

School of Environmental Biology

Conservation biology of the rare and threatened
Dryandra ionthocarpa*, *D. mimica* and *D. serra

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Abstract

The genus *Dryandra*, in the family Proteaceae, is endemic to south-western Australia. It consists of 92 named species and is an important component of some kwongan communities. Various aspects of the ecology of three threatened species of *Dryandra* (*Dryandra ionthocarpa*, *D. mimica* and *D. serra*) were studied. Threats to these species include weed invasion, inappropriate fire regimes, disturbance from roads, recreational activities, grazing, trampling, clearing and chemical drift from adjacent farms. Knowledge presented within on the ecology and biology of these three species is needed to develop appropriate conservation and management strategies.

Population measurements of plant dimensions and seed bank size were assessed. Seed banks of all three species were shown to increase with increasing plant size. *D. ionthocarpa* and *D. serra* produced large numbers of viable seeds which was related to their mode of regeneration after fire. Experimental fires killed both species and seedling recruitment occurred following the death of adult plants. This indicated that both species are nonsprouters. *D. mimica* produced extremely small numbers of seeds, and had a high level of barren cones. Following an experimental burn, resprouting of adult plants was observed, but no seedling recruitment, indicating that this species is a resprouter.

Granivore exclusion experiments showed that the seed banks of *D. ionthocarpa* and *D. serra* increased after the application of insecticide or bagging. Granivores are therefore considered to be a significant factor limiting the size of the seed bank. Timing of attack for *D. ionthocarpa* was shown to occur early in inflorescence development. However, the seed predators did not start to consume the seeds until after the infructescence was almost fully developed.

Translocation studies were used to investigate whether *D. ionthocarpa* could survive and grow on other soil types or under the same edaphic conditions in other areas. Survival after nine months was better in spongolite or heavy clay soils. The highest survival and growth was for spongolite soils in a nature reserve near to the two

known populations, indicating that this species will grow well, at least initially, in other areas, and that this area can be considered suitable for a larger scale translocation. Reciprocal translocations were used to assess whether *D. serra* shows adaptation to local conditions across its distribution. No clear pattern was found, with only seedlings from the South Sister population surviving better at their original locality. Monitoring over a longer time period is recommended to assess whether a clearer pattern develops after flowering and fruiting.

Plants of *D. ionthocarpa* with orange leaves were found to be under greater water stress during summer and autumn than green plants. The levels of chlorophyll *a* and *b* were also lower in orange plants in summer and autumn than green plants. These differences were attributed to a drought response, and the orange colour of this species during summer can therefore be used as an indicator of the health of the populations.

An important objective of these investigations was to provide baseline information that could be used in the development of conservation and recovery strategies for these species. Several management actions are recommended. The health of the *D. ionthocarpa* populations should be assessed regularly using the orange foliage colour and total plant numbers as indicators. In the event the population is in decline the use of small scale controlled burns in autumn is recommended to stimulate seedling recruitment. This should be undertaken in conjunction with the control of seed predators pre-burn, and the watering of any seedlings recruited post-burn, for at least the first summer. In addition, translocation to other matched sites, particularly the spongolite soils of the Kalgan Plains Nature Reserve is recommended. No exclusion from fire is deemed necessary for *D. mimica*, as this species appears to tolerate fire. Active management of *D. serra* is not considered necessary, instead the species should be monitored regularly.

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Chapter 1: General Introduction

The southwestern portion of Australia is considered a region of extraordinary botanical diversity. This region has a mediterranean-type climate and stretches from Point Culver in the south-east to Shark Bay in the north-west. It is considered to have a floristic diversity similar to that of the much acclaimed diversity of rainforests at the same scale (Hopper *et al.* 1990), but differs in that there are a large number of species in relatively few genera and a high species turn over (where similar habitats that are only a short distance apart have few, or no species in common).

In Australia there are 17,590 described species of indigenous vascular plants (Hnatiuk 1990) and it is estimated that 80% of these are endemic (Leigh and Briggs 1992). There were 7,125 described species in Western Australia in 1985 (Green 1985) and in 1988 this number was raised to 7725 (Green 1988). Beard (1969) first estimated the number of endemic species in southwestern Australia at 69% and Hopper (1979) suggested that the actual figure may be between 75 and 80% of the flora. Estimates place the number of undescribed species in Western Australia at 2000 (Hopper *et al.* 1990) and so the actual number of endemics may even be higher, and many of these are likely to be rare and geographically restricted.

The high number of endemic species in southwestern Australia has been attributed to geographic and climatic changes during the Tertiary (70 to 2 million years ago) and Quaternary (2 million years ago to present) periods (Hopper 1979, James and Hopper 1981). The flora of Australia during the Tertiary was thought to consist mainly of sub-tropical to temperate rainforest (Hopper 1979). Increased aridity associated with major climate changes during the Tertiary and Quaternary lead to the extinction of many rainforest species and adaption of others to the drier climate, gradually forming the dry sclerophyll forest that is now characteristic in Western Australia. It is thought that geological activity then caused a change in drainage patterns (Hopper *et al.* 1996). The uplifting of the Darling Scarp is believed to have

diverted the river systems from an eastern flow to a western and southern flow and resulted in the formation of chains of salt lakes in the old eastern flowing river systems (Hopper *et al.* 1996). Limestone laid down over the Nullabor Plain about 30 million years ago formed an edaphic barrier to plant species migration between eastern and western Australia. The typical soil types of the southwestern region (ie, leached, nutrient impoverished laterites), were also thought to have formed during the tertiary period.

Hopper (1979) divided southwestern Australia into three rainfall zones: high rainfall near the coast, low rainfall arid zone in inland regions and the transitional zone between the high and low rainfall zone. In the high rainfall zone broadscale laterite formation is thought to have occurred, whilst at the same time erosion of these lateritic soils was thought to have occurred in the transitional and low rainfall zones (Hopper *et al.* 1996). The changing drainage patterns and edaphic conditions may have resulted in the fragmentation of the landscape and hence large populations of plants. Habitat fragmentation may also have caused the genetic isolation of plant populations and hence favoured rapid speciation.

During the Quaternary it is believed that there were several periods of climatic fluctuations that caused changes in the sea level, and this affected coastal vegetation also favouring speciation. These arid phases may also have caused the climatic isolation of the southwestern flora from the northern and eastern flora, often resulting in further speciation. It is believed (Hopper *et al.* 1996) that the arid phases placed greater stress on species growing in the transitional rainfall zone as they may have experienced large fluctuations in rainfall. Extensive climatic fluctuations have been postulated as a major factor contributing to greater speciation in the transitional rainfall zone. These geological and climatic factors are considered to be critical reasons for the high vascular plant diversity found in southwestern Australia (Hopper *et al.* 1996).

Rarity

A particular feature of this botanical diversity is the large number of rare and geographically restricted species and species with small population sizes (Hopper *et al.* 1990). The term rare has been defined and discussed by numerous authors. Reveal (1981) defined rarity as the current status of an extant taxon, which through any combination of factors is restricted either in number or area to a level that is demonstrably less than the majority of other organisms of comparable taxonomic rank. A species may be quite rare, yet reproducing and competing adequately with others. A newly evolved species may be rare at present, but possess the potential for a greater range. Likewise, a widespread species may be locally scarce yet maintain itself well regionally. Harper (1981) suggested rarity is related to the number of sites a species occupies, the size of the sites, the carrying capacity of these sites, the time over which the site is habitable, the ability of the species to disperse from these sites and the effect of predators and pathogens. Rabinowitz (1981) considered rarity developed as a combination of factors: range (large or small), habitat specificity (wide or narrow) and local abundance. She identified seven forms of rarity from permutations of these factors.

Kunin and Gaston (1993) hesitated to define the term rare as it describes a wide range of spatial and temporal patterns of abundance, from sparsely populated species with a wide geographic range, to point endemics, which are locally abundant. Fiedler (1986) also steered away from defining rarity, and suggested that the definitions of rarity supplied by Harper (1981), Rabinowitz (1981) and Reveal (1981) had too narrow a focus. Fiedler (1986) suggested nine factors which need to be addressed before the causes and consequences of rarity are understood and a comprehensive approach to management could be developed. These are: age of the taxon, evolutionary history, taxonomic position, ecology, population biology, reproductive biology, land use history and recent human uses.

Fiedler (1987) cautioned against the single species approach to rare flora research. Specific features such as an unusual floral biology or seed dispersal may only be distinguished by comparisons between rare and more common (closely related) species. Kunin and Gaston (1993) also recommended that research on rare species incorporate a more common species for comparison. They suggested that differences between rare and common species may have evolved to cope with the condition of rarity or may indicate that a species is more prone to rarity. This, of course, is only the case if a species is naturally rare. Species which have become rare due to human intervention may not follow this pattern.

Much research has therefore focused on comparisons between closely related rare and common species to help address why a species is rare. Aplet and Laven (1993), using four species of closely related Hawaiian Asteraceae, investigated the proposal that poor competitive ability leads to rarity. They concluded that relative abundance and competitive ability are only one aspect that explains the rarity of some species. Snyder *et al.* (1994) also tested the idea that poor competitive ability was the factor that restricted rare species. They compared the rare species, *Echinacea tennesseensis*, to two closely related species, *E. angustifolia* var. *angustifolia* and *E. pallida*, using growth characteristics to test whether the two common species were competitively superior to the rare species. They concluded that poor competitive ability cannot account solely for the rarity of *E. tennesseensis*. The idea that rarity is explained by evaluating the competitive competency of a species was also examined by Rabinowitz *et al.* (1984). They compared sparse and common perennial grasses. They concluded that, as seedlings, sparse species were advantaged and common species disadvantaged by competition. As tillers, both common and sparse species were unaffected by competition. Therefore, competitive ability was not considered the cause of rarity; rather it is a way of offsetting the problems associated with low densities and makes persistence more likely. Witkowski and Lamont (1997) compared attributes of the rare *Banksia goodii* with its more widespread relative, *B. gardneri*. They concluded that the rarity of *B. goodii* may have more to do with its

recent origin and habitat fragmentation than inferior vegetative, reproductive or ecological attributes.

