is unlikely to eliminate a population. Seeds buried at critical depths below 1 -2 cm will not experience adequate heat stimulus for germination if temperatures are below 40°C - 60°C, but will be able to emerge following a hotter stimulus at a later time (Cavanagh 1980; Auld 1986b). Soil moisture content is particularly influential, with soils often failing to reach threshold temperatures during burns in cooler seasons (Hodgkinson 1991). In spite of some losses, the remaining seeds are likely to persist in the soil, and losses will be compensated for annually.

It is not known whether seeds are able to germinate after exposure to the heat of the sun. The absence of seedlings of *S. microphyllum* and *S. obcordatum* other than in areas which had received low intensity patch burns, and in fact the general absence of seedlings of associated flora at sites supporting the two species, suggests that favourable conditions for seedling establishment do not prevail. The most likely explanation is seeds germinating at or close to the soil surface in summer die as a result of drought stress, whereas those which have germinated below ground receive moisture stored in the soil.

Herbarium records suggest that both species were already rare at the time of European occupation. Aboriginal use of fire is unlikely to offer a feasible explanation for rarity. There is no evidence in the archaeological, ethnohistorical or palynological record to suggest that burning by Aboriginal people was so frequent as to explain rarity in the Tasmanian flora (Thomas 1992). However, the ongoing use of land management practices popular with Europeans throughout the nineteenth and twentieth centuries is likely to further endanger *S. microphyllum* and *S. obcordatum* populations.

#### *Phytosociological and environmental attributes of populations*

Numerous case studies of rare plants have shown that populations of the same rare species, including narrow endemics, frequently occur in habitats which differ in their topographic, edaphic and geological characteristics. *Spyridium microphyllum* and *S. obcordatum* are typical in this respect. *Spyridium microphyllum* and *S. obcordatum* populations occupy widely differing habitats and have varying phytosociological relationships. Similar habitats were relatively common within the ranges of both species. Consequently, neither was considered rare because of confinement to a rare habitat. Rarity in the two species appears to

be primarily related to confinement to ecologically narrow niches and the effects of competitive exclusion from more widespread taxa.

A postulated cause of narrow endemism is narrow ecological tolerance yet this is rarely substantiated in the literature, other than in the case of edaphic endemics (Kruckeberg & Rabinowitz 1985). However, the environmental correlates of *S. microphyllum* and *S. obcordatum* suggest that rarity might be explained by two ecological factors.

First, the light and temperature requirements of the two species may be poorly met in closed vegetation. Moisture levels are also likely to be higher in closed vegetation. The data suggested that *S. obcordatum* was able to establish large populations where moisture availability was not limiting, as well as on drier sites. *Spyridium microphyllum* occurs mainly in dry sites but is occasionally found on deeper or locally moist soils along the St Pauls and Swan River, providing these are well drained. Consequently it is likely that the two species are tolerators of droughty conditions rather than having a requirement for low soil moisture. Furthermore, limited moisture availability is likely to reduce net photosynthetic rates, observed in shallow rooted species in fynbos flora (van der Heyden 1988 in Stock *et al.* 1992). Therefore, relative competitive ability may be related to partitioning of subterranean resources.

First, the photosynthetic requirements of rare species have seldom been quantified and there is conflicting evidence in the literature that confinement to open vegetation is a result of a reduced ability to compete for light (Baskin & Baskin 1988; Baskauf & Eickmeier 1994). It is also unclear whether poor competitive ability is a cause or consequence of rarity, or whether a taxon is inherently a poor competitor, or a poor competitor only under a given climate regime. The phenological characteristics of both taxa suggest that *S. obcordatum* might successfully compete for pollinators and *S. microphyllum* might avoid competition, although this was not tested. Thus, although competition for resources related to photosynthesis is likely to exclude both species from more favourable and widespread sites, the two species may not be poor competitors in the overall sense. However, such traits have not been well demonstrated in Australian flora to date.

Second, the aggregated nature of *S. microphyllum* and *S. obcordatum* populations, also a feature of other rare or restricted Rhamnaceae in Tasmania (Coates 1991), suggests that favourable conditions for seedling establishment are spatially limited. This contrasts with populations of some common *Spyridium* species which are widely dispersed. For example, *S. subochreatum* var. *subochreatum*, found in mallee heath, is widespread but recorded in low numbers (D. Cheal, University of Melbourne, unpub. data). *Spyridium parvifolium* exhibits similar behaviour in Victoria, yet in northern Tasmania, where it is at the edge of its range and rare, populations are discrete (pers. obs.).

Safe sites (Harper *et al.* 1961) can include appropriate stimulus for regeneration, in this case disturbance. Disturbance provides the means by which dormancy is broken in seeds and provides appropriate conditions for seedling establishment and growth by creating an environment with high light levels. Sites have experienced

varying frequencies and intensities of disturbance, but fire has effected all populations at some time in the past. The locally unique nature of *S. microphyllum* and *S. obcordatum* habitat except the Douglas - Apsley implies that characteristics endemic to sites influence the outcome of disturbance in some cases. For example rocky or moist soils will modify the effects of fire.

*Spyridium microphyllum* populations at the Thumbs and Swan River sites were strongly associated with low litter cover. This would be removed as a result of disturbance, especially in the case of fire. Seedlings were observed in ash beds created by a patch burn at the Swan River. However, the quality and quantity of ash may effect seedling growth and development. Other than in the case of very hot fires, ash beds created by burning are much finer than in open forest, mainly owing to the absence of fallen branches. Litter levels also partially determine fire intensity and will consequently affect the heat flux through the soil profile and levels of post fire germination. Frequent floods at this site mean that bare ground will be created more frequently than in adjacent forested areas lying outside the flood zone.

*Spyridium obcordatum* showed a preference for clay rich non acidic soils at three sites which implies that soils supporting vegetation adjacent to *S. obcordatum* populations may be unsuitable for seedling establishment.

Environmental conditions for seedling establishment are undoubtedly different within the habitat of the two rare species compared to that of adjacent habitat. An unsuitable environment for seedling establishment may explain the apparent inability of *S. microphyllum* and *S. obcordatum* to become more widespread. The putative absence of safe sites in vegetation at present prompts consideration of vegetation dynamics and site histories. In other words, have phytosociological interactions contributed to the rarity of the two species in the long term, or are these factors only relevant since the most recent major changes in vegetation patterns in Tasmania? Consequently, this explanation seems closely linked with the broader theme of biogeographic history.

From the above discussion, it might be concluded that an phytosociological analysis of habitat and environmental correlates has limited explanatory power for causes of rarity. It is very difficult to determine whether the realised niches of the two rare species are the end result of rarity or whether they signify narrow ecological tolerances. There are numerous examples of species in habitats at the edge of their range which differ markedly from habitats where they are common. Yet, these are generally recognised as having inferior competitive abilities only when remote from optimal conditions. Examples include *Beyeria viscosa*, widespread and common in wet forest and rainforest in Tasmania but rare in New South Wales where it is confined to exposed environments having shallow, rocky soils (Keith & Ashby 1992; Harden 1990). *Psoralea adscendens*, a rare legume, is confined to three exposed coastal sites in northwestern Tasmania but found in wet forest in eastern Victoria (Lynch 1993). Thus, the environmental relationships of rare species might be a consequence, rather than a cause of rarity. A distinction needs to be made between the proximate and ultimate causes of rarity (Fiedler & Ahouse 1992). A more feasible explanation may be that the two rare species are at

the edge of their climatic range. Climate change rather than geographic isolation, and therefore temporal, rather than spatial remoteness from optimal conditions may explain the apparent inability of *S. microphyllum* and *S. obcordatum* to successfully compete with widespread taxa, or to extend populations beyond the limits of their realised niche at present.

### Biogeographical causes of rarity

#### *Are S. microphyllum and S. obcordatum occupying interglacial refugia?*

If *S. microphyllum* and *S. obcordatum* are refugial species today, then it can be argued that the vegetation in which they occur is likely to be relictual. To fit this hypothesis, the two rare species must be associated with aggregates of species with similarly restricted ranges (Hulthen, 1937; Daubenmire 1975; Kirkpatrick & Brown 1984a & b; Kirkpatrick 1986c), to rule out the possibility of long distance dispersal to suitable habitats (Macphail & Moscal 1981).

It is not possible to directly test the refugia hypothesis. Pollen and geomorphological evidence suggests that during the last glacial, when temperatures were 4°C - 6°C lower than at present (Macphail 1975; Goede *et al.* 1990), alpine flora shifted to lower altitudes in eastern Tasmania and forests took refuge from deteriorating climatic conditions, by migrating 200 - 300 m closer to the coast below their present positions on mountain slopes (Macphail 1975; Kirkpatrick & Brown 1984a & b; Potts & Reid 1985a; Kirkpatrick & Potts 1987). Thus, it could be expected that deeper soils than those that now exclude trees would have been treeless.

Palynological evidence from sites in the southern Midlands and in south eastern Tasmania near Hobart, suggest that at the height of the Last Glacial, 18,000 years BP, sparse steppe - grassland and savannah woodland were widespread in these areas (Colhoun 1978; Macphail 1975, 1979). No pollen evidence exists for the central east coast, seaward of the Eastern Tiers or for the Tasman Peninsula, where a number of endemics are also concentrated. Consequently, past floras of these regions are not known and the history of the shrubby east coast endemic flora in particular is poorly understood.

In the north, the vegetation of at least parts of the southwestern Bassian Plain during the Last Glacial is likely to have been low shrub heath dominated by Epacridaceae or heathy low open woodland, becoming increasingly more grassy toward the late Last Glacial Maximum, but including a shrubland phase dominated by woody composites (Hope 1978). This community has no apparent contemporary analogue, other than broad similarities with alpine shrubland in the Central Highlands (Hope 1978). Heathland communities may have been pushed upslope by rising sea levels (Thomas 1992). Further to the west, a heath community dominated by *Microstrobos* and *Casuarina* (probably *Allocasuarina*) has also been recorded during the same period (Colhoun 1977), again with no contemporary analogue. *Microstrobos* is known from alpine vegetation in

Tasmania and the genus *Allocasuarina* is widespread. In the far northeast, glacial grassland preceded the development of heathy eucalypt forests in the early Holocene, which were eventually replaced by coastal heathland as a result of Aboriginal burning and increased salt spray as Bass Strait stabilised (Thomas 1992; Thomas & Kirkpatrick 1995).

Were endemic shrubs part of forest communities that migrated to refugia during the late Pleistocene or did they persist and radiate during this period, being more suited to a colder, drier environment? If they retreated to refugia, then they might be expected to be associated with forests at present. Although some rare shrubby endemics occur in the understoreys of forest, none of these occur within *S. microphyllum* populations. Nor are there any rare endemics typically associated with forest in the central north which also occur with *S. obcordatum*. Rare or restricted endemic taxa which occur with *S. microphyllum* or *S. obcordatum* are frequently concentrated within riparian vegetation, on isolated rocky ridges which are often protected from frequent fires, or in gaps within forest where canopy cover is either minor or absent owing to disturbance or edaphic conditions. Localised communities which contain rare or restricted species are often dominated by shrubs, with eucalypts either absent or present in depauperate form, or as mallees. Thus, it seems unlikely that either of the two rare species have historically been components of forest vegetation.

#### *Phytochorological patterns*

*Spyridium microphyllum* occurs in low shrub dominated vegetation throughout its range. Extensive scrubs and shrublands seldom occur in areas which lie outside the arid and semi - arid regions (Parsons 1981). However, disjunct mallee shrublands are recorded from humid regions in Queensland and New South Wales (Jones 1964; McDonald & Elsol 1984 in Martin 1989). Scrubs are also known from East Gippsland in Victoria and the New South Wales Southern Tablelands (Beadle 1948; Forbes *et al.* 1981; Clayton - Greene & Wimbush 1988; Peel 1993).

The phytochorological composition of shrubland containing *S. microphyllum* differed from adjacent vegetation. Its composition suggests they are relict ecosystems confined to marginal environments within dry sclerophyll vegetation. Regular disturbance in riparian situations provide the light conditions necessary for the maintenance of these communities. Rocky sites having shallow soils which preclude the establishment of forest communities also provide similar conditions.

At the Douglas - Apsley and Swan River sites, *S. microphyllum* was strongly associated with other narrow endemics. At the Thumbs, *S. microphyllum* occurred with one other narrow endemic, endemics restricted to southeastern Tasmania, mediterranean - type taxa and taxa associated with the Great Dividing Range. Mediterranean type flora is poorly represented in Tasmania (Nelson 1981). The phytochorological composition of vegetation containing *S. microphyllum* at this site may reflect the scarcity of suitable habitat for rare, disjunct or endemic taxa and the degree of stochasticity which influences patterns of distribution in the area. The emplacement of forests in more mesic sites at lower altitudes since the late

Pleistocene and their subsequent radiation during the Holocene has left little opportunity for vegetation containing endemic or disjunct shrubs to expand. The discontinuous nature of the preferred habitat of *S. microphyllum* and its apparent inability to compete on deeper soils overlain by jumbled dolerite blocks, which are widespread throughout open forest in the area, may have further prevented its spread.

Similar biogeographic patterns have been recorded in rare shrubland vegetation elsewhere. Forbes *et al.* (1981) and Peel (1993) recorded scrubs containing rare species in areas long recognised for their high levels of endemic or disjunct flora in far eastern Victoria. These include *Pomaderris oraria* ssp. *calicicola* and *Spyridium eriocephalum*. Perhaps significantly, the region shares similar climatic characteristics to the central east coast of Tasmania (Bureau of Meteorology & Walsh 1993). In Tasmania, shrubland containing *S. eriocephalum* is dominated by the mallee *Eucalyptus risdonii* on skeletal mudstone ridges and steep slopes. A mallee form of *E. nitida* occurs in association with distinct shrub dominated vegetation, including the rare endemic *Spyridium gunnii*, on ultramafic rock outcrops in western Tasmania (Gibson *et al.* 1992). Soil fertility is likely to be the major factor influencing the physiognomic development of this community. However, the occurrence of rainforest on ultramafic soils nearby implies that soil depth, rockiness and fire history are also major factors in their development.

At Hawley and at Asbestos Range, the floristic composition of vegetation containing *S. obcordatum* suggests that there are close links between floristic elements at these sites and some mainland Australian elements. *Spyridium obcordatum* may formerly have been a component of heathland, shrubland or open woodland in northern Tasmania and possibly on sections of the Bassian Plain, during periods of lower sea level. Since the post glacial expansion of forests in northern Tasmania, these types are restricted to open sites where competition from adjacent vegetation is precluded by soils too shallow to support trees, or by continual environmental disturbance which prevents development of closed vegetation.

At Dans Hill, mining in the twentieth century has significantly altered the biogeographic composition of the vegetation. At present, deep soils supporting *S. obcordatum* populations are able to sustain both narrow endemics and widespread shrubby taxa. During the late Last Glacial Maximum, mesic sites in the associated foothills of the Dazzler and Asbestos Ranges may have provided a refugium for forest taxa, although the vegetation throughout most of the area, especially on ultramafic rock outcrops, was almost certain to have been more open. Even with increased precipitation in northern Tasmania during the Holocene (Colhoun *et al.* 1982; Thomas 1992), shallow rocky soils are likely to have precluded vigorous tree growth. To some extent these conditions are mimicked by recent artificial disturbance which has maintained open conditions but created a more favourable environment for *S. obcordatum* root penetration and uptake of moisture.

The phytochorological correlates of both rare species imply that there are underlying biogeographic reasons for their apparent inability to expand populations.

### *Geographic and bioclimatic patterns*

There are a high number of narrow endemics, disjunct taxa and taxa which are restricted in either their latitudinal or longitudinal range in the genus *Spyridium*. This suggests that it is associated with areas which have favoured speciation, refugial occupation or recent radiation. Fragmented or disjunct distributions suggest that some taxa may once have been more widespread. Regions which support centres of endemism and abundance within the genus have also been recognised for high levels of diversity in other taxonomic groups, or for high concentrations of narrow endemics and disjunctions associated with past climate change (Crocker & Wood 1947; Burbidge 1960; Marchant 1973; Lange 1976, 1983; Nelson 1981; Lange & Lang 1985). Examples include *Eucalyptus*, *Verticordia*, *Conospermum* (Speck 1958 in George *et al.* 1979; George 1991), *Banksia* and *Acacia* (Lamont *et al.* 1984; Hnatiuk & Maslin 1988). Of particular interest is the co -occurrence of disjunct taxa in the same local areas, namely the Barren and Stirling Ranges, Twilight Cove on the Nullarbor Plain, Kangaroo Island and the Eyre Peninsula (Crocker & Wood 1947; Marchant 1973; Nelson 1981 and references cited therein). These distributions are thought to have their origins in complicated migration events at times of lowered sea levels across the Great Australian Bight.