From the above it is clear that no one definition of rarity can cover the range of issues and concepts involved. However, for the purpose of management, a definition is needed. The comment of Harper (1981) that rarity as a conservation term is different from rarity as a legal term warrants attention. A purely conservation perspective eliminates calling a plant rare on one side of the political border and common on the other. However, for administrative reasons a legal definition using political borders is needed (Harper 1981). There have been several attempts to classify what a rare species is in Western Australia, in the legal sense. Marchant and Keighery (1979) used the criterion of poorly collected (less than five collections) to indicate rarity. From this, 2053 species were listed as actually or potentially at risk in Western Australia. Rye (1981) used the criterion of geographical restriction to define a rare species. As such, 527 native flowering plant species were considered to be restricted to a range of less than 100 km and a further 128 had a range of between 100 and 160 km in Western Australia.

However, the focus has now shifted from listing rare plants to listing threatened plants. Plants that are rare may not necessarily be at risk of extinction and therefore do not necessarily warrant special legal protection. Plants that are at risk of becoming extinct because they are threatened by one or more threatening processes do warrant special legal protection. For example *Banksia brownii* is a species represented by 15 populations, which range in size from 500 individuals to less than 10 plants. All populations are threatened by dieback (*Phytophthora cinnamomi*) and habitat loss due to extensive clearing. Despite the relatively large numbers of *B. brownii* populations and individuals, this species is at high risk of extinction and therefore warrants legal protection.

Accordingly, the criteria that are used now to define a threatened species are as follows (CALM Policy Statement No. 9 1992):

- a) The taxon is well-defined, readily identified and represented by a voucher specimen in the State or National Herbarium;
- b) Must have been searched for thoroughly in the wild; and
- c) Searches have established that the taxon is either:
 - 1) rare
 - 2) in danger of extinction
 - 3) deemed to be threatened and in need of special protection
 - 4) presumed extinct.

Using these criteria, 357 species were classified as Declared Rare Flora in 1998, of which 27 are considered extinct and a further 1926 are on the priority list for further surveys or monitoring to clarify their status (K. Atkins, pers. comm.).

Threats To Threatened Species In Western Australia

There are numerous threats to threatened species in southwestern Australia. They include problems associated with small population sizes, diseases such as *Phytophthora cinnamomi* and aerial canker, land clearing, mining activities, inappropriate fire regimes, grazing and trampling, introduced weeds and feral animals, accidental destruction, drought and altered hydroecology (particularly rising salinity) (Hopper *et al.* 1990, Coates and Atkins 1997, Brown *et al.* 1998).

1. Problems associated with small population sizes

Many rare species are known from populations with few individuals. The “Allee” effect is a form of density dependence that occurs when, below some critical level, individual fecundity declines as population density declines (Allee 1949). When populations become small, there may be a loss of genetic variation due to inbreeding among related individuals, this results in reduced viability and fecundity. This may also occur when populations are so sparsely spread that it is difficult to reach a 'mate'

(Burgman *et al.* 1993). The seed set of the threatened plant *Senecio integrifolius* decreased with decreasing population size demonstrating an example of the Allee effect (Widen 1993). Lamont *et al.* (1993a) demonstrated the existence of this effect for the rare *Banksia goodii*. Small populations of this species produced no, or fewer, seeds per unit crown cover in contrast to larger populations. They demonstrated this result was not due to resource limitations and suggested that it may be due to fewer pollinator visits, reducing pollen availability and quality, or inbreeding depression. The effect of small population sizes is not well documented for Western Australian flora, but poses a major problem in managing rare species (Coates and Atkins 1997). In addition to reduced fecundity, there is an increased risk of catastrophic events, such as fire or clearing along road verges, destroying these small populations. They are also vulnerable to edge effects such as weed invasion, herbicide drift, predation by introduced herbivores and disease (Hopper *et al.* 1990).

2. Diseases

A significant proportion of the southwestern Australian flora is under serious threat from the destructive root rot disease, *Phytophthora cinnamomi*. The disease is already well developed across extensive regions of the higher rainfall zone, with many hundreds of species considered to be susceptible (Shearer 1994). It was first recognised in the southwestern Australian flora in 1964 (Podger 1972). The disease is thought to be exotic (Podger 1972, Weste 1974) and may be of Indo-Malayan origin. It is presently known to have a distribution that covers much of the area bounded by Eneabba (300 km north of Perth), Dryandra (150 km south east of Perth) and Cape Arid (130 km east of Esperance) (Shearer 1994). A further six species of *Phytophthora* have also been isolated in Western Australian plant communities, but are not considered to be as serious a threat as *P. cinnamomi* (Hill 1990).

P. cinnamomi enters the host through its roots and invades the conducting elements of the plant, killing the phloem and cambium (Weste and Marks 1987) and blocking the xylem. It produces symptoms of wilting, dieback and leaf discoloration, which are

similar to that of drought stress and phosphorus toxicity (Grose 1991). Species infected by *P. cinnamomi* die as a result of drought stress, due to the inability of the roots to conduct water and nutrients. The maximum expression of disease characteristics occurs on shallow soils when there are wet periods at temperatures over 12°C (Weste 1974, Weste and Marks 1987).

The effects of this disease on the plant community are considered devastating. It converts evergreen forests to species poor and open communities of reduced productivity (Podger 1972). Up to 50-75% of species have been eliminated by the pathogen in certain Western Australian plant communities (Podger 1972).

P. cinnamomi and other *Phytophthora* diseases cause greatest impact among species that belong to the families Proteaceae, Epacridaceae, Myrtaceae, Dilleniaceae, Papilionaceae and Xanthorrhoeaceae (Hill 1990). Many species from the family Proteaceae have a high susceptibility to *P. cinnamomi* (Barker and Wardlow 1995, Podger and Brown 1989, Wills 1992, Shearer 1994). Cho (1983) tested 33 *Banksia* species: eight species were resistant to the fungus, 13 were moderately susceptible and 12 were highly susceptible. All resistant species were native to eastern Australia, whilst the moderately and highly susceptible species were restricted to Western Australia and southeastern Australia. McCredie *et al.* (1985) also confirmed this trend. They tested 39 species of Western Australian and 10 eastern Australian species of *Banksia* for resistance to *P. cinnamomi*. Eight of the 10 eastern Australian species showed resistance to *P. cinnamomi*, one species had low susceptibility and one species was highly susceptible. However, no Western Australian species showed resistance to the disease and the majority had medium to high susceptibility. The tests by Zentmyer (1980) included five species of *Dryandra*; all were considered hosts (able to be infected) for *P. cinnamomi*.

Many threatened species are susceptible to *P. cinnamomi*. Barker and Wardlow (1995) stated that of the genera most susceptible to *P. cinnamomi*, most are rare or

threatened species. They tested 47 species of rare Tasmanian flora: 36 species were susceptible, four species were resistant but hosts to the disease, 3 species were resistant and four species showed inconclusive results. The presence of *P. cinnamomi* is of particular importance in the management of rare or threatened plant species in southwestern Australian due to the high number of species threatened by this disease (Brown *et al.* 1998).

3. Other threats

The other threats to threatened flora include land clearing, mining activities, grazing and trampling by stock, inappropriate fire regimes, weeds, drought, accidental destruction and rising salinity. Inappropriate fire regimes will be discussed in Chapter 3.

Clearing for agriculture, housing, roads and mining has destroyed and fragmented the habitats of rare species. Habitat fragmentation has been documented as resulting in lower species diversity (Jennersten 1988). Over 90% of native vegetation has been destroyed in some districts in the wheatbelt, resulting in a highly fragmented landscape (Hopper *et al.* 1990).

About 19% of all endangered plant species in Western Australia occur on private land, many of these in unfenced remnants on farming properties (Coates and Atkins 1997). Grazing and trampling by stock is a problem for the threatened species that occur in these remnants. Most rare plant species do not have a tolerance to bruising and compression that many of the weed species (commonly grasses) have (Crawley 1986). Total vegetation cover, species diversity and total number of vascular plant species have been documented as decreasing following trampling by humans in coastal communities in Denmark (Andersen 1995). Grazing has also been documented as resulting in lower species diversity in Wandoo and Gimlet woodlands (Abensperg-Traun *et al.* 1998). Fencing of rare plant populations has been shown to have a positive effect on population size and habitat recovery (Coates and Atkins 1997).

Fencing of a population of *Darwinea carnea*, resulted in the population increasing from approximately five individuals in 1978 to a peak of almost 100 individuals in 1994 (Coates and Atkins 1997).

Invasive weeds are considered to be a major threat to threatened flora populations (Coates and Atkins 1997). Weeds outcompete the native flora, which can result in lower species diversity (Abensperg-Traun *et al.* 1998). In addition the flammability of the habitat often increases due to higher fuel loadings (Abensperg-Traun *et al.* 1998). Control is difficult due to the large number of weed species and the constant reinvasion from adjoining farms and road verges (Coates and Atkins 1997).

Soil salinity has increased following the widespread clearing of deep-rooted native perennials for the growing of short-lived shallow-rooted agricultural crops (Anon. 1996). The removal of deep-rooted perennials results in a rise in the watertable and as the watertable rises the large quantities of salt stored in the soils are brought closer to the surface causing the twin problems of waterlogging and increased salinity (George *et al.* 1996). Watertables are rising by between 0.05 and 0.5 metres per year, with a rise in the watertable of over 25 m in some areas since widespread clearing began approximately 80 years ago (George *et al.* 1996). Widespread clearing has resulted in over one million hectares of land in Western Australia becoming salt affected, almost 2 million hectares becoming waterlogged and the loss of 5 mm per decade of soil to erosion (Lefroy *et al.* 1993). Under present management practices it is estimated that approximately 25% of most landscapes in the southwest, and as much as between 40-50% of some landscapes low in the catchment, may become salt affected in the next 100 years. A consequence of this altered hydrology may be the loss of many reserves and numerous species of threatened flora (Coates and Atkins 1997, Brown *et al.* 1998).

The Genus *Dryandra*

Dryandra belongs to the family Proteaceae and is endemic to southwestern Australia. George (1996) described 92 species as belonging to *Dryandra*, 33 species for the first time. The *Dryandra* inflorescence is a compact head consisting of numerous flowers set on a curved woody receptacle and surrounded by prominent bracts (George 1996). It is considered to be closely allied to the genus *Banksia* (Johnson and Briggs 1975) but the latter flower head does not possess prominent involucre bracts and has a long woolly rachis. The inflorescences are usually yellow, but vary from cream to orange (Sainsbury 1985), with the main flowering period for the genus occurring during spring. *Dryandra*'s are mostly prostrate to low, sclerophyllous, perennial shrubs, with a few species attaining tree status. Highest species richness occurs around Eneabba (northern sandplains) and the Stirling Ranges (southern sandplains), with moderate species richness in between (Griffin 1985). These two regions have an annual rainfall between 400 and 600 mm and are dominated by scrub-heath (kwongan) vegetation. *Dryandra* species are usually restricted to well drained sandy or lateritic soils (Griffin 1985).

Five species of *Dryandra* are currently listed as Declared Rare Flora (Wildlife Conservation (Rare Flora) Notice 1998). A further 39 species are on the Priority Flora list, as they are considered at risk of depletion if action is not taken to protect them (Wildlife Conservation (Rare Flora) Notice 1998). *Dryandra* blooms are highly sought after in the wildflower industry, with 7.6% of the total of 13,814,000 flowering stems picked from all species being from *Dryandras* (Burgman and Hopper 1982). Currently about 32 species, mostly from wild populations, are exploited by the industry (Rye *et al.* 1980, Burgman and Hopper 1982). Diseases pose a great threat to *Dryandra* species. The dieback fungus (*P. cinnamomi*) is a threat to survival of plant communities along the southern coast of Western Australia where *Dryandras* are prominent. *Dryandra* is considered to be an important element of some kwongan and other sclerophyllous shrubland communities (Griffin 1985). Together with a reduction in reproductive potential via the wildflower industry and loss of plants via

dieback disease, it is important that research into the conservation biology of this significant genus is undertaken.

This study focused on three threatened *Dryandra* species: two prostrate Declared Rare species and one upright Priority Four species. They are described below.

Dryandra ionthocarpa A. S. George (Kamballup dryandra) occurs in only two known populations and is restricted to spongolite soils near Kamballup (Figures 1 and 2). *D. ionthocarpa* is a prostrate species and the leaves are pinnatifid, 80-250 mm long, 5-20 mm wide and with 15-35 triangular lobes on each side (George 1996). Inflorescences are terminal with 40-60 flowers per inflorescence. Flowers are pink-mauve with pale yellow limbs, and occur in September-October. Disease, chemical pollution from fertilisers and herbicides from the adjacent farm, together with weed invasion appear to be threats to this species.

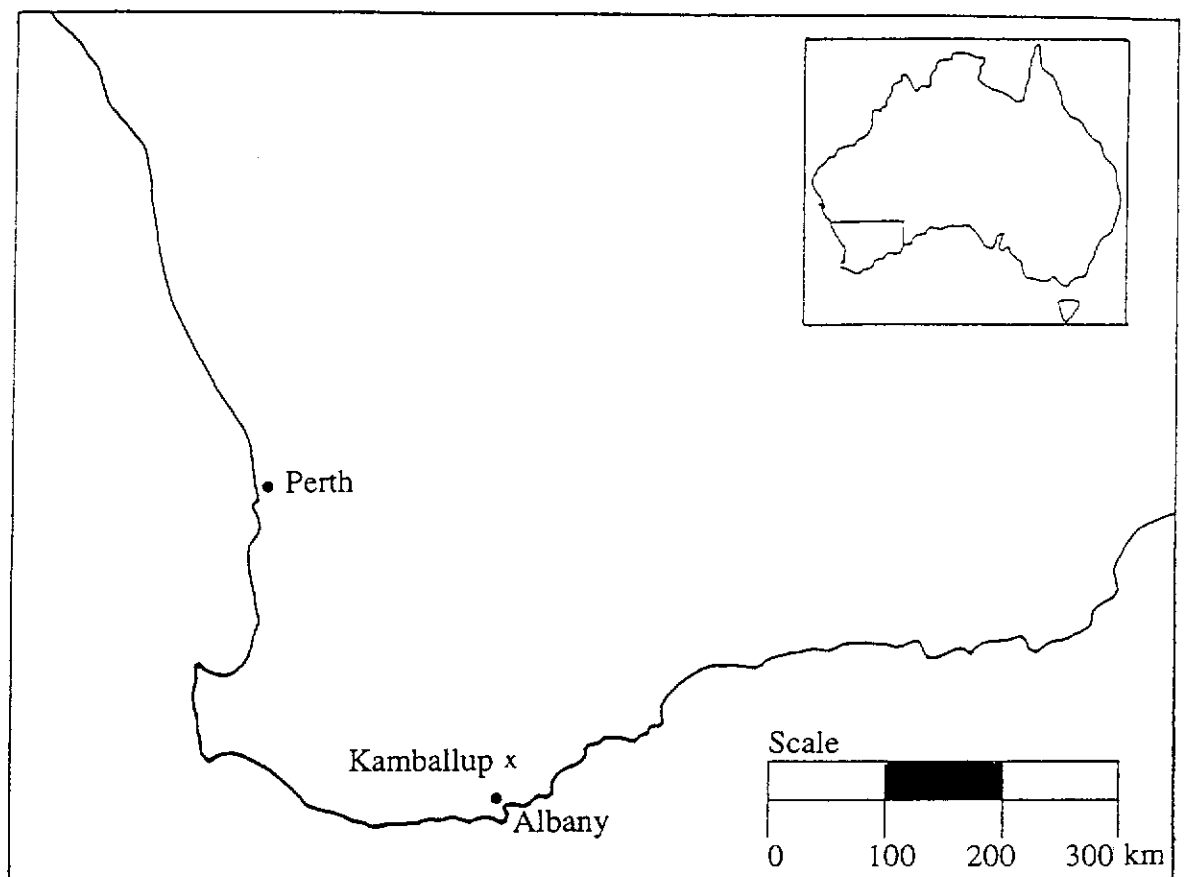


Figure 1. Map of southwestern Australia showing the location of the *Dryandra ionthocarpa* populations.



Figure 2. The low heathland habitat of *Dryandra ionthocarpa*. A plant (of 0.35m in height) is shown in the bottom right hand corner. The Porongurup Range is in the background.

Dryandra mimica A. S. George (summer honeypot) is a small prostrate shrub known from three disjunct localities on private properties at Mogumber and Welshpool (Perth) and in State Forest in the Whicher Range near Busselton (Figures 3 and 4). Leaves are 130-350 mm long and 5-15 mm wide with rounded sinuses between the lobes (George 1984). The yellow inflorescences are terminal with about 20 flowers per inflorescence. Flowering occurs in summer (Sainsbury 1985). From personal observations, threats to this species include grazing and trampling by stock, weed invasion, disease and clearing for agriculture.

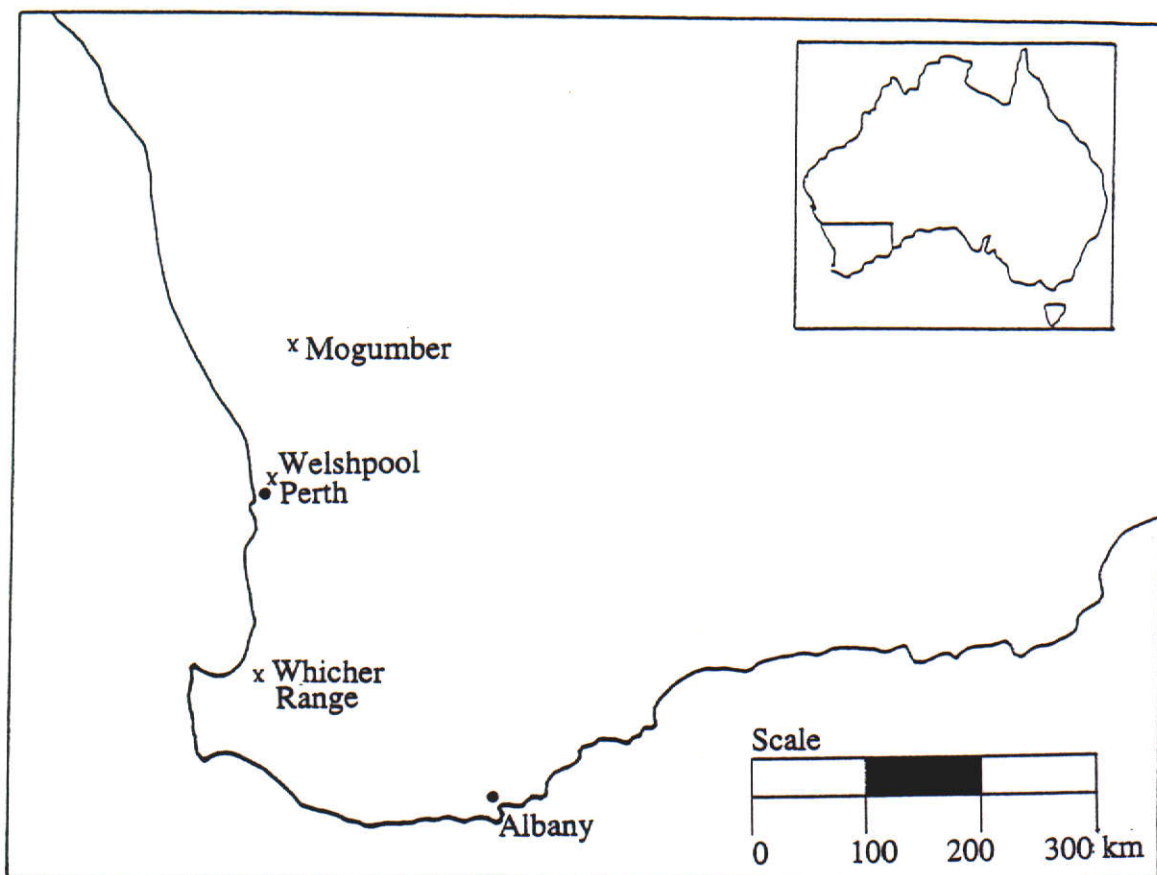


Figure 3. Map of southwestern Australia showing the location of the *Dryandra mimica* populations.



Figure 4. The scrubland habitat of *Dryandra mimica*. Arrow indicates an individual of *D. mimica*.