The interchange of widely separated taxa during times when land passages were temporarily available and conditions were suitable, can result in the subsequent evolution of endemics or disjunct populations following another disruption (Nelson 1981). These may not necessarily date to the same events, but rather to a series of events throughout the Quaternary and possibly earlier, including the Late Tertiary (Galloway & Kemp 1981). Disjunctions theoretically indicate recent migrations and endemics indicate migrations further back in time (Nelson 1981). However, complex and widespread disjunctions between ecologically unrelated areas, as evident in the distribution of populations of *S. cinereum* and *S. eriocephalum* for example, suggest it is equally likely that the genus may have had a continuous distribution prior to the Last Glacial, or, that its current distribution is a result of fragmentation by more recent geomorphic and climatic events.

There is surprisingly little narrow endemism known in *Spyridium* in eastern mainland Australia, in spite of the presence of the Great Dividing Range which has long been recognised as a major feature important in shaping the biogeography of the eastern Australian flora. The few disjunct southeastern Australian *Spyridium* taxa in the region are associated with elevated sites along the Great Dividing Range, suggesting that the distributions of *S. scortechinii*, *S. cinereum* and *S. eriocephalum* are associated with eastern Australia migrations and ecological processes which differ from biogeographic processes which took place in southern and western Australia.

*Spyridium* taxa are predominantly confined to shrub dominated vegetation in semi - arid regions. The genus is mainly mediterranean in its distribution. Most taxa have no edaphic, altitudinal or topographic preference within their climatic and



geographic range. Tasmanian *Spyridium* taxa differ from their mainland Australian congeners by occupying environments having relatively high winter and summer rainfall.

The most extreme of these is *Spyridium gunnii*, which is the only member of the genus confined to perhumid environments. Its presence on river banks within rainforest but also in shrubby vegetation on droughty, infertile substrates within high rainfall areas, suggests that it may be a very old taxon which has survived within insular cool temperate environments. Precursors of semi - arid shrub dominated vegetation such as mallee, chaparral and fynbos are thought to have existed within Tertiary plant communities in marginal sites where soils were rocky, infertile or prone to drought (Raven & Axelrod 1978; Martin 1989). The distribution of *S. gunnii* likewise suggests a formerly more widespread distribution. However, further speculation as to its evolutionary position rests on biosystematic, cytoevolutionary, allozyme and DNA analyses following revision of the genus.

The bioclimatic correlates of *S. microphyllum* and *S. obcordatum* showed that they occupy narrow climatic niches at present, as do a number of widespread *Spyridium* taxa. It is unlikely that rarity in *S. microphyllum* and *S. obcordatum* can be wholly explained by their current climatic distribution. Furthermore, it is unclear whether narrow climatic tolerance is a cause or consequence of narrow endemism. A comparison between the geographical and bioclimatic distributions of *S. microphyllum* and between those of *S. obcordatum* generated hypotheses which might explain causes of rarity in the two species. Narrow endemics occupying narrow climatic niches are likely to be relatively new species which have had inadequate time to expand populations. Alternatively, they are relatively old species with drastically reduced ranges; or they may have narrow physiological requirements. They may also lack the ability to successfully compete and disperse.

## Conclusions

Testable hypotheses of rarity rely on knowledge of the age of the taxon in question as well as on their geographic dispersion (Fiedler & Ahouse 1992). However, in the case of *S. microphyllum* and *S. obcordatum*, a combined ecological and biogeographical approach was useful in separating attributes likely to signify correlates of rarity from those likely to be a consequence of rarity. Explanations for rarity can be considered in light of currently held notions of scarcity and endangerment, and hypotheses constructed which might explain rarity in the two species.

A lack of fossil evidence precludes dating the time of origin of *S. microphyllum* and of *S. obcordatum*. The absence of populations from recent sediments in Tasmania and their isolation from centres of endemism and abundance in mainland Australia, strongly suggest that they are unlikely to have evolved in the 10,000 years since the end of the last glacial. In this respect, the two species have had adequate time to disperse. A more likely explanation for rarity is an inability to disperse because of biogeographical and ecological barriers set in place as a result of forest expansion during the Holocene.

The biological performance of both species demonstrated that they have ample reproductive resources and are adapted to fire regimes common in dry sclerophyll vegetation in Tasmania. Hence, lack of genetic fitness or poor reproductive effort is unlikely to be a cause of rarity in either *S. microphyllum* or *S. obcordatum*. A lack of habitat specificity suggests that neither of the two species has narrow physiological requirements.

The phytosociological and phytochorological correlates of *S. microphyllum* support the notion that it was formerly a member of shrub dominated vegetation, similar to extant mallee shrublands and heath and, as a result of the expansion of forests during the Holocene, is relictual under present climatic conditions. It is unclear whether its current environment constitutes interglacial refugia. Its phenological attributes and arrangement of floral organs imply that it may be the older of the two species, being adapted to a less seasonal climate than exists in southern Australia at present. It is disjunct within its present range, and is likely to have been more widespread in the past. The same phenological patterns are absent in *Spyridium* confined to eastern Australia but occur in some other Rhamnaceae taxa in southern and southwestern Australia.

Biogeographical explanations also offer the most likely explanation for rarity in *Spyridium obcordatum*. Populations may have been more or less continuous in the past, as part of a Bassian flora which is now extinct, the relicts of which have been incorporated into coastal heathland or open rocky environments which signify interglacial refugia. Stochastic events relating to local extinction, establishment and maintenance, together with European land practices, have influenced its survival and abundance. Alternatively, *S. obcordatum* may have a drastically reduced range, having been more widespread in the past. However, its phenological attributes imply it is well adapted to a more seasonal climate and is more recently evolved than *S. microphyllum*.

The most parsimonious explanation for rarity in both species is temporal remoteness from optimal conditions. Ecological explanations for rarity in the two species are most likely to be a consequence of their present relictual status. These relate to confinement to narrow ecological niches, poor competitive ability under conditions of improved soil moisture or in closed or undisturbed vegetation, and a lack of safe sites for seedling establishment. As a result, both species are dependent on disturbance for regeneration. Land use practices since European occupation of Tasmania further endanger populations at present.

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Taxon	SMISW	SMIDA	SOBDH	SOBH	SOV	SOO	SEE	SPA	SUL	SGU	SVV
Treatment											
40/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/10	NS	NS	NS	NS	↓53.5**	↓62.5***	NS	NS	NS	NS	NS
60/1	NS	NS	↑-73.0**	↑-60.00***	NS	NS	NS	↑-61.0**	↑-40.5*	↑47.5**	↑-41.5
60/5	NS	NS	↑-56.0**	↑-40.0**	NS	NS	NS	NS	NS	↑69.0***	NS
60/10	↑60.0*	NS	NS	↑-58.0***	NS	NS	NS	NS	↑-66.0***	↑77.5***	↑-76.0
80/1	NS	NS	NS	NS	NS	NS	NS	NS	↑-67.5***	↑62.0***	NS
80/5	NS	NS	NS	↑-32.5*	NS	NS	NS	NS	NS	↑74.0***	NS
80/10	NS	NS	NS	NS	NS	NS	NS	NS	↑-57.0***	↑83.0***	NS
100/1	↑55.0*	NS	NS	↑-34.5*	NS	NS	↑55.0*	NS	↑-53.0**	↑65.5***	NS
100/5	NS	NS	NS	NS	NS	↓49.0**	↓-42.5*	NS	NS	↑46.0**	NS
100/10	NS	↑50.5*	NS	NS	NS	NS	NS	NS	NS	↑56.5***	NS
120/1	NS	NS	NS	↑-35.5*	NS	NS	↑-46.5**	NS	NS	NS	NS
120/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
120/10	NS	NS	NS	↑-30.5*	NS	NS	NS	NS	NS	NS	NS

Appendix A.1. Incubation at 12<sup>0</sup>C. Tukey HSD simultaneous pairwise mean comparisons between *S. microphyllum* (Thumbs) and all other *Spyridium* taxa (df = 30). ↑ = *S. microphyllum* (Thumbs) percentage germination higher; ↓ = *S. microphyllum* (Thumbs) percentage germination lower.

**SMISW** = *S. microphyllum* (Swan River); **SMIDA** = *S. microphyllum* (Douglas - Apsley); **SOBDH** = *S. obcordatum* (Dans Hill); **SOBH** = *S. obcordatum* (Hawley); **SOO** = *S. obovatum* var. *obovatum*; **SOV** = *S. obovatum* var. *velutinum*; **SEE** = *S. eriocephalum*; **SPA** = *S. parvifolium*; **SUL** = *S. ulicinum*; **SGU** = *S. gunnii*; **SVV** = *S. vexilliferum*.

Taxon	SMISW	SMIDA	SOBDH	SOBH	SOV	SOO	SEE	SPA	SUL	SGU	SVV
Treatment											
40/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/5	NS	NS	NS	NS	NS	NS	↑16.0**	↑-16.0*	NS	NS	NS
40/10	↑59.0***	↑57***	↑-30.0**	↑-64.0***	NS	↑-61.0***	↑64.0***	↑-64.0***	↑-64***	↑58.0***	↑-62.0***
60/1	NS	↑60.0***	↑-42.5***	↑-84.0***	NS	NS	↑84.0***	↑-81.5***	↑-69.5***	↑52.5***	↑-64.5***
60/5	↑45.5**	↑57.5***	↑-41.5***	↑-85.5***	↑-60.0***	↑-57.0**	↑93.0***	↑-90.5***	↑-93.0***	↑86.5***	↑-86.5***
60/10	↑35.0*	↑64.5***	↑-39.0***	↑-93.0***	NS	NS	↑95.5***	↑-95.5***	↑-79.0***	↑76.5***	↑-58.5***
80/1	↑60.5***	↑38.5**	NS	↑-83.5***	↑-68.0***	↑-56.5**	↑95.5***	↑-93.5***	↑-57.5***	↑57.5***	↑-52.5***
80/5	↑62.5***	↑36.0**	NS	↑-95.0***	↑-69.5***	NS	↑93.5***	↑-97.5***	↑-73.5***	↑90.5***	↑-56.5***
80/10	↑51.0***	NS	NS	↑-67.5***	↑-63.0***	NS	↑93.5***	↑-91.0***	↑-72.0***	↑74.5***	↑-41.5***
100/1	↑40.5***	NS	NS	NS	NS	NS	↑70.5***	↑-68.0***	↑-42.0***	↑45.5***	↑-27.0*
100/5	NS	↑49.5***	↓29.0*	↑-45.0***	NS	NS	↑61.5***	↑-61.5***	↑-35.5***	↑61.5***	NS
100/10	NS	↑40.5***	↓43.5***	↑-36.0***	NS	NS	↑45.5***	↑-43.0***	↑-26.5**	↑45.5***	NS
120/1	↓-33.5*	↑NS	↓62.5***	NS	↓52.5***	NS	NS	NS	NS	NS	NS
120/5	NS	↑34.0**	NS	↑-26.5**	↓41.0**	NS	↑36.5***	↑-36.5***	↑-26.5**	↑36.5***	NS
120/10	↓-40.0**	NS	NS	NS	↓64.0***	NS	NS	NS	NS	NS	NS

Appendix A.6. Incubation at 20<sup>0</sup>C. Tukey HSD simultaneous pairwise mean comparisons between *S. microphyllum* (Thumbs) and all other *Spyridium* taxa (df = 30). ↑ = *S. microphyllum* (Thumbs) percentage germination higher; ↓ = *S. microphyllum* (Thumbs) percentage germination lower.

**SMITH** = *S. microphyllum* (Thumbs); **SMIDA** = *S. microphyllum* (Douglas - Apsley); **SOBDH** = *S. obcordatum* (Dans Hill); **SOBH** = *S. obcordatum* (Hawley); **SOO** = *S. obovatum* var. *obovatum*; **SOV** = *S. obovatum* var. *velutinum*; **SEE** = *S. eriocephalum*; **SPA** = *S. parvifolium*; **SUL** = *S. ulicinum*; **SGU** = *S. gunnii*; **SVV** = *S. vexilliferum*.

Taxon	SMITH	SMIDA	SOBDH	SOBH	SOV	SOO	SEE	SPA	SUL	SGU	SVV
Treatment											
40/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/10	NS	NS	NS	NS	NS	↓53.0*	NS	NS	NS	NS	NS
60/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
60/5	NS	NS	NS	NS	NS	NS	NS	↓60.0*	NS	NS	NS
60/10	↓60.0*	NS	NS	NS	NS	↓55.0*	NS	NS	NS	NS	NS
80/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
80/5	NS	NS	NS	NS	NS	NS	↓53.0*	NS	NS	NS	NS
80/10	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
100/1	↓55.0*	NS	NS	NS	NS	↓52.0*	NS	NS	NS	NS	↓53.5*
100/5	NS	NS	↓59.0*	NS	↓64.5**	↓72.0**	↓65.5**	NS	NS	NS	↓49.5*
100/10	NS	NS	↓62.5*	NS	↓65.0**	↓66.0**	↓62.0**	NS	NS	NS	↓74.0***
120/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
120/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
120/10	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Appendix A.2. Incubation at 12<sup>0</sup>C. Tukey HSD simultaneous pairwise mean comparisons between *S. microphyllum* (Swan River) and all other *Spyridium* taxa (df = 30). ↑ = *S. microphyllum* (Swan River) percentage germination higher; ↓ = *S. microphyllum* (Swan River) percentage germination lower.

**SMITH** = *S. microphyllum* (Thumbs); **SMIDA** = *S. microphyllum* (Douglas - Apsley); **SOBDH** = *S. obcordatum* (Dans Hill); **SOBH** = *S. obcordatum* (Hawley); **SOO** = *S. obovatum* var. *obovatum*; **SOV** = *S. obovatum* var. *velutinum*; **SEE** = *S. eriocephalum*; **SPA** = *S. parvifolium*; **SUL** = *S. ulicinum*; **SGU** = *S. gunnii*; **SVV** = *S. vexilliferum*.

Taxon	SMITH	SMIDA	SOBDH	SOBH	SOV	SOO	SEE	SPA	SUL	SGU	SVV
Treatment											
40/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/10	↓59.***	NS	NS	NS	↓53.5**	NS	NS	NS	NS	NS	NS
60/1	NS	↑36.0*	NS	↑-60.0***	NS	NS	↑60.0***	↑-57.5***	↑-45.5**	NS	↑-40.5*
60/5	↓45.5**	NS	NS	↑-40.0**	NS	NS	↑47.5***	↑-45.0***	↑-47.5***	↑41.0**	↑-41.0*
60/10	↓35.0*	NS	NS	↑-58.0***	NS	NS	↑60.5***	↑-60.5***	↑-44.0**	↑41.5**	NS
80/1	↓60.5***	NS	↓41.5**	NS	NS	NS	↑35.0**	↑-32.5*	NS	NS	NS
80/5	↓62.5***	NS	↓49.0***	↑-32.5*	NS	NS	↑37.5**	↑-35.0*	NS	NS	NS
80/10	↓51.0***	↓-50.5**	↓44.0**	NS	NS	NS	↑42.5**	↑-40.0**	NS	NS	NS
100/1	↓40.5**	↓-53.5***	↓55.0***	↓34.5*	NS	NS	↑30.0*	NS	NS	NS	NS
100/5	NS	NS	↓45.0**	NS	NS	NS	↑45.0***	↑-45.0***	NS	↑45.0**	↓39.5*
100/10	NS	NS	↓59.0***	NS	NS	NS	↑30.0*	NS	NS	NS	NS
120/1	↑-33.5*	↑37.5*	NS	↑-35.5*	NS	NS	↑45.0***	↑-45.0***	↑-35.0*	↑45.0	NS
120/5	NS	NS	NS	NS	NS	NS	↑37.5**	↑-37.5**	NS	↑37.5**	NS
120/10	↑-40.0**	↑40.0*	↑-40.0*	↑-40.0**	NS	NS	↑40.0**	↑-40.0**	↑-37.5**	↑40.0**	NS

Appendix A.7. Incubation at 20°C. Tukey HSD simultaneous pairwise mean comparisons between *S. microphyllum* (Swan River) and all other *Spyridium* taxa (df = 30). ↑ = *S. microphyllum* (Swan River) percentage germination higher; ↓ = *S. microphyllum* (Swan River) percentage germination lower.