Dryandra serra R. Br. occurs in 10 known populations from Bow River to Mount Manypeaks in the extreme south of Western Australia (Figures 5 and 6). *D. serra* is an erect multi-stemmed shrub to 6 m high. Leaves are 30-150 mm long, 5-15 mm wide, glabrous on the upper surface, and tomentose on the lower surface (George, unpublished). Leaves are divided almost to the midrib with 8-20 triangular lobes on each side. Inflorescences are 20 mm long and 10 mm wide, on short axillary branchlets surrounded by floral leaves. Flowers are pale yellow, 20-36 per inflorescence, and occur in July-October (Sainsbury 1985). Disease is considered to be the major threat to this species, as it is highly susceptible to *P. cinnamomi* and aerial canker, and five of the known populations are already infected with both pathogens (M. Grant pers. comm.). Disturbance from roads and recreational activities also appear to be threats to this species.

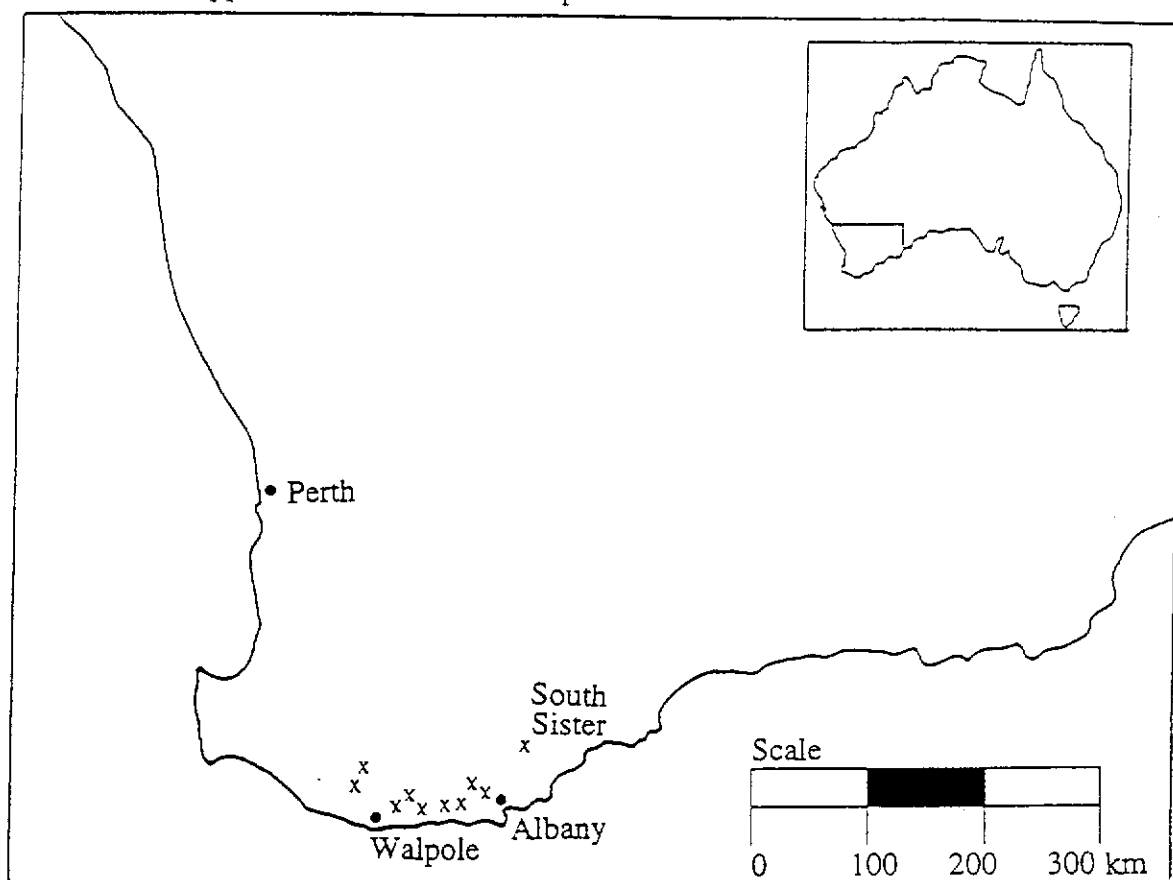


Figure 5. Map of southwestern Australia showing the location of the *Dryandra serra* populations.



Figure 6. The Eucalypt woodland habitat of *Dryandra serra*. Janine is standing to the right of a *D. serra* plant, which is almost double her height.

Aims and Objectives

Very little is known about the biology and ecology of the genus *Dryandra*. The research presented here aims to investigate the conservation biology of *D. mimica*, *D. ionthocarpa* and *D. serra*, with particular emphasis on the gathering of data for the future management and recovery planning of these species. The demography of the three species will be investigated in Chapter 2. In particular the fecundity to size relationship, the fate of the seed, the fecundity to age relationship in the case of *D. serra*, the age structure of the *D. serra* populations and comparisons between populations for *D. ionthocarpa* and *D. serra*. This information will provide baseline data for assessing population decline and the success of future translocations. The response to fire for all three species will be investigated in Chapter 3. This information will provide data for assessing the role of fire as part of a management program. The effect of granivory on seed bank size of *D. ionthocarpa* and *D. serra* will be assessed in Chapter 4. Granivore exclusion will be used to evaluate whether

granivores are limiting the size of the seed bank and whether these need to be controlled to reduce their impact. The ability of *D. ionthocarpa* and *D. serra* to survive following translocation to other, disease free, habitats will be investigated in Chapter 5. In particular the ability of *D. ionthocarpa* to survive and grow in soil types other than spongolite, and whether any adaptation to localized conditions has occurred in the widely distributed populations of *D. serra*. These preliminary translocations will be used to assess the suitability of the chosen translocation sites and whether translocations are a viable management option. Finally Chapter 6 focuses on whether the orange foliage colour of some *D. ionthocarpa* plants during summer is a response to water stress, and whether this foliage colour can be used as an indicator of population health.

Chapter 2: Demography

Introduction

The pattern of seedling recruitment over time controls the age structure of a plant population. This is influenced by the timing of seed release, which may be delayed for up to 30 years in some Proteaceous species (Lamont *et al.* 1991a). Little is known about the recruitment biology in *Dryandra*, however it is likely to be similar to the closely related and widely studied genus, *Banksia*.

Seeds for most southwestern Australian Proteaceae may be stored within the canopy, or on or in the soil (Lamont and Groom 1998). Seeds of *Banksia*, *Hakea*, *Isopogon* and *Petrophile* are commonly stored within woody fruits or infructescences (Lamont and Groom 1998). The length of time the seeds are retained is referred to as their level of serotiny (Lamont *et al.* 1991a). Storage in the soil is uncommon within these genera as the seeds are often short lived once released from the follicles (Lamont and Groom 1998). The genera *Conospermum*, *Persoonia*, *Adenanthos* and *Grevillea* have hard coated, long lived seeds which are stored on or in the soil (Lamont and Groom 1998). Little is known about seed storage in *Dryandra*. The seeds are contained within leathery follicles that appear to be retained in the canopy for some years (Bell *et al.* 1993). However, *D. sessilis* is known to release seeds as soon as they ripen and therefore stores its seeds on or in the soil until the first rains (Lamont and Groom 1998).

A strongly serotinous species will have an even-aged population with a peak in plant age corresponding to a major disturbance event, such as fire, which triggers general seed release. Lamont *et al.* (1991b) showed that *Banksia cuneata* followed this pattern. The ages of plants in one population corresponded to the timing of road works and fires in the area. *B. attenuata* and *B. leptophylla* (both strongly serotinous species), and *B.*

menziesii and *B. prionotes* (both weakly serotinous species), were shown to have most of their recruitment confined to the post-fire period (Cowling *et al.* 1987). Most seedlings, which resulted from the spontaneous release of seeds each year in the absence of fire, did not survive the first summer.

Fire is a common trigger for seed release among *Banksia* species (Siddiqi 1976). *Dryandra* is known to be closely allied to the genus *Banksia* (Johnson and Briggs 1975), and therefore fire is likely to be a trigger for seed release in *Dryandra* as well. The hot and drying effects of fire weaken the resin that holds the follicles closed (Enright and Lamont 1989a). The seeds are insulated from the heat of the fire in woody follicles and open post fire (Siddiqi 1976, Lamont 1985). The seeds of *Dryandra* are not protected within the confines of a woody follicle and therefore are believed to be able to withstand intense heat from fires (Bell *et al.* 1993). Death of adult plants is another common trigger for seed release. Significant seedling recruitment was observed following the drought-induced death of adult plants of 47% of proteaceous species studied (Hnatiuk and Hopkins 1980).

The number of juvenile plants recruited to a population is directly linked to seed bank size as controlled by plant age (Lamont *et al.* 1991b) and plant size (Aarssen and Taylor 1992). Cone production increased with age for *B. attenuata*, *B. leptophylla*, *B. menziesii* and *B. prionotes* (Cowling *et al.* 1987). Aarssen and Taylor (1992) showed fecundity was highly correlated with plant size. However, there was variability in reproductive effort exhibited by plants of the same species growing in different environments. Hartnett (1990) also showed a significant positive linear relationship between inflorescence mass and plant size. Harnett (1990) found that there was a pattern among the study species, where sexual reproductive effort increased with increasing ramet size, and concluded that this may be the pattern among clonal composites. In the serotinous *B. burdettii*, canopy seed storage increased exponentially with plant age to a mean of 830

viable seeds at 15 years of age (Lamont and Barker 1988). *B. speciosa* and *B. baxteri* were found to have a seed bank that increased exponentially, whereas *B. coccinea* was found to have a seed bank that increased quadratically, peaking at a plant age of 16 (Witkowski *et al.* 1991).

In this chapter, my aim was to investigate the pattern of seed bank storage and population recruitment among six populations of *D. serra*, two populations of *D. ionthocarpa* and one population of *D. mimica*. Differences between the populations of the same species were compared. These included plant height, plant age (*D. serra* only, as the other species could not be aged), crown volume and plant fecundity. This study will provide baseline ecological data that can ultimately be used for the management and conservation of these species, in particular these data will be essential for assessing the success of any future translocations.

Materials and Methods

Dryandra ionthocarpa

The two known populations of *D. ionthocarpa* were chosen as study sites. These populations are located 500 m apart in the Kamballup Recreation Reserve. Twenty plants were randomly selected within each of three height classes from these two populations. These height classes were 0.31-0.4 m, 0.41-0.5 m and 0.51-0.6 m (no plants were located outside these limits). For each of the 60 plants, height and crown width in two directions (north-south and east-west) were measured. A representative branch was removed from the plant and the number of branches of equivalent size counted. Cones were removed from the branch and categorised as either belonging to this year's crop (1996) or a previous year's crop (pre-1996). This was determined by the colour of the cones. Cones produced in the 1996 season had a reddish brown colour, whereas cones from previous years had a dark brown-grey colour. All follicles were removed from the

cones and counted as either intact, or eaten. Where all the follicles within a cone had been consumed, the number of follicles were estimated by averaging the number of follicles from those cones where it could be determined. Cones which did not have any follicles were classified as eaten when there was a presence of frass.

All intact seeds (one seed per follicle is produced by this species) were removed from the follicles and germinated. Seeds were placed on paper towelling in seedling trays and the trays covered in plastic bags to retain moisture. Seeds were moistened with distilled water whenever necessary and incubated in germination cabinets at 15°C in 24 hour darkness. Seeds were then classified as either viable (germinated) or nonviable (did not germinate). The number of follicles per branch were multiplied by the total number of branches, to provide an estimate of total follicles and seeds per plant. Total viable seed store was estimated by multiplying total number of branches by percentage germination.

Two way Analysis of Variance (ANOVA) were used to compare populations and height categories for all attributes. Paired *t*-tests were used to compared the differences between 1996 and pre-1996 cones for the attributes of open, intact and eaten/decayed follicles. Where appropriate posthoc analysis using Fishers PLSD test was undertaken. Arcsin transformations were undertaken on percentage data prior to analysis.

Soil was collected from around ten plants, five in each population, to assess the presence and size of a soil stored seed bank. Four quadrats of 0.25 m by 0.25 m were measured around each plant. All the soil, to a depth of 0.05 m, was collected from the quadrats, and bulked together for each plant. The soil for each plant was sieved and searched for seeds.

An opportunistic collection was also made of a whole dead plant that had been accidentally pulled from the ground following deep ripping for tree planting. The height

and crown width were measured and the number of cones and follicles counted using the same methods described above. The plant was aged using the growth increment method described by Lamont (1985).

A transect (N-S) was set up through the centre of each of the two populations. The transect started and finished approximately four metres into dense scrub on either side of the populations. The height and identity of the tallest species were recorded at two meter intervals along the transect. The identity of all other species within one meter of the point were also recorded.

Dryandra mimica

Twenty plants were randomly selected within each of three height classes. These height classes were 0.21-0.3 m, 0.31-0.4 m and 0.41-0.5 m (no plants were outside these limits). Height and crown width in two directions (north-south and east-west) were measured for each of the 60 plants. A representative branch was removed and the number of branches of equivalent size was counted for each plant. Cones were removed from the branch and scored as either intact or eaten. All follicles were removed from the cone and counted as either intact or eaten. Intact seeds were removed from the follicles and germinated, and then classified as either viable or nonviable as for *D. ionthocarpa*.

Only the large population at Mogumber was considered suitable for these studies. Other populations at Welshpool and Whicher Ranges were too small, and there was difficulty in identifying individual plants because of their prostrate and intertwining habit. The other population at Mogumber, was considered too disturbed by cattle to be representative for this studies purposes.

One way ANOVA's were used to compare height categories for height, crown width, crown volume, the number of fertile, eaten and intact cones, number of follicles, number

of eaten or intact seed, and percentage viable seed. Where appropriate posthoc analysis using Fishers PLSD test was undertaken. Arcsin transformations were undertaken on percentage data prior to analysis.

Dryandra serra

Ten plants were selected randomly within each of six height classes from the six populations. The height class boundaries were 0-0.5 m, 0.51-1 m, 1.01-1.50 m, 1.51-2 m, 2-3 m and greater than 3 m. Height and crown width in two directions (north-south and east-west) were measured, and age (using the growth increment method, Lamont 1985) and number of cones were recorded for each of the 60 plants. All cones were removed and the number of follicles within each cone counted for the smaller plants (< 2 m). For larger plants (> 2 m), all branches were counted, all cones were removed from five representative branches and the number of follicles within each cone was counted. Open, eaten and intact follicles were counted for each plant and the seeds removed. All intact seeds were germinated at 15°C on agar plates containing 10 mg/L of gibberellic acid and scored as either viable (germinated) or nonviable (did not germinate). A different germination method was used for this species, compared to the other two species, in the belief that the level of fungal attack might be reduced.

Two way Analysis of Variance (ANOVA) was used to compare populations and height categories for all attributes. Except where a three way ANOVA was used to compare populations, height categories and cone ages for percentage of open, eaten and intact follicles. Where appropriate posthoc analysis using Fishers PLSD test was undertaken. Arcsin transformations were undertaken on percentage data prior to analysis.

Results

Dryandra ionthocarpa

A two way ANOVA was used to compare populations and height categories for height and crown volume. No significant difference was found between the two populations for height ($P = 0.4913$), volume ($P = 0.9241$) (Table 1) or total number of cones ($P = 0.3223$) (Table 4). There was a significant difference ($P < 0.0001$) between the height categories for the attributes of height, volume (Table 1) and total number of cones (Table 4). Post-hoc testing showed all height categories were significantly different for height and crown volume at $P < 0.0001$.

Table 1. Mean height (m) and crown volume (m^3) (\pm standard deviation) of *Dryandra ionthocarpa* in two populations (1 and 2) and over four height categories.

Height category (m)	Height (m)		Crown volume (m^3)	
	1	2	1	2
0.31 - 0.40	0.36 ± 0.03	0.35 ± 0.03	0.10 ± 0.03	0.07 ± 0.03
0.41 - 0.50	0.45 ± 0.02	0.46 ± 0.03	0.16 ± 0.06	0.17 ± 0.05
0.51 - 0.60	0.53 ± 0.02	0.54 ± 0.02	0.25 ± 0.07	0.26 ± 0.09

Height and diameter at first cone production can be estimated when height or mean diameter is regressed against number of cones (Figure 7) and is shown below in Table 2.

Table 2. Height (m) and mean diameter (m) of *Dryandra ionthocarpa* in two populations (1 and 2) at first cone production.

Population	Height at first cone production (m)	Mean diameter at first cone production (m)
1	0.26	0.47
2	0.30	0.49

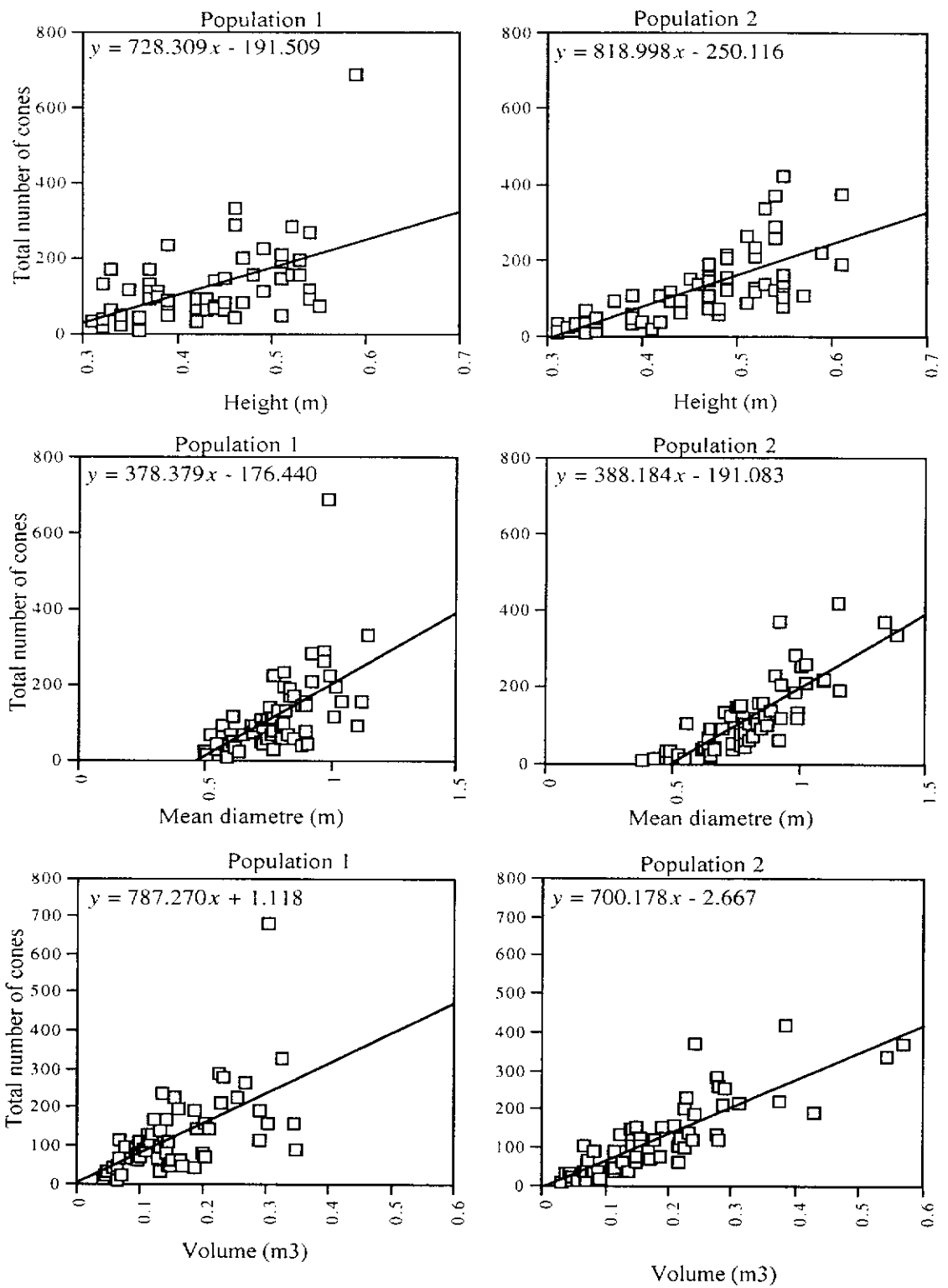


Figure 7. Regressions of height, diameter and crown volume against number of cones for the two study sites of *Dryandra ionthocarpa*.