**SMITH** = *S. microphyllum* (Thumbs); **SMIDA** = *S. microphyllum* (Douglas - Apsley); **SOBDH** = *S. obcordatum* (Dans Hill); **SOBH** = *S. obcordatum* (Hawley); **SOO** = *S. obovatum* var. *obovatum*; **SOV** = *S. obovatum* var. *velutinum*; **SEE** = *S. eriocephalum*; **SPA** = *S. parvifolium*; **SUL** = *S. ulicinum*; **SGU** = *S. gunnii*; **SVV** = *S. vexilliferum*.

Taxon	SMITH	SMISW	SOBDH	SOBH	SOV	SOO	SEE	SPA	SUL	SGU	SVV
Treatment											
40/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/5	NS	NS	NS	NS	NS	↓45.5*	NS	NS	NS	NS	NS
40/10	NS	NS	NS	NS	↓84.5***	↓93.5***	NS	NS	NS	NS	↓44.5*
60/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
60/5	NS	NS	NS	↑51.0**	NS	NS	NS	NS	NS	↑55.5**	NS
60/10	NS	↑60.0*	NS	NS	NS	NS	NS	NS	NS	↑45.5**	↑-44.0*
80/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
80/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	↑72.5***	NS
80/10	NS	NS	NS	↑50.0**	NS	NS	NS	NS	NS	↑49.5**	NS
100/1	NS	↑55.0*	NS	NS	NS	NS	NS	NS	NS	↑41.5*	NS
100/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	↑50.0**	NS
100/10	↓50.5*	NS	↓70.**	NS	↓73.0***	↓74.0***	↓70.***	NS	NS	NS	↓82.0***
120/1	NS	NS	NS	NS	NS	NS	↓46.5*	NS	NS	NS	NS
120/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
120/10	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Appendix A.3. Incubation at 12<sup>0</sup>C. Tukey HSD simultaneous pairwise mean comparisons between *S. microphyllum* (Douglas - Apsley) and all other *Spyridium* taxa (df = 30). ↑ = *S. microphyllum* (Douglas - Apsley) percentage germination higher; ↓ = *S. microphyllum* (Douglas - Apsley) percentage germination lower.

**SMITH** = *S. microphyllum* (Thumbs); **SMISW** = *S. microphyllum* (Swan River); **SMIDA** = *S. microphyllum* (Douglas - Apsley); **SOBDH** = *S. obcordatum* (Dans Hill); **SOBH** = *S. obcordatum* (Hawley); **SOO** = *S. obovatum* var. *obovatum*; **SOV** = *S. obovatum* var. *velutinum*; **SEE** = *S. eriocephalum*; **SPA** = *S. parvifolium*; **SUL** = *S. ulicinum*; **SGU** = *S. gunnii*; **SVV** = *S. vexilliferum*.



Taxon	SMITH	SMISW	SOBDH	SOBH	SOV	SOO	SEE	SPA	SUL	SGU	SVV
Treatment											
40/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/10	↓57.0***	NS	NS	NS	↓51.5**	NS	NS	NS	NS	NS	NS
60/1	↓60.0***	↓36.0*	NS	NS	NS	NS	↑24.0**	↑-25.0*	NS	NS	NS
60/5	↓57.5***	NS	NS	↑-28.0*	NS	NS	↑35.5***	↑-33.0***	↑-35.5***	↑29.0**	NS
60/10	↓64.5***	NS	NS	↑-28.5**	NS	NS	↑31.0***	↑-31.0**	NS	NS	NS
80/1	↓38.5**	NS	NS	↑-45.0***	NS	NS	↑57.0***	↑-54.5***	NS	NS	NS
80/5	↓36.0**	NS	NS	↑-59.0***	↑-62.5***	NS	↑64.0***	↑-61.5***	↑-37.5***	↑54.5***	NS
80/10	NS	↑-50.5**	NS	↑-67.0***	↑-53.0**	NS	↑93.0***	↑-90.5***	↑-71.5***	↑74.0***	↑-41.0**
100/1	NS	↑-53.5***	NS	NS	NS	NS	↑83.5***	↑-81.0***	↑-55.0***	↑58.5***	↑-40.00**
100/5	↓49.5***	NS	↓78.5***	NS	↓63.0***	NS	NS	NS	NS	NS	↓72.5***
100/10	↓40.5***	NS	↓84.0***	NS	↓47.5**	↓61.5**	NS	NS	NS	NS	↓58.0***
120/1	NS	↓37.5*	↓66.5***	NS	↓56.5***	NS	NS	NS	NS	NS	NS
120/5	↓34.0**	NS	↓46.5***	NS	↓75.0***	NS	NS	NS	NS	NS	NS
120/10	NS	↓40.0*	NS	NS	↓64.0***	NS	NS	NS	NS	NS	NS

Appendix A.8. Incubation at 20<sup>0</sup>C. Tukey HSD simultaneous pairwise mean comparisons between *S. microphyllum* (Douglas - Apsley) and all other *Spyridium* taxa (df = 30). ↑ = *S. microphyllum* (Douglas - Apsley) percentage germination higher; ↓ = *S. microphyllum* (Douglas - Apsley) percentage germination lower.

**SMITH** = *S. microphyllum* (Thumbs); **SMISW** = *S. microphyllum* (Swan River); **SOBDH** = *S. obcordatum* (Dans Hill); **SOBH** = *S. obcordatum* (Hawley); **SOO** = *S. obovatum* var. *obovatum*; **SOV** = *S. obovatum* var. *velutinum*; **SEE** = *S. eriocephalum*; **SPA** = *S. parvifolium*; **SUL** = *S. ulicinum*; **SGU** = *S. gunnii*; **SVV** = *S. vexilliferum*.

Taxon	SMITH	SMISW	SMIDA	SOBH	SOV	SOO	SEE	SPA	SUL	SGU	SVV
Treatment											
40/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/10	NS	NS	NS	NS	↓79.5***	↓88.5***	↓58.0**	NS	NS	NS	NS
60/1	↓-73.0**	NS	NS	NS	↓75.0**	↓79.5***	↓52.5*	↓75.0**	NS	NS	NS
60/5	↓-56.0*	NS	NS	NS	↓66.5**	↓63.0**	NS	NS	NS	NS	NS
60/10	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
80/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
80/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
80/10	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
100/1	NS	NS	NS	↑-45.5*	NS	NS	NS	NS	NS	↑52.0**	NS
100/5	NS	↑59.0*	NS	↑-69.5***	NS	NS	NS	NS	↑-69.0***	↑82.0***	NS
100/10	NS	↑62.5*	↑70.5**	↑-48.5*	NS	NS	NS	NS	↑-51.0**	↑76.5***	NS
120/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	↑42.5*	NS
120/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
120/10	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Appendix A.4. Incubation at 12<sup>0</sup>C. Tukey HSD simultaneous pairwise mean comparisons between *S. obcordatum* (Dans Hill) and all other *Spyridium* taxa (df = 30). ↑ = *S. obcordatum* (Dans Hill) percentage germination higher; ↓ = *S. obcordatum* (Dans Hill) percentage germination lower.

**SMITH** = *S. microphyllum* (Thumbs); **SMISW** = *S. microphyllum* (Swan River); **SMIDA** = *S. microphyllum* (Douglas - Apsley); **SOBH** = *S. obcordatum* (Hawley); **SOO** = *S. obovatum* var. *obovatum*; **SOV** = *S. obovatum* var. *velutinum*; **SEE** = *S. eriocephalum*; **SPA** = *S. parvifolium*; **SUL** = *S. ulicinum*; **SGU** = *S. gunnii*; **SVV** = *S. vexilliferum*.

Taxon	SMITH	SMISW	SMIDA	SOBH	SOV	SOO	SEE	SPA	SUL	SGU	SVV
Treatment											
40/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/10	↓-30.0**	NS	NS	↑-34.0***	NS	NS	↑34.0***	↑-34.0***	↑-34.0***	↑28.0**	↑-32.0**
60/1	↓-42.5***	NS	NS	↑-41.5***	NS	NS	↑41.5***	↑-39.0***	↑-27.1**	NS	NS
60/5	↓-41.5***	NS	NS	↑-44.0***	NS	NS	↑56.5***	↑-49.0***	↑-51.5***	↑45.0***	↑-45.5***
60/10	↓-39.0***	NS	NS	↑-54.0***	NS	NS	↑56.5***	↑-56.5***	↑-40.0***	↑37.5***	NS
80/1	NS	↑41.5*	NS	↑-64.5***	↑-49.0**	NS	↑51.5***	↑-74.0***	↑-38.5***	↑30.5***	↑-33.5**
80/5	NS	↑49.0**	NS	↑-81.5***	↑-75.5***	NS	↑76.5***	↑-84.5***	↑-60.0***	↑77.0***	↑-43.0***
80/10	NS	↑44.0**	NS	↑-60.5***	↑-56***	NS	↑76.5***	↑-84.0***	↑-65.0***	↑67.5***	↑-34.5**
100/1	NS	↑55.0***	NS	NS	NS	NS	↑85.0***	↑-82.5***	↑-56.5***	↑60.0***	↑-41.5***
100/5	↑29.0**	↑45.5**	↑78.5***	↑-74.0***	NS	↑-57.0**	↑90.5***	↑-90.5***	↑-64.5***	↑90.5***	NS
100/10	↑43.5***	↑59.0***	↑84.0***	↑-79.5***	↑-36.5*	NS	↑89.0***	↑-86.5***	↑-70.0***	↑89.0***	NS
120/1	↑62.5***	NS	↑66.5***	↑-64.5***	NS	NS	↑74.0***	↑-74.0***	↑-64.0***	↑74.0***	↑-50.5***
120/5	NS	NS	↑46.5***	↑-39.0***	NS	NS	↑49.0***	↑-49.***	↑-39.0***	↑49.0***	↑-33.5**
120/10	NS	↓-40.0*	NS	NS	↓64.0***	NS	NS	NS	NS	NS	NS

Appendix A.9. Incubation at 20°C. Tukey HSD simultaneous pairwise mean comparisons between *S. obcordatum* (Dans Hill) and all other *Spyridium* taxa (df = 30). ↑ = *S. obcordatum* (Dans Hill) percentage germination higher; ↓ = *S. obcordatum* (Dans Hill) percentage germination lower.

**SMITH** = *S. microphyllum* (Thumbs); **SMISW** = *S. microphyllum* (Swan River); **SMIDA** = *S. microphyllum* (Douglas - Apsley); **SOBH** = *S. obcordatum* (Hawley); **SOO** = *S. obovatum* var. *obovatum*; **SOV** = *S. obovatum* var. *velutinum*; **SEE** = *S. eriocephalum*; **SPA** = *S. parvifolium*; **SUL** = *S. ulicinum*; **SGU** = *S. gunnii*; **SVV** = *S. vexilliferum*.

Taxon	SMITH	SMISW	SMIDA	SOBDH	SOV	SOO	SEE	SPA	SUL	SGU	SVV
Treatment											
40/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/5	NS	NS	NS	NS	NS	↓34.0*	NS	NS	NS	NS	NS
40/10	NS	NS	NS	NS	↓82.5***	↓91.5*	↓30.0*	NS	NS	NS	↓42.5***
60/1	↓-60.00***	NS	NS	NS	NS	↓41.0**	NS	NS	NS	NS	NS
60/5	↓-40.0**	NS	↓-51.0**	NS	↓75.0***	↓71.5***	↓-61.0***	↓83.5***	↓28.5*	NS	↓36.0**
60/10	↓-58.0***	NS	NS	NS	↓41.0*	↓58.5***	↓-28.0*	↓53.5**	NS	NS	NS
80/1	NS	NS	NS	NS	↓53.5**	↓61.0***	↓-58.0***	↓58.0**	NS	NS	↓49.0***
80/5	↓-32.5*	NS	NS	NS	NS	NS	↓-31.5*	NS	NS	↑59.0***	NS
80/10	NS	NS	↓-50.0**	NS	↓74.5***	↓71.5***	↓-79.0***	↓76.0***	NS	NS	↓60.5***
100/1	↓-34.5*	NS	NS	↓-45.5*	↓56.5***	↓56.0***	NS	NS	NS	NS	↓57.5***
100/5	NS	NS	NS	↓-69.5***	↓75.0***	↓82.5***	↓-76.0***	↓65.0***	NS	NS	↓60.0***
100/10	NS	NS	NS	↓-48.5*	↓51.0**	↓52.0***	↓-48.0***	NS	NS	NS	↓60.0***
120/1	↓-35.5*	NS	NS	NS	NS	NS	↓-41.5***	NS	NS	NS	NS
120/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
120/10	↓-30.5*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Appendix A.5. Incubation at 12<sup>0</sup>C. Tukey HSD simultaneous pairwise mean comparisons between *S. obcordatum* (Hawley) and all other *Spyridium* taxa (df = 30). ↑ = *S. obcordatum* (Hawley) percentage germination higher; ↓ = *S. obcordatum* (Hawley) percentage germination lower.

**SMITH** = *S. microphyllum* (Thumbs); **SMISW** = *S. microphyllum* (Swan River); **SMIDA** = *S. microphyllum* (Douglas - Apsley); **SOBDH** = *S. obcordatum* (Dans Hill); **SOO** = *S. obovatum* var. *obovatum*; **SOV** = *S. obovatum* var. *velutinum*; **SEE** = *S. eriocephalum*; **SPA** = *S. parvifolium*; **SUL** = *S. ulicinum*; **SGU** = *S. gunnii*; **SVV** = *S. vexilliferum*.

Taxon	SMITH	SMISW	SMIDA	SOBDH	SOV	SOO	SEE	SPA	SUL	SGU	SVV
Treatment											
40/1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
40/10	↓-64.0***	NS	NS	↓-34.0***	↓58.5***	NS	NS	NS	NS	NS	NS
60/1	↓-84.0***	↓-60.0***	NS	↓-41.5***	↓53.0***	↓56.0***	NS	NS	NS	↓-31.5***	NS
60/5	↓-85.5***	↓-40.0**	↓-28.0*	↓-44.0***	NS	NS	NS	NS	NS	NS	NS
60/10	↓-93.0***	↓-58.0***	↓-28.5**	↓-54.0***	↓61.5***	↓59.0***	NS	NS	NS	NS	↓34.5**
80/1	↓-83.5***	NS	↓-45.0***	↓-64.5***	NS	NS	NS	NS	↓26.0**	↓-26.0**	↓31.0**
80/5	↓-95.0***	↑32.5*	↓-59.0***	↓-81.5***	NS	↓73.0***	NS	NS	↓21.5*	NS	↓38.5**
80/10	↓-67.5***	NS	↓-67.0***	↓-60.5***	NS	NS	↑26.0***	↑-23.5***	NS	NS	NS
100/1	NS	↑34.5*	NS	NS	NS	NS	↑64.5***	↑-62.5***	↑-36.5***	↑39.5***	NS
100/5	↓-45.0***	NS	NS	↓-74.0***	↓58.5***	NS	↑16.5**	↑-16.5*	NS	NS	↓68.0***
100/10	↓-36.0***	NS	NS	↓-79.5***	↓43.0**	↓57.0**	NS	NS	NS	NS	↓53.5***
120/1	NS	↓-35.5*	NS	↓-64.5***	↓54.5***	NS	NS	NS	NS	NS	NS
120/5	↓-26.5**	NS	NS	↓-39.0***	↓67.5***	NS	NS	NS	NS	NS	NS
120/10	NS	↓-40.0**	NS	NS	↓64.0***	NS	NS	NS	NS	NS	NS

Appendix A.10. Incubation at 20<sup>0</sup>C. Tukey HSD simultaneous pairwise mean comparisons between *S. obcordatum* (Hawley) and all other *Spyridium* taxa (df = 30). ↑ = *S. obcordatum* (Hawley) percentage germination higher; ↓ = *S. obcordatum* (Hawley) percentage germination lower.

**SMITH** = *S. microphyllum* (Thumbs); **SMISW** = *S. microphyllum* (Swan River); **SMIDA** = *S. microphyllum* (Douglas - Apsley); **SOBDH** = *S. obcordatum* (Dans Hill); **SOO** = *S. obovatum* var. *obovatum*; **SOV** = *S. obovatum* var. *velutinum*; **SEE** = *S. eriocephalum*; **SPA** = *S. parvifolium*; **SUL** = *S. ulicinum*; **SGU** = *S. gunnii*; **SVV** = *S. vexilliferum*.

## Appendix B. Taxa currently included under *Spyridium*

*Spyridium* currently under revision in Australia (K. Thiele, CSIRO, in prep.)

\*Core = +

Not core = |

Uncertain = ?

\*A core species has characters currently considered to differentiate *Spyridium* from closely related taxa.