There was a relatively linear relationship between plant height, crown diameter, volume and total number of cones, with the number of cones increasing as height, crown diameter and volume increased (Table 3).

Table 3. Regression statistics of number of cones of *Dryandra ionthocarpa* against height, diameter and volume.

Attribute	r^2	P
Plant height	0.353	< 0.0001
Crown diameter	0.497	< 0.0001
Crown volume	0.461	< 0.0001

There was no significant difference between populations for the number of cones produced in the 1996 fruiting season ($P = 0.1730$). In contrast there was a significant difference between populations with those cones produced prior to the 1996 fruiting season ($P = 0.7627$) (Table 4). There was a significant difference between all height categories for cones produced in the 1996 fruiting season ($P < 0.0001$) and those produced prior to the 1996 fruiting season ($P < 0.0001$), with the number of cones increasing from the smallest height category to the tallest height category (Table 4).

Table 4. Mean number of cones (\pm standard deviation) of *Dryandra ionthocarpa* in two populations (1 and 2) and over four height categories. Cones are classified as those produced in the 1996 fruiting season and those produced in prior fruiting seasons.

Height category (m)	Number of cones in 1996		Number of cones pre-1996	
	1	2	1	2
0.31 - 0.40	47.74 \pm 35.71	24.25 \pm 17.51	37.22 \pm 27.65	15.45 \pm 11.69
0.41 - 0.50	70.68 \pm 42.79	65.65 \pm 35.89	52.14 \pm 46.49	50.10 \pm 34.47
0.51 - 0.60	123.93 \pm 90.55	112.80 \pm 72.91	65.07 \pm 79.02	81.60 \pm 46.94

The percentage of open follicles was significantly different between those cones classified as produced in the 1996 fruiting season with those produced in earlier fruiting seasons ($P = 0.0074$) and between populations ($P < 0.0001$), but not significant between height categories ($P = 0.0782$) (Table 5). There was no interaction effect between population and height category ($P = 0.1230$). Where follicles were classified as eaten there was a significant difference between cones classified as produced in the 1996 fruiting season and those produced in earlier fruiting seasons ($P < 0.0001$), between height categories ($P = 0.0092$), but no significant difference between the two populations ($P < 0.2490$). There was a significant interaction effect between population and height category ($P < 0.0001$). For those follicles classified as intact there was a significant difference between cones classified as produced in the 1996 fruiting season and those produced in earlier fruiting seasons ($P < 0.0001$), between populations ($P < 0.0001$), and between the height categories ($P = 0.0130$). However, there was no significant interaction effect between height category and population ($P = 0.5832$).

Those cones produced in the 1996 season had fewer open (4.0% compared with 5.8%), fewer eaten (51.4% compared with 88.0%) and more intact (44.6% compared with 6.3%) follicles than cones produced in earlier fruiting seasons. Population 1 had more open (9.0% compared with 0.4%), fewer eaten (54.0% compared with 79.0%) and more intact (37.1% compared with 20.7%) follicles than population 2. There was no significant difference between height categories ($P = 0.8891$) or populations ($P = 0.7321$) for percentage viability of the seeds (Table 6). No soil stored seed bank was found (Table 7).

Table 5. Mean number (% in brackets) of open, eaten, intact and total follicles per cone for *Dryandra ionthocarpa* in two populations (1 and 2) and three height categories. Follicles are from cones classified as those produced in the 1996 fruiting season and those produced in earlier fruiting seasons (Pre-1996).

Height category (m)	1996		Pre-1996	
	1	2	1	2
Open follicles/cone				
0.31 - 0.40	0.50 (5.5)	0.00 (0.0)	0.53 (5.8)	0.00 (0.0)
0.41 - 0.50	0.95 (10.3)	0.00 (0.0)	1.16 (12.6)	0.00 (0.0)
0.51 - 0.60	0.66 (7.1)	0.00 (0.0)	1.30 (14.1)	0.23 (2.1)
Eaten follicles/cone				
0.31 - 0.40	4.49 (49.1)	8.60 (77.6)	7.91 (86.5)	10.93 (97.6)
0.41 - 0.50	2.89 (31.4)	7.97 (71.6)	7.70 (84.3)	10.84 (96.6)
0.51 - 0.60	3.02 (33.7)	6.42 (57.6)	6.53 (71.6)	10.30 (92.6)
Intact follicles/cone				
0.31 - 0.40	4.58 (45.4)	2.97 (22.4)	0.61 (7.9)	0.15 (2.4)
0.41 - 0.50	4.68 (58.3)	3.45 (28.5)	0.32 (3.2)	0.26 (3.4)
0.51 - 0.60	6.01 (59.0)	4.99 (42.2)	1.12 (14.3)	0.38 (5.4)

Table 6. Total number of viable seeds and mean percentage viability of *Dryandra ionthocarpa* seeds per plant in three height categories and two populations (1 and 2).

Height category (m)	1	2
Total number of viable seeds/height category		
0.31 - 0.40	668	353
0.41 - 0.50	905	583
0.51 - 0.60	1392	1145
Mean viability (%) / height category		
0.31 - 0.40	72	79
0.41 - 0.50	83	73
0.51 - 0.60	74	82

Table 7. Number of seeds of *Dryandra ionthocarpa* identified in soil samples collected from around five plants in each of two populations (1 and 2).

Plant number	1	2
1	0	0
2	0	0
3	0	0
4	0	0
5	0	0

The dead plant found pulled from the ground was not significantly different in height from plants in population 1, height category 2 (0.41 - 0.50 m) ($P = 0.1240$) (Table 8). However, it was shown to have a significantly different crown volume ($P = 0.0399$), total number of cones ($P = 0.0171$) and number of cones pre-1996 ($P < 0.0001$). There was no significant difference for the number of cones produced in 1996 ($P = 0.7576$). The whole plant was aged as being approximately 24 years old.

Table 8. Attributes of the whole plant of *Dryandra ionthocarpa* collected from population 1.

Attribute	Pre-1996	1996
Height (m)	0.42	
Volume (m ³)	0.03	
Total number of intact cones	26	23
Total number of eaten cones	258	57
Total number of intact follicles	204	188
Total number of eaten follicles	122	476

D. ionthocarpa was only recorded in vegetation that was less than 1.15 m in height. Associated species that were present in the seven, 1 m² quadrats with *D. ionthocarpa* were all small shrubs or herbaceous species. These were: *Acacia assimilis*, *Agonis spathulata*, *Allocasuarina microstachys*, *Astroloma pallidum*, *Borya* sp., *Drosera erythrorhiza* subsp. *squamosa*, *Drosera menziesii*, various grasses, *Hibbertia microphylla*, *Jacksonia humilis*, *Lepidosperma* sp., *Leucopogon polymorphus*, *Melaleuca carrii*, *M. bracteosa*, *Opercularia vaginata*, *Petrophile teretifolia*, *Stylidium repens*, *Stypandra glauca* and *Verticordia pennigera* (see Table 9 and 10). No indicator species were apparent, and further analyses, such as ordination, were not considered warranted.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
										0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
<i>Acacia assimilis</i>	+	+	+	+	+						+	+							+					+	+	
<i>Agonis spathulata</i>	+										+	+	+		+	+	+	+					+	+	+	+
<i>Allocasuarina microstachys</i>				+	+	+	+	+	+	+	+	+	+		+	+	+	+					+	+	+	
<i>Astroloma pallidum</i>					+		+				+		+													
<i>Argentipallium niveum</i>		+																								
<i>Borja</i> sp.														+								+	+	+		
<i>Calytrix</i> sp.					+																			+		
<i>Dampiera sacculata</i>	+	+																								
<i>Desmocladus flexuosus</i>					+					+				+			+	+	+	+	+	+	+			
<i>Drosera erythrorhiza</i> subsp. <i>squamosa</i>													+			+								+		
<i>Drosera menziesii</i>														+	+									+		
<i>Dryandra ionthocarpa</i>							+				+															
<i>Elythranthera brunosis</i>									+																	
<i>Eucalyptus redunca</i>																		+	+							
Various Grasses		+	+					+																		
<i>Hibbertia microphylla</i>									+			+	+							+			+			
<i>Hypocalymma angustifolium</i>	+																		+							
<i>Jacksonia humilis</i>										+	+			+					+			+	+			
<i>Lepidosperma</i> sp.	+	+	+	+	+	+	+	+	+			+	+	+	+	+		+	+		+		+	+	+	
<i>Leucopogon polymorphus</i>				+		+		+																		
<i>Melaleuca carrii</i>													+	+	+					+	+					
<i>Melaleuca spathulata</i>	+																			+						
<i>Petrophile teretifolia</i>	+					+			+		+							+				+	+		+	
<i>Stylidium repens</i>																				+						
<i>Stypandra glauca</i>					+	+	+	+	+		+											+				
<i>Verticordia pennigera</i>				+	+							+	+	+	+					+	+	+	+	+	+	

Table 10. Associated species of *Dryandra ionthocarpa* in population 2 along a 26 m x 1 m transect. Authorities follow Green (1985, 1988).

Dryandra mimica

The height categories were significantly different by one way ANOVA for height ($P < 0.0001$) and volume ($P = 0.0006$) (Table 11).

Table 11. Mean height and volume (\pm standard deviation) for *Dryandra mimica* in population 1 of the two Mogumber populations. Means are for three height categories.

Height category (m)	Mean height (m)	Mean diameter (m)	Mean volume (m ³)
0.21 - 0.30	0.27 \pm 0.02	0.59 \pm 0.12	0.08 \pm 0.03
0.31 - 0.40	0.34 \pm 0.03	0.75 \pm 0.17	0.16 \pm 0.09
0.41 - 0.50	0.42 \pm 0.01	0.76 \pm 0.26	0.21 \pm 0.14

No significant differences were shown between height categories for the number of fertile, eaten and intact cones, number of follicles, number of eaten or intact seed, and percentage viable seed (Table 12). However, there was a significant difference between height categories for the total number of cones, and number of barren cones (Table 12). Post-hoc testing showed that there was no significant difference between all height categories for the number of fertile, barren, eaten, intact cones, with the exception of height categories 1-2 of barren cones ($P = 0.0051$), height categories 1-2 for eaten cones ($P = 0.0193$), height categories 1-2 of whole cones ($P = .00006$) and 1-3 ($P = 0.0377$). Post-hoc testing also showed no significant difference between any height categories for eaten or intact seeds.

Table 12. Mean number (% of total in brackets) of intact, eaten, whole cones, follicles and seeds and seed viability data (\pm standard deviation) for *Dryandra mimica* from population 1 at Mogumber.

Attribute	Height category (m)			<i>P</i>
	0.21 - 0.30	0.31 - 0.40	0.41 - 0.50	
Mean number of barren cones	43.90 \pm 33.87	87.60 \pm 56.03	88.00 \pm 50.85	0.0125
Mean number of fertile cones				
- eaten cones	3.65 \pm 5.85	16.70 \pm 22.78	14.20 \pm 19.78	0.5610
- intact cones	1.20 \pm 2.98	8.25 \pm 17.81	5.20 \pm 11.63	0.2235
Mean number of cones	48.75 \pm 35.22	112.55 \pm 69.88	107.40 \pm 47.88	0.0018
Mean number of follicles/plant	0.15 \pm 0.37	0.55 \pm 1.10	0.40 \pm 0.89	0.3176
Mean number of intact seeds/ plant	0.05 \pm 0.22 (33.33)	0.55 \pm 1.10 (100.00)	0.40 \pm 0.89 (100.00)	0.1519
Mean number of eaten seeds/ plant	0.10 \pm 0.31 (66.67)	0.00 (0.00)	0.00 (0.00)	0.2843
Total number of viable seeds	0	4	0	-
Mean % germination	0.00	9.60	0.00	0.2101

Height and crown diameter at first cone production could be estimated when height or mean diameter was regressed against number of cones (Figure 8). Height at first cone production was 0.14 m and mean diameter at first cone production was 0.30 m.

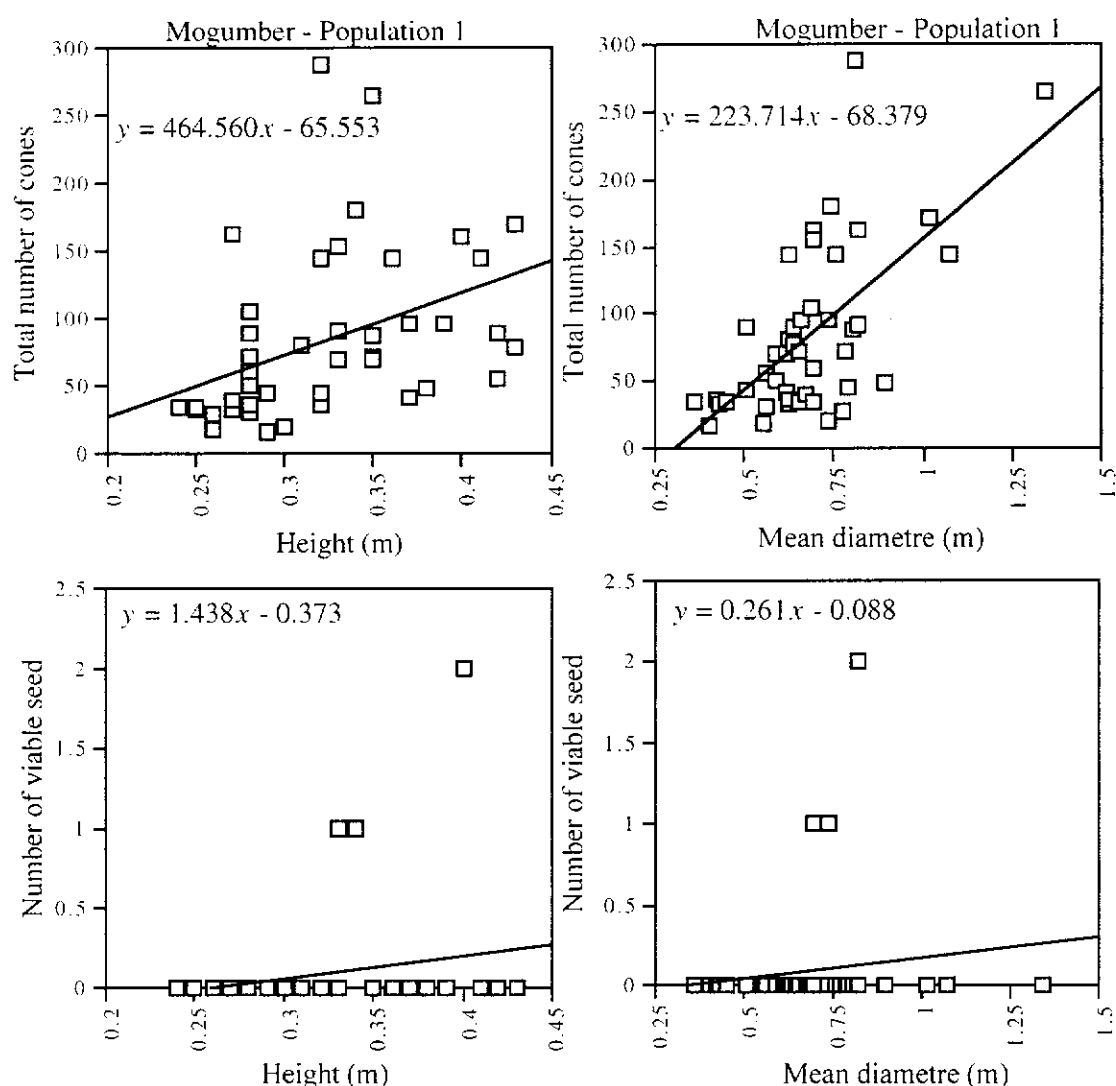


Figure 8. Regressions of height against number of cones and mean diameter against number of cones for *Dryandra mimica*.

There was an increase in the number of cones with increasing plant height, diameter and volume for *D. mimica* (Table 13).

Table 13. Regression statistics of number of cones of *Dryandra mimica* against height, diameter and volume.

Attribute	<i>p</i>	<i>r</i> ²
Height	0.0057	0.164
Crown diameter	<0.0001	0.404
Crown volume	<0.0001	0.414

Dryandra serra

A two way ANOVA was used to compare the heights of *D. serra* between the six populations and six height categories. Analysis showed that the populations were significantly different from each other ($P = 0.0121$) and the height categories were significantly different ($P < 0.0001$). (Table 14). Further pairwise comparisons using Fisher's PLSD test showed that all populations were significantly different at $P < 0.0001$, except for South Sister and Down Road ($P = 0.6646$), Hunwick Road and Mount Hallowell ($P = 0.6804$), Hunwick Road and Kordabup Road ($P = 0.0177$), and Mount Hallowell and Kordabup Road ($P = 0.0495$).

Table 14. Mean height (m) (\pm standard deviation) of the six height categories of *Dryandra serra* at the six study sites.

Height category (m)	South Sister	Down Road	Hunwick Road	Mount Hallowell	Kordabup Road	Rose Road
0.0-0.5	0.25 \pm 0.13	0.25 \pm 0.12	0.24 \pm 0.15	0.32 \pm 0.13	0.26 \pm 0.13	0.20 \pm 0.12
0.51-1.0	0.73 \pm 0.16	0.74 \pm 0.18	0.84 \pm 0.10	0.84 \pm 0.12	0.76 \pm 0.11	0.73 \pm 0.14
1.01-1.5	1.30 \pm 0.16	1.27 \pm 0.16	1.24 \pm 0.14	1.31 \pm 0.24	1.19 \pm 0.13	1.39 \pm 0.20
1.51-2.0	1.76 \pm 0.13	1.71 \pm 0.15	1.64 \pm 0.13	1.80 \pm 0.14	1.77 \pm 0.19	1.74 \pm 0.13
2.01-3.0	2.42 \pm 0.26	2.59 \pm 0.35	2.32 \pm 0.24	2.41 \pm 0.34	2.56 \pm 0.32	2.50 \pm 0.28
> 3.0	3.23 \pm 0.20	3.32 \pm 0.11	3.85 \pm 0.60	3.58 \pm 0.45	4.36 \pm 0.76	3.68 \pm 0.53

A two way ANOVA was used to compare the ages of *D. serra* between the six populations and six height categories. Comparisons of ages between the populations showed that all populations were significantly different ($P < 0.0001$) (Table 15). Of the fifteen possible pairwise comparisons the Fisher's PLSD showed only four were not significant. These were South Sister and Rose Road ($P = 0.4471$), Down Road and Mount Hallowell ($P = 0.0917$), Hunwick Road and Kordabup Road ($P = 0.3860$), and

Mount Hallowell and Kordabup Road ($P = 0.0942$). On comparison of the ages, height categories were significantly different ($P < 0.0001$). Further analysis, using Fisher's PLSD showed that all the height categories were significantly different ($P < 0.0001$), however the pairwise comparison of Hunwick Road and Mount Hallowell was significant at $P = 0.0006$.

Table 15. Mean age (years) (\pm standard deviation) of the six height categories of *Dryandra serra* at the six study sites.

Height category (m)	South Sister	Down Road	Hunwick Road	Mount Hallowell	Kordabup Road	Rose Road
0.0-0.5	2.70 \pm 1.25	2.30 \pm 0.67	2.40 \pm 0.97	2.40 \pm 0.84	2.20 \pm 0.79	2.06 \pm 1.00
0.51-1.0	5.30 \pm 0.95	4.10 \pm 0.74	4.90 \pm 0.88	3.80 \pm 0.63	3.70 \pm 0.68	4.90 \pm 1.45
1.01-1.5	7.20 \pm 2.20	5.00 \pm 0.47	5.30 \pm 1.42	5.50 \pm 0.97	4.30 \pm 0.82	6.50 \pm 2.07
1.51-2.0	8.90 \pm 1.97	5.90 \pm 1.29	6.70 \pm 1.49	6.30 \pm 0.95	5.70 \pm 1.16	6.30 \pm 1.42
2.01-3.0	11.20 \pm 1.99	9.00 \pm 2.26	8.80 \pm 1.39	7.30 \pm 1.16	8.60 \pm 2.37	7.82 \pm 1.24
>3.0	15.67 \pm 1.15	10.33 \pm 1.15	12.60 \pm 1.51	11.00 \pm 2.45	14.70 \pm 2.75	10.97 \pm 2.60

A significant difference between the populations ($P < 0.0001$, $\chi^2=194.14$, $df=45$) was shown when the data in Figure 9. were compared. This is clear from the graphs of the ages (Figure 9) where Down Road, Hunwick Road and Kordabup Road have age peaks in the graphs around one to six years of age, Mount Hallowell and Rose Road have peaks in the age graphs around five to ten years, and South Sister has two peaks around one to two years and ten to 14 years. If the ages of the plants within the different populations are compared using one-way ANOVA there is also a significant difference ($P < 0.0001$). Further analysis using Fisher's PLSD showed that Down Road is significantly younger than all other populations, Rose Road is significantly older than South Sister, Hunwick Road and Kordabup Road, and Mount Hallowell is significantly older than Hunwick Road.