- + *Spyridium bifidum* (F. Muell.) Benth.
- + *Spyridium bifidum* (F. Muell.) Benth. var. *bifidum*
- + *Spyridium bifidum* (F. Muell.) Benth. var. *integrifolium* J. Black
- + *Spyridium cinereum* Wakef.
- + *Spyridium coactilifolium* Reisseck
- | *Spyridium complicatum* F. Muell.
- ? *Spyridium cordatum* (Turcz) Benth.
- | *Spyridium denticuliferum* Diels
- | *Spyridium divaricatum* Benth.
- + *Spyridium eriocephalum* Fenzl
- + *Spyridium eriocephalum* Fenzl var. *eriocephalum*
- + *Spyridium eriocephalum* Fenzl var. *glabrisepalum* J. Black
- + *Spyridium globulosum* (Labill.) Benth.
- + *Spyridium gunnii* (J. D. Hook.) Benth.
- + *Spyridium halmaturinum* (F. Muell.) Benth.
- + *Spyridium halmaturinum* (F. Muell.) Benth. var. *halmaturinum*
- + *Spyridium halmaturinum* (F. Muell.) Benth. var. *integrifolium* J. Black
- + *Spyridium halmaturinum* (F. Muell.) Benth. var. *scabridum* (Tate) J. Black
- ? *Spyridium kalganese* Diels
- + *Spyridium leucopogon* (Reisseck) F. Muell.
- ? *Spyridium microcephalum* (Turcz) Benth.
- + *Spyridium microphyllum* (Reisseck) Druce
- + *Spyridium nitidum* Wakef.
- + *Spyridium obcordatum* (J. D. Hook.) W. M. Curtis
- + *Spyridium obovatum* (Hook. ) Benth.
- + *Spyridium oligocephalum* (Turcz) Benth.
- + *Spyridium parvifolium* (Hook.) F. Muell.
- + *Spyridium phlebophyllum* (F. Muell.) F. Muell.
- + *Spyridium phyllicoides* Reisseck
- ? *Spyridium rotundifolium* F. Muell.
- + *Spyridium spadiceum* (Fenzl) Benth.
- + *Spyridium spathulatum* (F. Muell.) Benth.
- + *Spyridium subochreatum* Reisseck
- + *Spyridium subochreatum* Reisseck var. *laxiusculum* J. Black
- + *Spyridium subochreatum* Reisseck var. *subochreatum*
- ? *Spyridium thymifolium* Reisseck
- | *Spyridium tridentatum* (Steudel) Benth.

- + *Spyridium ulicinum* (Hook.) Benth.
- + *Spyridium vexilliferum* (Hook.) Reisseck
- + *Spyridium vexilliferum* (Hook.) Reisseck var. *latifolium* Benth.
- + *Spyridium vexilliferum* (Hook.) Reisseck var. *vexilliferum*
- ? *Spyridium westringifolium* (Steudel) Benth.

**Recently described or resurrected taxa in Western Australia (B. Rye, Western Australian Herbarium, pers. comm.).**

	Notes
<i>Spyridium cordatum</i> (Turcz.) Benth.	
<i>Spyridium divaricatum</i> Benth.	Conservation status P2 in WA, 1 record only
<i>Spyridium glaucum</i> Rye ms	Conservation status P1 in WA
<i>Spyridium globulosum</i> (Labill.) Benth.	
<i>Spyridium majoranifolium</i> (Fenzl) Rye var. <i>majoranifolium</i> ms	
<i>Spyridium majoranifolium</i> (Fenzl) Rye var. <i>pediacum</i> ms	
<i>Spyridium microcephalum</i> (Turcz.) Benth.	
<i>Spyridium minutum</i> Rye ms	Conservation status P1 in WA
<i>Spyridium montanum</i> Rye ms	
<i>Spyridium mucronatum</i> Rye ssp. <i>mucronatum</i> ms	
<i>Spyridium mucronatum</i> Rye ssp. <i>multiflorum</i> ms	
<i>Spyridium mucronatum</i> Rye ssp. <i>recurvum</i> ms	
<i>Spyridium oligocephalum</i> (Turcz.) Benth.	
<i>Spyridium polycephalum</i> (Turcz.) Rye ms	
<i>Spyridium spadiceum</i> (Fenzl) Benth.	
<i>Spyridium subochreatum</i> (F. Muell.) Reisseck var. <i>subochreatum</i>	
<i>Spyridium tricolor</i> W. R. Barker & Rye ms	
<i>Spyridium villosum</i> (Turcz.) Benth.	
Plus:	
<i>Spyridium microcephalum/cordatum</i>	
<i>Spyridium</i> sp.	
<i>Spyridium</i> sp. <i>frank hann</i>	
<i>Spyridium rotundifolium</i> F. Muell.	

**Taxa to be transferred from *Cryptandra* (K. Thiele, Australian National Herbarium, pers. comm.).**

*Cryptandra buxifolia* Fenzl = *S. buxifolium*

*Cryptandra scortechinii* F. Muell. = *S. scortechinii*

*Cryptandra* sp. A = *S. "burraborang"*

**Taxa used for BIOCLIM analysis**

**Distribution**

<i>Spyridium bifidum</i> var. <i>bifidum</i>	SA, VIC
<i>Spyridium bifidum</i> var. <i>integrifolium</i>	SA
<i>Spyridium cinereum</i>	VIC NSW
<i>Spyridium coactilifolium</i>	SA
<i>Spyridium cordatum</i>	WA
<i>Spyridium divaricatum</i>	WA
<i>Spyridium eriocephalum</i> var. <i>eriocephalum</i>	SA, VIC, NSW, TAS
<i>Spyridium eriocephalum</i> var. <i>glabrisepalum</i>	SA
<i>Spyridium erymnocaulum</i> W. R. Barker sp. nov.	SA
<i>Spyridium glaucum</i>	WA
<i>Spyridium globulosum</i>	WA
<i>Spyridium gunnii</i>	TAS
<i>Spyridium halmaturinum</i> var. <i>halmaturinum</i>	SA
<i>Spyridium halmaturinum</i> var. <i>integrifolium</i>	SA
<i>Spyridium halmaturinum</i> var. <i>scabridum</i>	SA
<i>Spyridium leucopogon</i>	SA
<i>Spyridium majoranifolium</i> var. <i>majoranifolium</i>	WA
<i>Spyridium majoranifolium</i> var. <i>pediacum</i>	WA
<i>Spyridium microcephalum</i>	WA
<i>Spyridium microcephalum/cordatum</i>	WA
<i>Spyridium microphyllum</i>	TAS
<i>Spyridium minutum</i>	WA
<i>Spyridium montanum</i>	WA
<i>Spyridium mucronatum</i> var. <i>mucronatum</i>	WA
<i>Spyridium mucronatum</i> var. <i>multiflorum</i>	WA
<i>Spyridium mucronatum</i> var. <i>recurvum</i>	WA
<i>Spyridium nitidum</i>	SA
<i>Spyridium obcordatum</i>	TAS
<i>Spyridium obovatum</i> var. <i>obovatum</i>	TAS
<i>Spyridium obovatum</i> var. <i>velutinum</i>	TAS
<i>Spyridium oligocephalum</i>	WA
<i>Spyridium parvifolium</i>	SA, VIC, TAS, NSW
<i>Spyridium phlebophyllum</i>	SA
<i>Spyridium phyllicoides</i>	SA
<i>Spyridium polycephalum</i>	WA
<i>Spyridium spadiceum</i>	WA



<i>Spyridium spathulatum</i>	SA VIC
<i>Spyridium subochreatum</i> var <i>laxiusculum</i>	SA
<i>Spyridium subochreatum</i> var <i>subochreatum</i>	WA SA VIC
<i>Spyridium thymifolium</i>	SA
<i>Spyridium tricolor</i>	WA SA
<i>Spyridium ulicinum</i>	TAS
<i>Spyridium vexilliferum</i> var. <i>latifolium</i>	SA
<i>Spyridium vexilliferum</i> var. <i>vexilliferum</i>	SA VIC TAS
<i>Spyridium villosum</i>	WA

***Taxa excluded from the analysis***

***Notes***

*Spyridium* sp.

No details available to distinguish this as a single taxon.

*Spyridium* sp. *frank hann*

1 Herbarium record only, status unclear.

*Spyridium rotundifolium* F. Muell.

1 Herbarium record only, no location known.

Taxon	Number of records	Region	Mean annual precip. (mm)	Precip. wettest month (mm)	Precip. driest month (mm)	Coefficient variation monthly precip.	Precip. wettest quarter (mm)	Precip. driest quarter (mm)	Precip. coolest quarter (mm)	Precip. warmest quarter (mm)
			SD	SD	SD	SD	SD	SD	SD	SD
<i>S. divaricatum</i>	1	WA	265 0	72 0	1 0	10.3.2 0	171 0	7 0	150 0	39 0
<i>S. glaucum</i>	2	WA	360 9.2	45 0	16 0	31 0.1	124 2.8	57 0.7	123 2.8	57 0.7
<i>S. montanum</i>	2	WA	768 103	116 22	21 1	51.6 4.0	314 54	73 3	314 54	73 3
<i>S. oligocephalum</i>	5	WA	460 86	59 8	17 2	40 4.7	166 27	55 7	163 24	62 15
<i>S. spadiceum</i>	4	WA	939 61	145 16	24 1	54.3 4.5	387 43	82 2	379 39	84 2
<i>S. villosum</i>	2	WA	716 74	105 16	20 1	50.5 3.9	288 42	69 2	277 26	69 2
<i>S. mucronatum</i> var. <i>multiflorum</i>	3	WA	446	55	19	36.4	160	62	160	62
<i>S. majoranifolium</i> var. <i>pediacum</i>	3	WA	75 564	10 72	2 18	5.4 42.5	33 207	3 61	33 203	3 61
			15	1	1	0.6	3	1	3	1

Appendix C.1. Bioclimatic profiles of *Spyridium* taxa (precipitation).

Taxon	Number of records	Region	Mean annual precip. (mm)	Precip. wettest month (mm)	Precip. driest month (mm)	Coefficient variation monthly precip.	Precip. wettest quarter (mm)	Precip. driest quarter (mm)	Precip. coolest quarter (mm)	Precip. warmest quarter (mm)
			SD	SD	SD	SD	SD	SD	SD	SD
<i>S. mucronatum</i> var. <i>recurvum</i>	3	WA	418 22	52 2.6	16 1.7	38 6.3	150 5.7	52 5.2	147 4.6	52 5.2
<i>S. mucronatum</i> var. <i>mucronatum</i>	14	WA	381 45	47 6	16 2	32.5 4.2	131 19	55 5	130 19	55 5
<i>S. globulosum</i>	146	WA	957 281	179 55	15.6 7	74 17.8	481 149	58 23	407 122	66 24
<i>S. majoranifolium</i> var. <i>majoranifolium</i>	32	WA	617 193	87 36	19 3	46.2 9.4	243 96	65 9	235 86	71 13
<i>S. microcephalum</i>	29	WA	391 78	52 12	15 3	38.5 10.5	143 32	52 10	141 32	52 11
<i>S. minutum</i>	13	WA	391 80	49 13	16 3	32.9 6.9	135 40	55 5	135 40	56 6
<i>S. cordatum</i>	16	WA	406 92	53 16	16 2	36.9 7.1	148 45	54 6	146 45	55 8
<i>S. "micord"</i>	5	WA	466 58	59 11	16 2	38.5 5.2	166 29	58 4	166 30	62 11
<i>S. polycephalum</i>	11	WA	399 81	61 9	13 3	49.8 7.5	166 31	47 10	163 32	49 13

Appendix C.1 continued. Bioclimatic profiles of *Spyridium* taxa (precipitation).

Taxon	Number of records	Region	Mean annual precip. (mm)	Precip. wettest month (mm)	Precip. driest month (mm)	Coefficient variation monthly precip.	Precip. wettest quarter (mm)	Precip. driest quarter (mm)	Precip. coolest quarter (mm)	Precip. warmest quarter (mm)
			SD	SD	SD	SD	SD	SD	SD	SD
<i>S. erymnocaula</i>	2	SA	399 41	51 4	16 4	39.6 1.4	148 12	55 8	148 12	55 8
<i>S. leucopogon</i>	6	SA	502 60	84 12	12 1	61.3 4	232 34	46 4	232 34	46 4
<i>S. halmaturinum</i> var. <i>integrifolium</i>	27	SA	665	113	18	61.9	307	63	267	65
			36	6	1	1.5	19	3	22	3
<i>S. eriocephalum</i> var. <i>glabrisepalum</i>	5	SA	524	84	17	55.7	230	57	230	57
			41	6	2	1.3	14	5	14	5
<i>S. halmaturinum</i> var. <i>halmaturinum</i>	28	SA	609	102	18	58.3	273	63	250	63
			45	10	1.0	3.3	26	3	12	3
<i>S. halmaturinum</i> var. <i>scabridum</i>	7	SA	605	101	18	59.3	274	61	255	62
			59	12	1	3.8	34	3	25	3
<i>S. tricolor</i>	11	WA/SA	326 94	39 13	15 4	29.1 9.7	111 36	53 10	108 37	54 12
<i>S. bifidum</i> var. <i>bifidum</i>	37	SA	406 106	56 21	15 4	42.7 12.8	160 59	53 10	160 59	53 11

Appendix C.1 continued. Bioclimatic profiles of *Spyridium* taxa (precipitation)

Taxon	Number of records	Region	Mean annual precip. (mm)	Precip. wettest month (mm)	Precip. driest month (mm)	Coefficient variation monthly precip.	Precip. wettest quarter (mm)	Precip. driest quarter (mm)	Precip. coolest quarter (mm)	Precip. warmest quarter (mm)
			SD	SD	SD	SD	SD	SD	SD	SD
<i>S. bifidum</i> var. <i>integrifolium</i>	9	SA	582 78	95 18	16 3.0	59.8 8.4	264 47	57 9.0	249 41	57 9.0
<i>S. subochreatum</i> var. <i>subochreatum</i>	164	WA/SA/VIC	391	44	18.7	28.8	128.	64	127	67
<i>S. subochreatum</i> var. <i>laxiusculum</i>	7	SA	71 493	11 63	2.0 21	6.3 37.2	31 179	7 66	32 178	7 67
<i>S. coactilifolium</i>	15	SA	140 651 108	26 95 19	2.0 23 3	9.4 50.2 5.4	70 266 52	7.0 71 7	71 266 52	7.0 72 6
<i>S. nitidum</i>	29	SA	556 57	89 13	17 3	55.5 6.4	242 31	59 8	234 22	59 8
<i>S. phlebophyllum</i>	30	SA	318 65	37 9	17 2	24.2 5.7	105 28	62 8	99 34	76 9
<i>S. phyllicoides</i>	83	SA	512 109	81 24	16 3	53.6 8.6	221 59	55 9	211 50	56 9
<i>S. spathulatum</i>	51	SA/VIC	638 164	97 26	21 6	52.7 7.7	268 71	69 16	264 71	69 16
<i>S. thymifolium</i>	146	SA	764 97	113 16	25 3	52.4 4	316 41	81 9	313 43	82 9

Appendix C.1 continued. Bioclimatic profiles of *Spyridium* taxa (precipitation).

Taxon	Number of records	Region	Mean annual precip. (mm)	Precip. wettest month (mm)	Precip. driest month (mm)	Coefficient variation monthly precip.	Precip. wettest quarter (mm)	Precip. driest quarter (mm)	Precip. coolest quarter (mm)	Precip. warmest quarter (mm)
			SD	SD	SD	SD	SD	SD	SD	SD
<i>S. vexilliferum</i> var. <i>latifolium</i>	22	SA	633	98	20	53	268	66	256	67
<i>S. "burraborang"</i>	4	NSW	85 807	23 93	1 39	8.5 28.5	59 261	3 119	51 162	3 252
<i>S. buxifolium</i>	11	NSW	20 641	5 77	1 36	1.6 25.3	10 218	4 120	5 130	9 218
<i>S. scortechinii</i>	47	NSW/QLD	79 948	12 120	4 47	4.2 30.	32 332	12 161	16 190	32 315
<i>S. cinereum</i>	11	VIC/NSW	277 880	40 99	13 58	10.8 17.4	115 267	45 192	61 254	95 199
<i>S. microphyllum</i>	17	TAS	179 714	18 70	18 46	7.7 12.3	44 196	56 155	38 185	58 160
<i>S. obcordatum</i>	8	TAS	139 850	14 110	7 39	1.2 31.9	40 302	31 133	39 302	29 133
<i>S. obovatum</i> var. <i>obovatum</i>	46	TAS	81 872	13 88	3 54	1.5 13.8	34 247	10 184	34 235	10 186
<i>S. obovatum</i> var. <i>velutinum</i>	28	TAS	200 752	23 75	9 50	3.2 12.4	68 210	32 162	74 193	30 163
			119	12	7	1	34	23	36	21

Appendix C.1 continued. Bioclimatic profiles of *Spyridium* taxa (precipitation).

Taxon	Number of records	Region	Mean annual precip. (mm)	Precip. wettest month (mm)	Precip. driest month (mm)	Coefficient variation monthly precip.	Precip. wettest quarter (mm)	Precip. driest quarter (mm)	Precip. coolest quarter (mm)	Precip. warmest quarter (mm)
			SD	SD	SD	SD	SD	SD	SD	SD
<i>S. ulicinum</i>	38	TAS	926	93	59	14.3	262	188	251	188
			322	31	21	4	87	71	83	71
<i>S. gunnii</i>	18	TAS	2175	247	104	25.2	690	359	678	359
			507	58	23	4.1	156	80	148	80
<i>S. vexilliferum</i> var. <i>vexilliferum</i>	75	SA/VIC/TAS	728	97	29	40.4	272	99	266	101
			188	29	11	15	79	36	81	39
<i>S. parvifolium</i>	707	SA/VIC/TAS/ NSW	992	112	51	26.7	318	168	303	174
			216	49	21	13	384	141	388	165
<i>S. eriocephalum</i> var. <i>eriocephalum</i>	129	SA/VIC/TAS/ NSW	405	47	20	28.1	135	67	130	70
			110	19	6	12.5	51	19	50	22

Appendix C.1 continued. Bioclimatic profiles of *Spyridium* taxa (precipitation).

Taxon	Number of records	Region	Annual mean temp. (°C)	Min. temp. coolest month (°C)	Max temp. warmest month (°C)	Annual temp. range (°C)	Mean temp. coolest quarter (°C)	Mean temp. warmest quarter (°C)	Mean temp. wettest quarter (°C)	Mean temp. driest quarter (°C)
			SD	SD	SD	SD	SD	SD	SD	SD
<i>S. divaricatum</i>	1	WA	22 0	10.4 0	34.5 0	24.1 0	16.8 0	27.6 0	18 0	23.1 0
<i>S. glaucum</i>	2	WA	15.7 0	4.6 0.07	30 0.07	25.4 0.1	10.2 0.1	21.4 0.07	11.3 0.07	21.4 0.07
<i>S. montanum</i>	2	WA	13.6 0.6	2.8 0.7	28 0.2	25.3 0.5	7.6 0.8	20 0.2	7.6 0.8	20 0.2
<i>S. oligocephalum</i>	5	WA	15.5 0.3	5.3 1.0	28.2 1.5	22.9 2.4	10.8 1.0	20.5 0.6	11.3 0.7	20.2 0.7
<i>S. spadiceum</i>	4	WA	14.4 0.7	4.8 1.5	27.0 0.9	22.2 2.4	9.7 1.6	19.5 0.2	9.7 1.7	19.5 0.3
<i>S. villosum</i>	2	WA	14.8 0.8	5.2 1.9	27.5 1.1	22.3 3.0	10.2 2.0	19.9 0.3	10.7 1.3	19.9 0.3
<i>S. mucronatum</i> var. <i>multiflorum</i>	3	WA	16.3 0.2	5.7 0	28.8 0.7	23.1 0.8	11.6 0.1	20.9 0.4	11.6 0.1	20.9 0.4
<i>S. majoranifolium</i> var. <i>pediacum</i>	3	WA	15.1 0.1	5.4 0.1	27.4 0.2	22 0.3	10.8 0.1	19.8 0.1	11.8 0.1	19.8 0.1

Appendix C.2. Bioclimatic profiles of *Spyridium* taxa (temperature).



Taxon	Number of records	Region	Annual mean temp. (°C)	Min. temp. coolest month (°C)	Max temp. warmest month (°C)	Annual temp. range (°C)	Mean temp. coolest quarter (°C)	Mean temp. warmest quarter (°C)	Mean temp. wettest quarter (°C)	Mean temp. driest quarter (°C)
			SD	SD	SD	SD	SD	SD	SD	SD
<i>S. mucronatum</i> var. <i>recurvum</i>	3	WA	15.8 0.4	5.5 0.6	28.3 0.4	22.8 0.9	11.3 0.7	20.6 0	12.3 0.7	20.6 0
<i>S. mucronatum</i> var. <i>mucronatum</i>	14	WA	16.3 0.2	5.3 0.3	29.8 0.6	24.4 0.8	11.2 0.4	21.4 0.3	11.4 0.5	21.3 0.4
<i>S. globulosum</i>	146	WA	16.5 1.1	8.1 1.3	27.5 1.7	19.4 1.8	12.7 0.9	20.8 1.5	13.2 1.2	20.7 1.3
<i>S. majoranifolium</i> var. <i>majoranifolium</i>	32	WA	15.7 0.4	6.0 0.7	27.1 1.2	21.0 1.9	11.6 0.7	20.0 0.6	12.0 0.7	20.0 0.6
<i>S. microcephalum</i>	29	WA	16.1 0.7	5.2 0.6	29.4 1.0	24.2 1.3	11.0 0.9	21.3 0.8	11.7 1.0	21.1 0.7
<i>S. minutum</i>	13	WA	16.3 0.2	5.3 0.3	29.9 1.0	24.5 1.2	11.2 0.3	21.4 0.6	11.3 0.3	21.3 0.7
<i>S. cordatum</i>	16	WA	16.0 0.3	5.1 0.7	29.2 1.2	24.0 1.9	11.0 0.8	21.1 0.6	11.7 0.9	21.1 0.6
<i>S. "micord"</i>	5	WA	15.9 0.3	5.6 0.4	28.3 0.8	22.7 1.1	11.4 0.4	20.6 0.4	11.6 0.3	20.3 0.8
<i>S. polycephalum</i>	11	WA	16 0.3	4.9 0.7	30.1 1.6	25.2 2.2	10.6 0.8	21.7 0.9	11.5 0.7	21.3 0.7

Appendix C.2 continued. Bioclimatic profiles of *Spyridium* taxa (temperature).

Taxon	Number of records	Region	Annual mean temp. (°C)	Min. temp. coolest month (°C)	Max temp. warmest month (°C)	Annual temp. range (°C)	Mean temp. coolest quarter (°C)	Mean temp. warmest quarter (°C)	Mean temp. wettest quarter (°C)	Mean temp. driest quarter (°C)
			SD	SD	SD	SD	SD	SD	SD	SD
<i>S. erymnocaula</i>	2	SA	15.9 1.1	5.3 1.2	29.5 0.4	24.1 0.9	10.4 1.3	21.3 0.8	10.4 1.3	21.3 0.8
<i>S. leucopogon</i>	6	SA	16.1 0.3	7.8 0.8	26.4 0.9	18.6 1.6	12 0.6	20.3 0.3	12 0.6	20.3 0.4
<i>S. halmaturinum</i> var. <i>integrifolium</i>	27	SA	14.9 0.3	8.7 0.7	23 0.6	14.3 1.2	11.7 0.5	18.4 0.1	11.8 0.6	18.1 0.2
<i>S. eriocephalum</i> var. <i>glabrisepalum</i>	5	SA	15.1 0.3	8.2 0.6	23.6 0.5	15.3 1	11.7 0.5	18.9 0.1	11.7 0.5	18.9 0.1
<i>S. halmaturinum</i> var. <i>halmaturinum</i>	28	SA	15.0 0.2	8.6 0.6	22.8 0.5	14.2 1.1	11.8 0.4	18.4 0.2	11.9 0.5	18.3 0.3
<i>S. halmaturinum</i> var. <i>scabridum</i>	7	SA	15 0.3	8.6 0.8	23.1 0.6	14.5 1.3	11.7 0.5	18.6 0	11.8 0.6	18.3 0.3
<i>S. tricolor</i>	11	WA/SA	17.1 0.6	6.0 0.2	29.6 0.9	23.6 0.8	12.2 0.4	21.8 0.8	12.8 0.6	21.5 0.8
<i>S. bifidum</i> var. <i>bifidum</i>	37	SA	16.2 0.9	5.7 1.3	29.6 1.8	23.9 2.7	10.8 1.0	21.5 1.1	10.9 1.1	21.3 1.2

Appendix C.2 continued. Bioclimate profiles of *Spyridium* taxa (temperature).

Taxon	Number of records	Region	Annual mean temp. (°C)	Min. temp. coolest month (°C)	Max temp. warmest month (°C)	Annual temp. range (°C)	Mean temp. coolest quarter (°C)	Mean temp. warmest quarter (°C)	Mean temp. wettest quarter (°C)	Mean temp. driest quarter (°C)
			SD	SD	SD	SD	SD	SD	SD	SD
<i>S. bifidum</i> var. <i>integrifolium</i>	9	SA	15.4 0.7	7.7 1.6	25.2 2.7	17.5 4.2	11.5 0.8	19.4 1.1	11.6 0.9	19.2 1.2
<i>S. subochreatum</i> var. <i>subochreatum</i>	164	WA/SA/VIC	15.5 0.9	4.3 0.8	30.4 1.3	26.1 1.8	9.8 0.7	21.3 1.1	11.1 2.3	21 1.1
<i>S. subochreatum</i> var <i>laxiusculum</i>	7	SA	15.1 0.6	5.4 1.0	28.3 1.4	22.9 2.3	10.2 0.6	20.2 0.7	10.9 1.2	20.2 0.7
<i>S. coactilifolium</i>	15	SA	15.3 0.7	6.8 0.4	26.2 1.7	19.4 2.0	10.9 0.4	19.8 1.0	10.9 0.4	19.8 1.0
<i>S. nitidum</i>	29	SA	15.2 0.6	7.9 1.3	24.4 2	16.4 3.1	11.6 0.8	19.1 0.8	11.6 0.8	19 0.8
<i>S. phlebophyllum</i>	30	SA	15.8 1.2	3.0 1	31.6 1.3	28.6 0.8	8.8 1.2	22.8 1.3	11.9 5.7	18.4 3.8
<i>S. phyllicoides</i>	83	SA	15.6 0.9	7.8 1.4	25.3 2.7	17.4 4.0	11.8 0.8	19.7 1.3	11.8 0.8	19.6 1.4
<i>S. spathulatum</i>	51	SA/VIC	14.7 0.9	6.4 1.9	25.9 2.2	19.5 3.8	10.4 1.4	19.3 0.8	10.6 1.3	19.2 0.9
<i>S. thymifolium</i>	146	SA	14.5 0.5	6 0.9	26.5 1.3	20.5 2.1	10 0.7	19.2 0.6	10.2 0.8	19.2 0.7

Appendix C.2 continued. Bioclimatic profiles of *Spyridium* taxa (temperature).

Taxon	Number of records	Region	Annual mean temp. (°C)	Min. temp. coolest month (°C)	Max temp. warmest month (°C)	Annual temp. range (°C)	Mean temp. coolest quarter (°C)	Mean temp. warmest quarter (°C)	Mean temp. wettest quarter (°C)	Mean temp. driest quarter (°C)
			SD	SD	SD	SD	SD	SD	SD	SD
<i>S. vexilliferum</i> var. <i>latifolium</i>	22	SA	14.5	6.3	25.8	19.5	10.5	18.9	10.5	18.8
			0.3	1.6	2.2	3.9	0.8	0.6	0.8	0.8
<i>S. "burraborang"</i>	4	NSW	15.5	2.6	28.0	25.4	9.7	21.0	20.8	10.5
			0.3	0.2	0.1	0.3	0.4	0.2	0.2	0.4
<i>S. buxifolium</i>	11	NSW	16.0	2.5	29.0	26.5	9.7	21.9	21.8	10.7
			1.2	1.1	1.4	1.5	1.2	1.2	1.5	0.7
<i>S. scortechinii</i>	47	NSW/QLD	14.3	1.7	25.8	24.1	8.6	19.5	18.9	10.5
			1.8	2.4	1.3	2.4	2.3	1.5	1.8	2.4
<i>S. cinereum</i>	11	VIC/NSW	14.8	6.5	23.9	17.4	10.7	19.1	11.5	18.4
			0.3	1.6	2.6	4.2	1	0.5	1.5	0.8
<i>S. microphyllum</i>	17	TAS	11.7	2.8	22.3	19.5	7.5	15.9	9.7	12.8
			1	0.9	1	1	1	0.9	2.1	3.4
<i>S. obcordatum</i>	8	TAS	12.4	3.5	23.1	19.6	8.3	16.7	8.3	16.7
			0.2	0.4	0.2	0.5	0.3	0.1	0.3	0.1
<i>S. obovatum</i> var. <i>obovatum</i>	46	TAS	11.2	2.7	21.5	18.8	7.1	15.3	9.7	13.2
			1.2	0.9	1.4	1	1.2	1.3	2.6	2.9
<i>S. obovatum</i> var. <i>velutinum</i>	28	TAS	10.9	2.4	21.4	18.9	6.8	15.1	10.9	13.7
			1.2	0.8	1.4	1	1.1	1.3	2.3	2.5

Appendix C.2 continued. Bioclimatic profiles of *Spyridium* taxa (temperature).

Taxon	Number of records	Region	Annual mean temp. (°C)	Min. temp. coolest month (°C)	Max temp. warmest month (°C)	Annual temp. range (°C)	Mean temp. coolest quarter (°C)	Mean temp. warmest quarter (°C)	Mean temp. wettest quarter (°C)	Mean temp. driest quarter (°C)
			SD	SD	SD	SD	SD	SD	SD	SD
<i>S. ulicinum</i>	38	TAS	9.5 1.7	1.6 1.1	20 2.1	18.4 1.4	5.6 1.5	13.7 1.8	7.9 2.4	13.7 1.8
<i>S. gunnii</i>	18	TAS	10 1.9	2.8 2.1	20.1 1.6	17.3 1.3	6.5 2.2	14 1.5	6.8 2.2	14 1.5
<i>S. vexilliferum</i> var. <i>vexilliferum</i>	75	SA/VIC/TAS	13.7 1.4	4.9 1.8	25.5 2.6	20.6 3.4	9.2 1.6	18.4 1.7	9.9 1.8	17.7 2.9
<i>S. parvifolium</i>	707	SA/VIC/TAS/ NSW	13.4 1.7	4 1.3	26 3.2	22 3.2	8.5 1.4	18.5 2.3	9.8 1.9	18.3 2.4
<i>S. eriocephalum</i> var. <i>eriocephalum</i>	129	SA/VIC/TAS/ NSW	15.8 0.9	4.9 1.4	29.6 2.4	24.7 3.6	10.3 0.8	21.4 1.5	12.5 3.1	19.9 3.3

Appendix C.2 continued. Bioclimatic profiles of *Spyridium* taxa (temperature).

## Appendix D.1. Vascular taxa recorded at *Spyridium microphyllum* sites

T = Tasmanian endemic

\* = Introduced species

Conservation status (Kirkpatrick *et al.* 1991). Lower case applies to Tasmania only. **E** = taxa that are likely to become extinct if present land use changes and patterns and other causal factors of decline continue. **V** = taxa that are likely to become extinct over a longer period of time than those classified E. **R** = taxa that have limited distributions nationally following Briggs & Leigh (1988), where "1" denotes a distribution in Tasmania that does not exceed 100 km x 100 km and "2" denotes taxa that occur in 20 or less 10 km x 10 km National Mapping grid squares in Tasmania. **U** = taxa not known from any secure reserve (World Heritage Area and reserves requiring the approval of both houses of parliament for revocation).

### Pteridophyta

#### ADIANTACEAE

*Cheilanthes austrotenuifolia* H. Quirk & T. C. Chambers

#### ASPLENIACEAE

*Asplenium flabellifolium* Cav.

### Gymnospermae

#### CUPRESSACEAE

T Vv *Callitris oblonga* A. & L. Rich.

*C. rhomboidea* R.Br. ex A. & L. Rich.

### Angiospermae: Monocotyledoneae

#### CYPERACEAE

*Carex appressa* R. Br.

*C. breviculmis* R.Br.

T Rr2 *Gahnia rowayi* F. Muell. ex Rodway

*Lepidosperma curtisiae* K. L. Wilson & D.I. Morris

*L. gunnii* Boeckler

*L. ensiforme* (Rodway) D. I. Morris

T *L. inops* F.Muell.

*L. laterale* R.Br.

*Schoenus apogon* Roemer & Schultes

IRIDACEAE

*Diplarrena moraea* Labill.

LILIACEAE

*Arthropodium milleflorum* (DC) MacBride

*Bulbine bulbosa* (R. Br.) Haw.

*B. glauca* (Raf.) E. M. Watson

*Chamaescilla corymbosa* (R. Br.) F. Muell. ex Benth.

*Dianella tasmanica* Hook. f.

*Laxmannia orientalis* Keighery

*Thysanotus patersonii* R. Br.

*Wurmbea dioica* (R. Br.) F. Muell.

ORCHIDACEAE

*Chiloglottis* sp.

*Curtostylis reniformis* (R. Br.) Schlecht.

*Dipodium punctatum* (Smith) R. Br.

*Pterostylis furcata* Lindley

*P. longifolia* R. Br.

*Pterostylis* sp.

*Thelymitra* sp.

POACEAE

*Agrostis venusta* Trin.

\* *Aira caryphyllea* L.

\* *A. elegantissima* Schur.

\* *Dactylis glomerata* L.

*Danthonia caespitosa* Gaudich.

T *D. dimidiata* Vick.

*D. laevis* Vick.

*D. penicillata* (Labill.) P. Beauv.

*D. racemosa* R. Br.

T Rr1 *Deyeuxia apsleyensis* D. Morris

*D. monticola* (Roemer & Schultes) Vick.

*D. quadriseta* (Labill.) Benth.

r2 *Dichelachne inaequiglumis* (Hack ex Cheeseman) Edgar & Connor

*D. rara* (R. Br.) Vick.

*Ehrharta distichophylla* Labill.

*E. stipoides* Labill.

*Elymus scabrus* (Labill.) A. Love

\* *Holcus lanatus* L.

*Pentapogon quadrifidus* (Labill.) Baillon var. *quadrifidus* (Benth.) D. Morris

*Poa hookeri* Vick.

- \* *P. infirma* Kunth.
- T *P. labillardieri* Steudel var. *acris* Vick.
- P. labillardieri* Steudel var. *labillardieri*
- P. rodwayi* Vick.
- P. sieberiana* Sprengel
- Poa* sp.
- P. tenera* F. Muell. ex Hook. f.
- Stipa flavescens* Labill.
- S. rudis* Sprengel
- Themeda triandra* Forsskal

## RESTIONACEAE

- Leptocarpus brownii* Hook.
- L. tenax* (Labill.) R.Br.

## XANTHORRHOEACEAE

- Lomandra longifolia* Labill.
- L. nana* (A. Lee) A. Lee
- Xanthorrhoea australis* R. Br.

## Angiospermae: Dicotyledoneae

## APIACEAE

- Daucus glochidiatus* (Labill.) Fischer *et al.*
- r2 *Hydrocotyle callicarpa* Bunge
- H. hirta* R. Br. ex A. Rich.
- Xanthosia pilosa* Rudge

## ASTERACEAE

- T *Bedfordia salicina* (Labill.) DC
- Brachyscome* sp.
- Brachyscome tenuiscapa* Hook. f.
- Cassinia aculeata* (Labill.) R. Br.
- Craspedia glauca* (Labill.) Sprengel
- Euchiton gymnocephalus* (DC.) A. Anderb.
- Helichrysum scorpioides* Labill.
- \* *Hypochoeris radicata* L.
- Lagenifera stipitata* (Labill.) Druce
- Leptorhynchos squamatus* (Labill.) Less.
- Millotia tenuifolia* Cass.
- Olearia myrsinoides* (Labill.) F. Muell. ex Benth.
- T Rur1 *Ozothamnus lycopodioides* Hook. f.
- \* *Sonchus asper* (L.) Hill



## CAMPANULACEAE

*Wahlenbergia* sp.

## CARYOPHYLLACEAE

\* *Cerastium vulgare* Hartm.

\* *Sagina apetala* Ard.

## CASUARINACEAE

*Allocasuarina littoralis* (Salisb.) L. Johnson

*A. verticillata* (Lam.) L. Johnson

## CLUSIACEAE

*Hypericum gramineum* Forst.f.

*H. japonicum* Thunb.

## CONVOLVULACEAE

*Convolvulus erubescens* Sims

*Dichondra repens* Forst. & Forst. f.

## CRASSULACEAE

*Crassula sieberana* (Schult & Schult. f) Druce.

## DILLENIACEAE

T *Hibbertia hirsuta* (Hook.) Benth.

*H. prostrata* Hook.

*H. riparia* (R.Br. ex DC.) Hoogl.

*H. sericea* (R. Br. ex DC) Benth.

## DROSERACEAE

*Drosera macrantha* Endl.

*D. peltata* Thunb. ssp. *auriculata* (Backh. ex Planchon) Conn

## EPACRIDACEAE

*Acrotriche serrulata* (Labill.) R.Br.

*Astroloma humifusum* (Cav.) R.Br.

T *Cyathodes divaricata* Hook. f.

T *C. glauca* Labill.

T *Epacris apsleyensis* Crowden

*E. impressa* Labill.

T *E. tasmanica* W.M. Curtis

*Leucopogon collinus* (Labill.) R. Br.

*Lissanthe strigosa* (Smith) R.Br.

## EUPHORBIACEAE

*Beyeria viscosa* (Labill.) Miq.

*Epilobium* sp.  
*Micrantheum hexandrum* Hook. f.  
*Phyllanthus australis* Hook.f.  
*Poranthera microphylla* Brongn.

#### FABACEAE

*A. dealbata* Link  
*A. genistifolia* Link  
*A. mearnsii* De Willd.  
*A. mucronata* Willd. ex Wendl.f.  
*A. myrtifolia*(Smith) Willd.  
*A. verticillata* (L'Herit) Willd.  
*Bossiaea prostrata* R.Br.  
*Daviesia ulicifolia* Andrews  
*Dillwynia glaberrima* Smith  
*D. sericea* A.Cunn  
*Hovea linearis* (Smith) R.Br.  
*Pultenaea gunnii* Benth.  
*P. juniperina* Labill.  
*P. prostrata* Benth ex Hook.  
T Vv *P. selaginoides* Hook. f.  
*Sphaerolobium vimineum* Smith  
\* *Trifolium* sp.

#### GENTIANACEAE

\* *Centaurium erythraea* Rafn.

#### GERANIACEAE

*Pelargonium australe* Willd.

#### GOODENIACEAE

*Goodenia lanata* R. Br.

#### HALORAGACEAE

*Gonocarpus tetragynus* Labill.  
*G. teucreoides* DC.

#### LAMIACEAE

*Prostanthera lasianthos* Labill.  
\* *Prunella vulgaris* L.  
r2 *Teucrium corymbosum* R. Br.

#### LAURACEAE

*Cassytha pubescens* R. Br.

## MYRTACEAE

- Baeckea ramosissima* A. Cunn.  
*Callistemon pallidus* (Bonpl.) DC  
ur2 *C. sieberi* F. Muell.  
T *C. viridiflorus* (Sims) Sweet  
*Calytrix tetragona* DC..  
T *Eucalyptus amygdalina* Labill.  
T Rr2 *E. barberi* L. Johnson & Blaxell  
*E. globulus* Labill.  
*E. ovata* Labill.  
T *E. pulchella* Desf.  
*E. viminalis* Labill.  
T *Leptospermum grandiflorum* Lodd.  
*L. scoparium* Forst. & Forst. f.  
*L. lanigerum* (Aiton) Smith  
*Melaleuca gibbosa* Labill.  
T Rr1 *M. pustulata* Hook.f.

## OLEACEAE

- Notelaea ligustrina* Vent.

## OXALIDACEAE

- Oxalis perennans* Haw.

## PITTOSPORACEAE

- Billardiera longiflora* Labill.  
*Bursaria spinosa* Cav.  
*Rhytidosporum procumbens* (Hook.) F. Muell.

## PLANTAGINACEAE

- \* *Plantago coronopus* L.  
\* *P. lanceolata* L.  
*P. varia* R.Br.

## POLYGALACEAE

- Comesperma volubile* Labill.

## POLYGONACEAE

- Rumex brownii* Campdera

## PRIMULACEAE

- \* *Anagallis arvensis* L.

## PROTEACEAE

- Banksia marginata* Cav.

- T r2 *Grevillea australis* R.Br. var. *linearifolia*  
*Hakea lissosperma* R. Br.  
T r1 *H. megadenia* R. M. Barker.  
*H. microcarpa* R.Br.  
T *Lomatia tinctoria* R. Br.

#### RANUNCULACEAE

- T *Clematis gentianoides* DC.  
*C. microphylla* DC.

#### RHAMNACEAE

- Pomaderris apetala* Labill.  
ur2 *P. phyllicifolia* Lodd. var. *phyllicifolia*  
*P. pilifera* Wakef.  
T Vv *Spyridium microphyllum* (F. Muell. ex Reisseck) Druce  
T *S. obovatum* (Hook.) Benth. var. *obovatum*  
T *S. obovatum* (Hook.) Benth. var. *velutinum* (Reisseck) Benth.  
T Vv *Stenanthemum pimeleoides* (Hook. f.) Benth.

#### ROSACEAE

- Acaena echinata* Nees  
*A. novae-zelandiae* Kirk  
\* *Aphanes arvensis*  
\* *Rosa rubiginosa* L.

#### RUBIACEAE

- Coprosma quadrifida* (Labill.) Robinson  
*Galium australe* DC.  
*G. gaudichaudii* DC.  
*Opercularia varia* Hook.f.

#### RUTACEAE

- Correa reflexa* (Labill.) Vent.

#### SANTALCAEAE

- Exocarpos cupressiformis* Labill.

#### SAPINDACEAE

- Dodonaea viscosa* Jacq.

#### SCROPHULARIACEAE

- Veronica calycina* R.Br.  
T *V. formosa* R. Br.  
*V. gracilis* R. Br.

**STERCULIACEAE**

T Vuv *Lasiopetalum micranthum* Hook.f.

**STYLIDIACEAE**

*Stylidium graminifolium* Swartz in Willd.

**THYMELAEACEAE**

*Pimelea humilis* R.Br.

T *P. nivea* Labill.

**TREMANDRACEAE**

*Tetratheca pilosa* Labill.

**VIOLACEAE**

*Viola hederacea* Labill.

## Appendix D.2. Vascular taxa recorded at *Spyridium obcordatum* sites

T = Tasmanian endemic

\* = Introduced species

Conservation status (Kirkpatrick *et al.* 1991). Lower case applies to Tasmania only. E = taxa that are likely to become extinct if present land use changes and patterns and other causal factors of decline continue. V = taxa that are likely to become extinct over a longer period of time than those classified E. R = taxa that have limited distributions nationally following Briggs & Leigh (1988), where "1" denotes a distribution in Tasmania that does not exceed 100 km x 100 km and "2" denotes taxa that occur in 20 or less 10 km x 10 km National Mapping grid squares in Tasmania. U = taxa not known from any secure reserve (World Heritage Area and reserves requiring the approval of both houses of parliament for revocation).

### Pteridophyta

#### ADIANTACEAE

*Adiantum aethiopicum* L.

*Cheilanthes austrotenuifolia* H. Quirk & T. C. Chambers

#### DENNSTAEDTIACEAE

*Pteridium esculentum* (Forst.f.) Cockayne

#### LINDSAEACEAE

*Lindsaea linearis* Swartz

#### SELAGINELLACEAE

*Selaginella uliginosa* (Labill.) Spring

### Angiospermae: Monocotyledoneae

#### CENTROLEPIDACEAE

*Centrolepis aristata* (R.Br.) Roemer & Schultes

*C. strigosa* (R.Br.) Roemer & Schultes

#### CYPERACEAE

*Carex breviculmis* R. Br.

*Gahnia grandis* (Labill.) S.T. Blake

*Isolepis marginata* (Thunb.) A. Dietr.

*Lepidosperma concavum* (R.Br.)

*L. curtisiae* K. L. Wilson & D.I. Morris

*L. elatius* Labill.

*L. filiforme* Labill.

- T     *L. gunnii* Boeckler  
       *L. inops* F. Muell  
       *L. laterale* R.Br.  
 ?r3   *L. viscidum* R. Br.  
       *Schoenus apogon* Roemer & Schultes  
       *S. nitens* Roemer & Schultes

#### IRIDACEAE

- Diplarrena moraea* Labill.  
       *Patersonia fragilis* (Labill.) Ashers & Graebner

#### JUNCACEAE

- Juncus planifolius* R. Br.

#### JUNCAGINACEAE

- Triglochin centrocarpa* Hook.

#### LILIACEAE

- Chamaescilla cormbosa* (R. Br.) F. Muell. ex Benth.  
       *Dianella revoluta* R. Br.  
       *Dianella tasmanica* Hook. f.  
 ur2   *Hypoxis vaginata* Schdl. var. *brevistigma* R. Henderson  
       *Laxmannia orientalis* Keighery  
       *Thysanotus patersonii* R.Br.  
       *Wurmbea dioica* (R.Br.) F. Muell. ssp. *dioica*

#### ORCHIDACEAE

- Acianthus exsertus* R. Br.  
       *Cyrtostylis reniformis* R. Br.  
       *Microtis* sp.  
       *Thelymitra* sp.

#### POACEAE

- \*     *Aira elegantissima* Schur  
 T     *Danthonia dimidiata* Vick.  
       *D. penicillata* (Labill.) P.Beauv.  
       *Danthonia setacea* R.Br. var. *setacea*  
       *D. tenuior* (Steudel) Conert  
       *Danthonia* sp.  
       *Deyeuxia quadriseta* (Labill.) Benth  
       *Dichelachne crinita* (L. f.) Hook.  
       *D. rara* (R. Br.) Vick.  
       *Ehrharta distichophylla* Labill.  
       *E. stipoides* Labill.  
       *Pentapogon quadrifidus* (Labill.) Baillon  
 r2    *Poa clelandii* Vick.  
       *P. rodwayi* Vick.  
       *Stipa mollis* R.Br.  
       *Stipa pubinodis* Trin. & Rupr.

- Stipa stiposa* Hughes
- Themeda triandra* Forsskal
- \* *Vulpia bromoides* (L.) Gray

#### RESTIONACEAE

- Leptocarpus tenax* (Labill.) R.Br.
- Hypolaena fastigiata* R. Br.

#### XANTHORRHOEACEAE

- Lomandra longifolia* Labill.

#### Angiospermae: Dicotyledoneae

#### APIACEAE

- Daucus glochidiatus* (Labill.) Fischer *et al.*
- r2 *Hydrocotyle callicarpa* Bunge
- H. hirta* R. Br. ex A. Rich.
- Xanthosia pilosa* Rudge
- X. pusilla* Bunge

#### ASTERACEAE

- r2 *Angianthus preissianus* (Steetz) Benth.
- Brachyscome aculeata* (Labill.) Less.
- \* *Chrysanthemoides monilifera* (L.) Norlindh.
- Euchiton gymnocephalus* (DC.) A. Anderb.
- Helichrysum scorpioides* Labill.
- \* *Hypochoeris radicata* L.
- Lagenifera stipitata* (Labill.) Druce
- Olearia lirata* (Sims) Hutch.
- \* *Vellereophyton dealbatum* (Thunb.) Hilliard & B.L. Burt

#### CAMPANULACEAE

- Lobelia alata* Labill.
- Wahlenbergia gracilentia* Loth
- W. gracilis* (Forst. f.) Schrader

#### CASUARINACEAE

- Allocasuarina littoralis* (Salisb.) L. Johnson
- A. monilifera* (L. Johnson) L. Johnson
- A. verticillata* (Lam.) L. Johnson

#### CLUSIACEAE

- Hypericum gramineum* Forst. f.
- H. japonicum* Thunb.

#### CONVOLVULACEAE

- Convolvulus erubescens* Sims



## CRASSULACEAE

*Crassula sieberiana* (Schult. & Schult. f.) Druce

## DILLENIACEAE

- T *Hibbertia hirsuta* (Hook.) Benth.  
*H. riparia* (R. Br. ex DC.) Hoogl.  
*H. sericea* (R. Br. ex DC.) Benth.

## DROSERACEAE

*Drosera peltata* Thunb. ssp. *auriculata* (Backh. ex Planchon) Conn  
*Drosera peltata* Thunb. ssp. *peltata*  
*D. pygmaea* DC.

## EPACRIDACEAE

- Acrotriche serrulata* (Labill.) R.Br.  
*Astroloma humifusum* (Cav.) R.Br.  
*Epacris impressa* Labill.  
T Vv *E. virgata* Hook. f.  
*Leucopogon australis* R. Br.  
*L. collinus* (Labill.) R.Br.  
*L. virgatus* (Labill.) R. Br.  
*Styphelia adscendens* R. Br.

## EUPHORBIACEAE

*Amperea xiphoclada* (Sieber ex Sprengel) Druce  
*Poranthera microphylla* Brongn.

## FABACEAE

*Acacia dealbata* Link  
*A. mearnsii* De Wild.  
*A. myrtifolia* (Smith) Willd.  
*A. sophorae* (Labill.) R. Br.  
*A. suaveolens* (Smith) Willd.  
*A. terminalis* (Salisb.) Macbr.  
*A. verticillata* (L'Herit) Willd.  
*Bossiaea prostrata* R.Br.  
*Dillwynia cinerascens* R. Br.  
*D. glaberrima* Smith  
*D. sericea* A. Cunn.  
*Hovea linearis* (Smith) R.Br.  
*Kennedia prostrata* R.Br.  
*Platylobium triangulare* R. Br.  
*Pultenaea daphnoides* J. Wendle ssp. *obcordata* (Andrews) Benth.  
*P. gunnii* Benth.

## GENTIANACEAE

- \* *Centaurium erythraea* Rafn

GERANIACEAE

*Pelargonium australe* Willd.

GOODENIACEAE

*Goodenia lanata* R.Br.

HALORAGACEAE

*Gonocarpus humilis* Orch.

*G. micranthus* Thunb.

*G. tetragynus* Labill.

*G. teucrioides* DC.

LAURACEAE

*Cassytha glabella* R. Br.

*C. melantha* R. Br.

LINACEAE

*Linum marginale* A. Cunn. ex Planchon

MYRTACEAE

*Baeckea ramosissima* A. Cunn.

*Calytrix tetragona* Labill.

e *Eucalyptus amygdalina* Labill.

*E. obliqua* L'Herit.

*E. ovata* Labill.

*Leptospermum scoparium* Forst & Forst. f. var. *scoparium*

*Melaleuca ericifolia* Smith

*M. squarrosa* Donn ex Smith

OXALIDACEAE

*Oxalis perennans* Haw.

PITTOSPORACEAE

*Billardiera scandens* Smith

*Bursaria spinosa* Cav.

*Rhytidosporum procumbens* (Hook.) F. Muell.

PLANTAGINACEAE

*Plantago varia* R. Br.

POLYGALACEAE

*Comesperma calymega* Labill.

*C. volubile* Labill.

PRIMULACEAE

*Anagallis arvensis* L.

*Samolus repens* (J. R. & G. Forster) Pers.

PROTEACEAE

- Banksia marginata* Cav.  
e *Lomatia tinctoria* R.Br.  
*Persoonia juniperina* Labill.

RHAMNACEAE

- ?Vuv *Pomaderris* aff. *apetala* (coastal form)  
*P. elliptica* Labill.  
*P. oraria* F. Muell. ex Reisseck ssp. *oraria*  
T *Spyridium obcordatum* (Hook. f.) W.M. Curtis

ROSCAEAE

- Acaena echinata* Nees

RUBIACEAE

- G. gaudichaudii* DC.  
*Opercularia varia* Hook. f.

RUTACEAE

- Boronia parviflora* Smith  
*Correa reflexa* (Labill.) Vent.

SANTALACEAE

- Exocarpos cupressiformis* Labill.  
*E. strictus* R. Br.  
*Leptomeria drupacea* (Labill.) Druce

SAPINDCEAE

- Dodonaea viscosa* Jacq

SCROPHULARIACEAE

- Veronica gracilis* R. Br.

STACKHOUSIACEAE

- Stackhousia monogyna* Labill.

STERCULIACEAE

- r1 *Lasiopetalum baueri* Steetz in Lehm.

STYLIDIACEAE

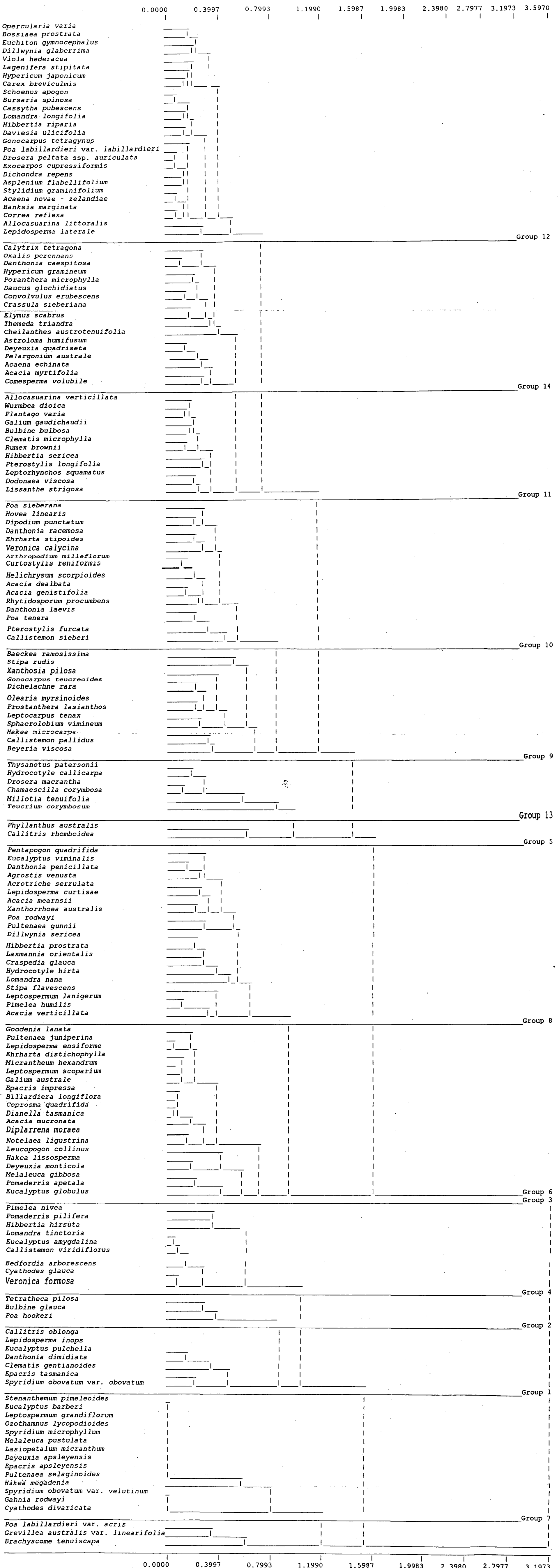
- Stylidium graminifolium* Swartz in Willd.  
r2 *S. perpusillum* Hook. f.

THYMELAEACEAE

- Pimelea humilis* R.Br.  
T *P. nivea* Labill.

VIOLACEAE

- Viola hederacea* Labill.



GROUP 1		GROUP 2		GROUP 3		GROUP 4	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
T2	7.14	T2	16.67	V11	11.11	SC	50.00
T4B	7.14	T4A	66.67	V16	11.11	NT	25.00
T7A	100.00	T4B	16.67	T2	22.22	CT	25.00
T7B	21.43	T7A	100.00	T3	77.78	ST	50.00
		T7B	66.67	T4A	88.89	V11	25.00
		T8	16.67	T4B	77.78	V12	25.00
		T10A	16.67	T5	77.78	V14	25.00
		T10B	100.00	T6	77.78	V16	75.00
				T7A	100.00	T3	50.00
				T7B	100.00	T4A	100.00
				T8	66.67	T4B	75.00
				T9	55.56	T7A	100.00
				T10A	55.56	T7B	75.00
				T10B	100.00	T10B	50.00

Appendix E.2. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 5		GROUP 6		GROUP 7		GROUP 8	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
YP	50.00	W11	5.00	DD	33.33	W11	5.00
SL	100.00	EP	10.00	SC	33.33	W17	5.00
KI	100.00	YP	5.00	NT	33.33	W19	15.00
SE	50.00	KI	5.00	V15	33.33	W20	10.00
FR	50.00	SE	15.00	T3	33.33	W21	5.00
NC	50.00	DD	5.00	T6	66.67	EP	20.00
CC	50.00	NC	5.00	T7A	100.00	NL	20.00
SC	50.00	CC	10.00	T8	100.00	MU	35.00
NT	50.00	SC	40.00	T10A	33.33	YP	20.00
CT	50.00	NT	30.00			SL	70.00
V2	50.00	CT	20.00			KI	40.00
V3	50.00	ST	55.00			SE	80.00
V4	100.00	V3	15.00			FR	15.00
V5	100.00	V4	40.00			DD	10.00
V7	50.00	V5	70.00			CC	10.00
V16	50.00	V7	60.00			SC	60.00

Appendix E.2. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 5		GROUP 6		GROUP 8	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
T2	50.00	V8	30.00	NT	30.00
T4B	50.00	V9	60.00	CT	35.00
T7A	100.00	V10	70.00	ST	45.00
		V11	85.00	NWS	5.00
		V12	70.00	CWS	5.00
		V13	55.00	SWS	20.00
		V14	65.00	NFWP	5.00
		V15	45.00	V1	5.00
		V16	85.00	V2	10.00
		T1	80.00	V3	55.00
		T2	85.00	V4	85.00
		T3	85.00	V5	80.00
		T4A	95.00	V6	35.00
		T4B	80.00	V7	90.00
		T5	100.00	V8	90.00
		T6	80.00	V9	90.00
		T7A	100.00	V10	80.00
		T7B	85.00	V11	80.00
		T8	75.00	V12	100.00
		T9	90.00	V13	35.00
		T10A	85.00	V14	70.00
		T10B	90.00	V15	60.00

Appendix E.2 continued. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 8

REGION	PCT	FREQ
V16	85.00	
T1	40.00	
T2	40.00	
T3	55.00	
T4A	90.00	
T4B	85.00	
T5	75.00	
T6	50.00	
T7A	100.00	
T7B	90.00	
T8	40.00	
T9	45.00	
T10A	40.00	
T10B	70.00	

Appendix E.2 continued. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.



GROUP 9		GROUP 10		GROUP 11		GROUP 12	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
W16	8.33	W17	18.75	W16	8.33	W10	3.85
W17	16.67	W18	6.25	W21	8.33	W17	3.85
W19	8.33	W19	18.75	W22	8.33	W19	7.69
W20	16.67	W20	18.75	W23	8.33	W20	11.54
W21	16.67	W21	12.50	NU	8.33	W21	7.69
W23	8.33	NU	6.25	SLE	25.00	W22	3.85
EP	8.33	SLE	6.25	GT	8.33	NW	3.85
MU	8.33	EP	12.50	EA	33.33	NU	3.85
SL	25.00	NL	12.50	EP	91.67	SLE	3.85

Appendix E.2 continued. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 9		GROUP 10		GROUP 11		GROUP 12	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
KI	8.33	MU	6.25	NL	100.00	GT	3.85
SE	25.00	YP	6.25	MU	100.00	EP	53.85
BN	8.33	SL	31.25	YP	91.67	NL	57.69
DD	50.00	KI	31.25	SL	91.67	MU	34.62
MO	58.33	SE	43.75	KI	75.00	YP	42.31
WB	33.33	FR	6.25	SE	100.00	SL	88.46
NC	75.00	BN	6.25	FR	91.67	KI	73.08
CC	75.00	CO	12.50	BN	16.67	SE	96.15
SC	100.00	DD	43.75	DD	66.67	FR	42.31
NT	75.00	GN	6.25	QLE	33.33	BN	34.62
CT	91.67	GS	6.25	MA	33.33	CO	30.77
ST	83.33	QLE	25.00	MI	8.33	DD	61.54
NWS	16.67	MA	6.25	MO	50.00	QLE	42.31
CWS	25.00	MI	12.50	NK	8.33	MA	7.69
SWS	16.67	MO	31.25	SK	8.33	MO	84.62
SWP	16.67	NK	12.50	WB	8.33	NK	34.62
V4	33.33	PC	6.25	NC	75.00	PC	34.62
V5	41.67	SK	12.50	CC	75.00	SK	7.69
V6	8.33	WA	6.25	SC	50.00	WA	3.85
V7	41.67	WB	12.50	NT	83.33	WB	50.00
V8	8.33	NC	81.25	CT	100.00	NC	96.15

Appendix E.2 continued. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 9		GROUP 10		GROUP 11		GROUP 12	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
V9	41.67	CC	93.75	ST	83.33	CC	96.15
V10	41.67	SC	87.50	NWS	66.67	SC	96.15
V15	33.33	CWS	93.75	NFWP	33.33	CWS	69.23
V11	100.00	NT	75.00	CWS	100.00	NT	80.77
V12	66.67	CT	93.75	SWS	83.33	CT	96.15
V13	8.33	ST	100.00	NWP	66.67	ST	92.31
V14	50.00	NWS	68.75	SWP	83.33	NWS	69.23
V16	91.67	SWS	81.25	SFWP	33.33	SWS	57.69
T1	8.33	NWP	18.75	V1	50.00	NWP	30.77
T2	16.67	SWP	18.75	V2	75.00	SWP	23.08
T3	66.67	V2	12.50	V3	91.67	SFWP	3.85
T4A	83.33	V3	25.00	V4	91.67	V1	11.54
T4B	75.00	V4	75.00	V5	91.67	V2	53.85
T5	66.67	V5	93.75	V6	100.00	V3	61.54
T6	41.67	V6	62.50	V7	100.00	V4	88.46
T7A	100.00	V7	100.00	V8	91.67	V5	92.31
T7B	75.00	V8	87.50	V9	83.33	V6	46.15
T8	66.67	V9	81.25	V10	66.67	V7	92.31
T9	25.00	V10	75.00	V11	83.33	V8	84.62
T10A	50.00	V11	100.00	V12	91.67	V9	96.15
T10B	75.00	V12	100.00	V13	41.67	V10	100.00

Appendix E.2 continued. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 9		GROUP 10		GROUP 11	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
V13	75.00	V14	91.67	V11	100.00
V14	68.75	V15	66.67	V12	100.00
V15	93.75	V16	100.00	V13	69.23
V16	100.00	T1	33.33	V14	92.31
T2	43.75	T2	75.00	V15	76.92
T3	68.75	T3	58.33	V16	100.00
T4A	62.50	T4A	100.00	T1	92.31
T4B	87.50	T4B	83.33	T2	80.77
T5	62.50	T5	83.33	T3	88.46
T6	37.50	T6	25.00	T4A	100.00
T7A	100.00	T7A	100.00	T4B	100.00
T7B	62.50	T7B	83.33	T5	100.00
T8	31.25	T8	16.67	T6	84.62
T9	31.25	T9	16.67	T7A	100.00
T10A	56.25	T10A	33.33	T7B	96.15

Appendix E.2 continued. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 9		GROUP 10		GROUP 11		GROUP 12	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
		T10B	50.00	T10B	41.67	T8	92.31
						T9	73.08
						T10A	76.92
						T10B	100.00

Appendix E.2 continued. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

## GROUP 13

REGION	PCT FREQ
W13	16.67
W14	16.67
W15	66.67
W16	83.33
W17	83.33
W18	66.67
W19	66.67
W20	66.67
W21	83.33
W22	83.33
W23	83.33
W24	83.33
NT29	16.67
NW	16.67
NU	16.67
SLE	16.67
GT	33.33
EA	16.67
EP	83.33

## GROUP 14

REGION	PCT FREQ
W1	23.53
W2	23.53
W3	5.88
W4	11.76
W6	5.88
W8	5.88
W9	23.53
W11	41.18
W12	11.76
W13	11.76
W14	23.53
W15	35.29
W16	29.41
W17	58.82
W18	64.71
W19	64.71
W20	47.06
W21	76.47
W22	70.59

Appendix E.2 continued. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 13		GROUP 14	
REGION	PCT FREQ	REGION	PCT FREQ
NL	83.33	W23	70.59
MU	66.67	W24	58.82
YP	66.67	NT25	23.53
SL	66.67	NT26	17.65
KI	66.67	NT27	5.88
SE	66.67	NT28	23.53
FR	83.33	NT29	29.41
MO	16.67	NW	29.41
CT	33.33	NU	35.29
ST	33.33	SLE	23.53
NWS	33.33	GT	41.18
CWS	50.00	EA	35.29
SWS	50.00	EP	76.47
SWP	50.00	NL	70.59
SFWP	33.33	MU	76.47
V1	33.33	YP	88.24
V2	50.00	SL	100.00
V3	83.33	KI	82.35
V4	83.33	SE	76.47
V5	83.33	FR	64.71
V6	50.00	BK	23.53
V7	100.00	BN	35.29

Appendix E.2 continued. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 13		GROUP 14	
REGION	PCT FREQ	REGION	PCT FREQ
V8	83.33	CO	11.76
V9	66.67	DD	52.94
V10	66.67	GN	17.65
V11	100.00	QLE	29.41
V12	100.00	MA	41.18
V13	16.67	MI	29.41
V14	50.00	MO	52.94
V16	83.33	NK	11.76
T3	50.00	PC	23.53
T4A	66.67	SK	17.65
T4B	16.67	WA	29.41
T5	50.00	WB	17.65
T7A	100.00	NC	76.47
T7B	66.67	CC	100.00
T10B	16.67	SC	94.12
		NT	70.59
		CT	94.12
		ST	100.00
		NWS	64.71

Appendix E.2 continued. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.



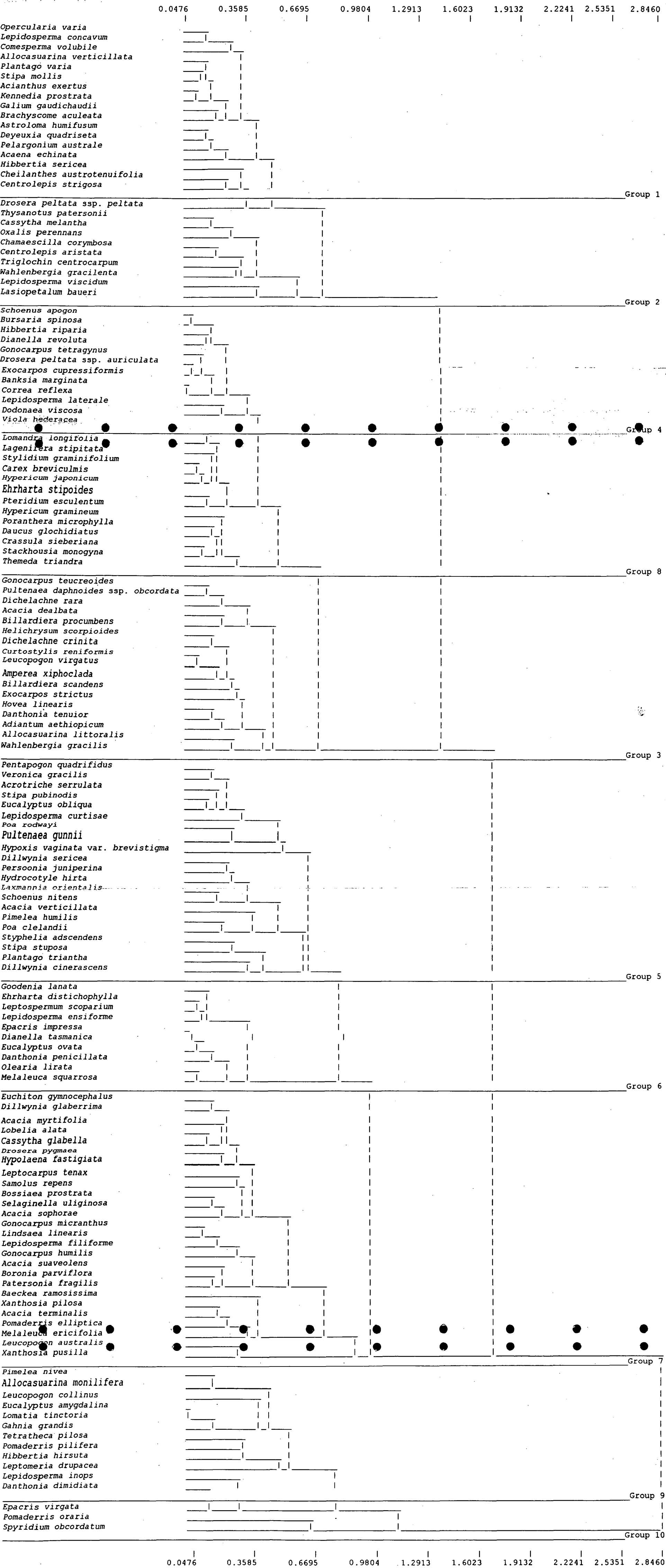
GROUP 14

REGION	PCT FREQ
CWS	70.59
SWS	82.35
NWP	47.06
SWP	58.82
NFWP	47.06
SFWP	58.82
V1	64.71
V2	76.47
V3	100.00
V4	94.12
V5	100.00
V6	82.35
V7	100.00
V8	88.24
V9	88.24
V10	100.00
V11	100.00
V12	94.12
V13	58.82
V14	88.24
V15	82.35
V16	94.12

Appendix E.2 continued. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

T1	58.82
T2	82.35
T3	88.24
T4A	94.12
T4B	88.24
T5	82.35
T6	70.59
T7A	100.00
T7B	94.12
T8	47.06
T9	58.82
T10A	35.29
T10B	82.35

Appendix E.2 continued. Phytochorological analysis (*S. microphyllum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.



Appendix E.3. Phytochorological analysis. Dendrogram from hierarchical clustering of taxa recorded with, and adjacent to, *S. obcordatum* populations.

GROUP 1		GROUP 2		GROUP 3		GROUP 4	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
W1	5.56	W5	11.11	W17	5.88	W11	8.33
W2	5.56	W7	11.11	W18	11.76	W16	8.33
W4	5.56	W9	11.11	W19	5.88	W17	8.33
W6	5.56	W11	22.22	W20	11.76	W19	8.33
W8	5.56	W13	11.11	W21	5.88	W21	8.33
W9	5.56	W14	22.22	EP	5.88	W22	8.33
W10	5.56	W15	44.44	MU	11.76	W23	8.33
W11	5.56	W16	66.67	YP	5.88	NW	8.33
W12	5.56	W17	66.67	SL	29.41	SLE	16.67
W13	5.56	W18	77.78	KI	17.65	EA	8.33
W15	11.11	W19	66.67	SE	41.18	EP	91.67
W17	27.78	W20	55.56	FR	5.88	NL	91.67
W18	11.11	W21	77.78	BN	35.29	MU	58.33
W19	33.33	W22	77.78	CO	11.76	YP	75.00
W20	16.67	W23	88.89	DD	82.35	SL	100.00
W21	27.78	W24	77.78	GN	5.88	KI	91.67
W22	22.22	NT29	11.11	GS	5.88	SE	100.00
W23	27.78	NW	22.22	QLE	35.29	FR	75.00
W24	22.22	NU	33.33	MA	5.88	BN	58.33
NT25	5.56	SLE	33.33	MI	5.88	CO	25.00
NT26	5.56	GT	44.44	MO	76.47	DD	75.00
NT28	5.56	EA	44.44	NK	11.76	QLE	58.33
NT29	5.56	EP	100.00	PC	11.76	MA	25.00

Appendix E.4. Phytochorological analysis (*S. obcordatum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 1		GROUP 2		GROUP 3		GROUP 4	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
NU	5.56	NL	88.89	SK	5.88	MO	91.67
EA	5.56	MU	88.89	WA	11.76	NK	33.33
EP	83.33	YP	100.00	WB	17.65	PC	41.67
NL	66.67	SL	100.00	NC	94.12	SK	8.33
MU	66.67	KI	100.00	CC	100.00	WB	50.00
YP	94.44	SE	100.00	SC	100.00	NC	91.67
SL	100.00	FR	66.67	NT	94.12	CC	100.00
KI	94.44	MO	11.11	CT	100.00	SC	83.33
SE	88.89	WA	11.11	ST	100.00	NT	83.33
FR	61.11	NC	11.11	NWS	58.82	CT	100.00
DD	27.78	CC	22.22	CWS	82.35	ST	100.00
QLE	11.11	SC	11.11	SWS	52.94	NWS	83.33
MA	5.56	CT	44.44	NWP	5.88	CWS	83.33
MO	22.22	ST	33.33	SWP	23.53	SWS	83.33
WB	5.56	NWS	44.44	SFWP	11.76	NWP	41.67
NC	72.22	CWS	44.44	V2	17.65	SWP	50.00
CC	94.44	SWS	44.44	V3	52.94	NFWP	8.33
SC	88.89	NWP	22.22	V4	64.71	SFWP	8.33
NT	44.44	SWP	55.56	V5	82.35	V1	25.00
CT	94.44	NFWP	11.11	V6	47.06	V2	58.33
ST	94.44	SFWP	33.33	V7	88.24	V3	66.67
NWS	22.22	V1	88.89	V8	64.71	V4	83.33

Appendix E.4 continued. Phytochorological analysis (*S. obcordatum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 1		GROUP 2		GROUP 3		GROUP 4	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
CWS	50.00	V2	88.89	V9	76.47	V5	91.67
SWS	77.78	V3	100.00	V10	64.71	V6	58.33
NWP	27.78	V4	55.56	V11	100.00	V7	91.67
SWP	44.44	V5	88.89	V12	100.00	V8	83.33
SFWP	16.67	V6	44.44	V13	64.71	V9	83.33
V1	50.00	V7	100.00	V14	82.35	V10	91.67
V2	77.78	V8	66.67	V15	41.18	V11	100.00
V3	100.00	V9	66.67	V16	100.00	V12	100.00
V4	88.89	V10	66.67	T1	23.53	V13	66.67
75	94.44	V11	77.78	T2	64.71	V14	75.00
V6	77.78	V12	77.78	T3	70.59	V15	83.33
V7	100.00	V13	22.22	T4A	100.00	V16	100.00
V8	88.89	V14	44.44	T4B	88.24	T1	83.33
V9	100.00	V15	22.22	T5	82.35	T2	83.33
V10	88.89	V16	66.67	T6	29.41	T3	100.00
V11	100.00	T1	11.11	T7A	94.12	T4A	100.00
V12	94.44	T2	22.22	T7B	76.47	T4B	100.00
V13	55.56	T3	55.56	T8	35.29	T5	100.00
V14	88.89	T4A	100.00	T9	29.41	T6	91.67
V15	61.11	T4B	33.33	T10A	47.06	T7A	100.00
V16	94.44	T5	66.67	T10B	58.82	T7B	91.67
T1	27.78	T6	11.11			T8	91.67

Appendix E.4 continued. Phytochorological analysis (*S. obcordatum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 1		GROUP 2		GROUP 3		GROUP 4	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
T2	61.11	T7A	77.78			T9	58.33
T3	38.89	T7B	33.33			T10A	75.00
T4A	100.00	T9	11.11			T10B	100.00
T4B	88.89	T10A	22.22				
T5	77.78	T10B	22.22				
T6	27.78						
T7	94.44						
T8	83.33						
T9	22.22						
T9	11.11						
T10A	5.56						
T10B	44.44						

Appendix E.4 continued. Phytochorological analysis (*S. obcordatum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 5		GROUP 6		GROUP 7		GROUP 8	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
W17	14.29	SL	10.00	W12 12	3.85	W1	23.08
W18	4.76	KI	10.00	W13 13	3.85	W2	23.08
W19	4.76	SE	30.00	W14 14	3.85	W3	7.69
W20	9.52	CC	20.00	W15 15	3.85	W4	7.69
W21	4.76	SC	70.00	W16 16	11.54	W9	15.38
W23	4.76	NT	30.00	W17 17	19.23	W11	23.08
NL	14.29	CT	50.00	W18 18	7.69	W14	15.38
MU	23.81	ST	60.00	W19 19	26.92	W15	38.46
YP	9.52	SWS	10.00	W20 20	23.08	W16	30.77
SL	71.43	NFWP	10.00	W21 21	34.62	W17	46.15
KI	28.57	V3	30.00	W22 22	7.69	W18	46.15
SE	76.19	V4	70.00	W23 23	15.38	W19	46.15
FR	9.52	V5	90.00	SLE 32	3.85	W20	46.15
DD	9.52	V7	70.00	EP 35	26.92	W21	53.85
NC	4.76	V8	40.00	NL 36	15.38	W22	38.46
CC	4.76	V9	100.00	MU 37	11.54	W23	38.46
SC	52.38	V10	100.00	YP 38	11.54	W24	30.77
NT	23.81	V11	100.00	SL 39	53.85	NT25	23.08
CT	23.81	V12	100.00	KI 40	50.00	NT26	15.38
ST	52.38	V13	80.00	SE 41	61.54	NT27	7.69
SWS	14.29	V14	80.00	FR 42	7.69	NT28	15.38
SWP	9.52	V15	40.00	CO 45	7.69	NT29	23.08

Appendix E.4 continued. Phytochorological analysis (*S. obcordatum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.



GROUP 5		GROUP 6		GROUP 7		GROUP 8	
REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ	REGION	PCT FREQ
V1	9.52	V16	100.00	DD 46	3.85	NW	15.38
V2	19.05	T1	100.00	QLE 49	7.69	NU	15.38
V3	61.90	T2	90.00	MO 52	61.54	SLE	15.38
V4	85.71	T3	100.00	PC 54	7.69	GT	23.08
V5	80.95	T4A	100.00	SK 55	3.85	EA	15.38
V6	33.33	T4B	100.00	WB 57	42.31	EP	38.46
V7	90.48	T5	90.00	NC 58	92.31	NL	53.85
V8	80.95	T6	100.00	CC 59	92.31	MU	46.15
V9	80.95	T7A	100.00	SC 60	92.31	YP	30.77
V10	57.14	T7B	100.00	NT 61	38.46	SL	100.00
V11	85.71	T8	90.00	CT 62	65.38	KI	76.92
V12	95.24	T9	90.00	ST 63	38.46	SE	84.62
V13	42.86	T10A	70.00	CWS 65	3.85	FR	30.77
V14	61.90	T10B	90.00	SWS 66	3.85	BK	30.77
V15	42.86			V1 71	3.85	BN	53.85
V16	66.67			V2 72	26.92	CO	46.15
T1	23.81			V3 73	30.77	DD	92.31
T2	19.05			V4 74	84.62	GN	15.38
T3	57.14			V5 75	65.38	QLE	69.23
T4A	100.00			V6 76	26.92	MA	30.77
T4B	66.67			V7 77	69.23	MI	23.08
T5	80.95			V8 78	42.31	MO	92.31

Appendix E.4. Phytochorological analysis (*S. obcordatum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 5		GROUP 7			GROUP 8	
REGION	PCT FREQ	REGION	PCT FREQ		REGION	PCT FREQ
T6	33.33	V9	79	88.46	NK	46.15
T7A	95.24	V10	80	57.69	PC	53.85
T7B	76.19	V11	81	73.08	SK	53.85
T8	33.33	V12	82	96.15	WA	23.08
T9	38.10	V13	83	38.46	WB	61.54
T10A	47.62	V14	84	84.62	NC	100.00
T10B	61.90	V15	85	19.23	CC	100.00
		V16	96.15		SC	100.00
		T1	57.69		NT	100.00
		T2	38.46		CT	100.00
		T3	100.00		ST	100.00
		T4A	100.00		NWS	76.92
		T4B	42.31		CWS	84.62
		T5	88.46		SWS	69.23
		T6	19.23		NWP	46.15
		T7A	100.00		SWP	38.46
		T7B	53.85		NFWP	30.77
		T8	30.77		SFWP	23.08
		T9	57.69		V1	38.46
		T10A	57.69		V2	53.85
		T10B	80.77		V3	61.54

Appendix E.4. Phytochorological analysis (*S. obcordatum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

## GROUP 8

REGION	PCT FREQ
V4	100.00
V5	100.00
V6	69.23
V7	100.00
V8	100.00
V9	100.00
V10	100.00
V12	100.00
V11	100.00
V13	100.00
V14	100.00
V15	100.00
V16	100.00
T1	69.23
T2	69.23
T3	84.62
T4A	100.00
T4B	100.00
T5	100.00
T6	92.31
T7A	100.00
T7B	100.00

Appendix E.4. Phytochorological analysis (*S. obcordatum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

## GROUP 8

REGION	PCT FREQ
T8	92.31
T9	76.92
T10A	84.62
T10B	100.00

## GROUP 9

REGION	PCT FREQ
NC	8.33
SC	8.33
NT	8.33
CT	16.67
ST	8.33
V11	25.00
V12	8.33
V14	16.67
V16	33.33
T1	8.33
T2	25.00
T3	75.00
T4A	100.00
T4B	58.33
T5	75.00

## GROUP 10

REGION	PCT FREQ
V14 84	33.33
V12 82	33.33
T4A 90	100.00

Appendix E.4. Phytochorological analysis (*S. obcordatum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

GROUP 9

REGION	PCT FREQ
T6	33.33
T7A	100.00
T7B	83.33
T8	50.00
T9	41.67
T10A	50.00
T10B	100.00

Appendix E.4. Phytochorological analysis (*S. obcordatum*). Percentage occurrence of phytochorological groups (compound averages) in each region. See Appendix E.5 for a key to regions.

**Appendix E.5. Key to biogeographic regions used in the phytochorological analysis.**