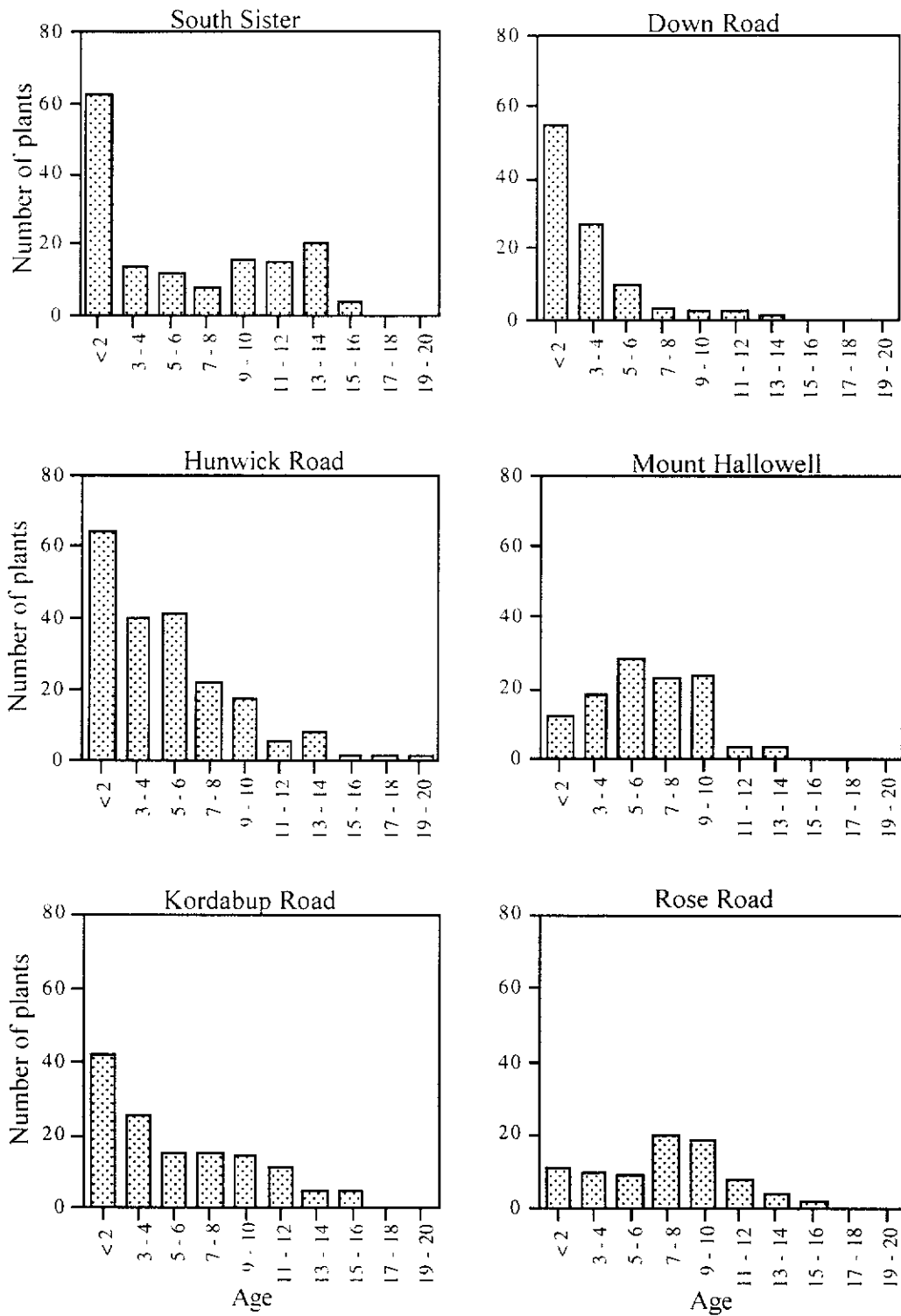


Figure 9. Age distribution graphs for *Dryandra. serra* for the six study sites.

All populations and all height categories were significantly different ($P < 0.0001$), for crown volume, with volume increasing with increasing age (Table 16).

Table 16. Mean crown volume (m^3) (\pm standard deviation) of the six height categories of *Dryandra serra* at the six study sites.

Height category (m)	South Sister	Down Road	Hunwick Road	Mount Hallowell	Kordabup Road	Rose Road
0.0-0.5	0.005 \pm 0.005	0.007 \pm 0.007	0.004 \pm 0.005	0.005 \pm 0.004	0.008 \pm 0.007	0.003 \pm 0.004
0.51-1.0	0.025 \pm 0.014	0.050 \pm 0.028	0.031 \pm 0.011	0.028 \pm 0.008	0.040 \pm 0.010	0.026 \pm 0.026
1.01-1.5	0.125 \pm 0.143	0.094 \pm 0.043	0.070 \pm 0.031	0.040 \pm 0.012	0.078 \pm 0.037	0.138 \pm 0.218
1.51-2.0	0.400 0.369 \pm	0.156 \pm 0.065	0.145 \pm 0.154	0.099 \pm 0.051	0.153 \pm 0.079	0.114 \pm 0.114
2.01-3.0	0.300 \pm 1.889	1.588 \pm 1.268	0.488 \pm 0.403	0.366 \pm 0.238	0.610 \pm 0.572	0.588 \pm 0.599
>3.0	12.100 \pm 1.543	5.031 \pm 2.326	4.372 \pm 2.231	2.018 \pm 1.613	8.128 \pm 7.477	3.061 \pm 2.558

A two-way ANOVA was used to compare the number of cones of *D. serra* between populations and between height categories (Table 17). There was a significant difference between populations and between height categories ($P < 0.0001$).

Table 17. Mean number of cones (\pm standard deviation) of the six height categories of *Dryandra serra* at the six study sites.

Height category (m)	South Sister	Down Road	Hunwick Road	Mount Hallowell	Kordabup Road	Rose Road
0.0-0.5	0.00 \pm 0.00	0.10 \pm 0.32	0.40 \pm 1.26	0.19 \pm 0.32	0.39 \pm 0.68	0.00 \pm 0.00
0.51-1.0	3.70 \pm 3.62	1.50 \pm 1.72	5.40 \pm 3.34	3.80 \pm 2.90	2.00 \pm 2.87	1.00 \pm 2.83
1.01-1.5	8.40 \pm 7.76	2.60 \pm 2.76	6.80 \pm 4.02	17.10 \pm 14.39	10.50 \pm 21.01	4.10 \pm 6.57
1.51-2.0	45.50 \pm 34.49	22.80 \pm 17.86	16.20 \pm 13.28	34.67 \pm 19.64	14.70 \pm 22.40	10.20 \pm 11.27
2.01-3.0	653.04 \pm 622.42	438.00 \pm 506.15	35.70 \pm 22.44	95.30 \pm 56.58	63.14 \pm 53.26	74.24 \pm 101.23
>3.0	1264.00 \pm 829.20	1290.67 \pm 1165.06	279.66 \pm 160.46	379.90 \pm 456.75	1493.50 \pm 866.98	188.79 \pm 173.29

A two-way ANOVA was used to compare the percentage of open, eaten and intact follicles of *D. serra* between populations and between height categories. The percentage of open follicles were not significantly different between the populations ($P = 0.0618$), but were significantly different between the height categories ($P < 0.0001$) (Table 18). Significant differences were found for the percentage of eaten follicles, for between populations, and height categories ($P < 0.0001$) (Table 18). Percentage of intact follicles were also shown to have significant differences between populations, ($P = 0.0104$) and height categories ($P < 0.0001$) (Table 18).

Table 18. Mean number (% in brackets) of open, eaten and intact follicles per plant of *Dryandra serra* at the six study sites.

Height category (m)	South Sister	Down Road	Hunwick Road	Mount Hallowell	Kordabup Road	Rose Road
Mean number of open follicles/plant						
0.0-0.5	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.06 (8.3)
0.51-1.0	0.10 (12.5)	2.40 (24.6)	0.50 (13.1)	0.30 (4.3)	0.00 (0.0)	0.00 (0.0)
1.01-1.5	0.20 (14.3)	0.60 (9.2)	0.40 (12.5)	3.40 (17.4)	1.80 (33.4)	0.00 (0.0)
1.51-2.0	3.06 (18.3)	5.10 (37.8)	2.20 (27.4)	1.90 (9.5)	0.50 (26.6)	0.30 (4.5)
2.01-3.0	19.86 (14.3)	40.58 (18.4)	3.60 (15.6)	6.00 (14.9)	1.25 (4.0)	3.69 (16.2)
>3.0	5.20 (4.2)	98.00 (22.0)	9.38 (9.8)	8.02 (9.9)	163.83 (27.4)	8.03 (22.0)
Mean number of eaten follicles/plant						
0.0-0.5	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	7.00 (58.3)
0.51-1.0	0.00 (0.0)	3.90 (34.8)	0.00 (0.0)	0.40 (6.5)	0.50 (30.0)	0.00 (0.0)
1.01-1.5	0.10 (7.1)	0.00 (0.00)	0.20 (2.5)	2.90 (26.0)	1.70 (17.8)	0.60 (50.0)
1.51-2.0	1.60 (10.6)	4.60 (28.0)	0.40 (3.3)	6.00 (33.3)	2.80 (17.8)	3.10 (27.6)
2.01-3.0	12.94 (21.4)	78.12 (25.7)	2.50 (22.0)	13.40 (38.0)	11.25 (46.7)	11.71 (47.2)
>3.0	37.60 (26.8)	90.53 (22.3)	14.58 (13.5)	41.95 (36.0)	190.63 (35.9)	24.74 (38.6)
Mean number of intact follicles/plant						
0.0-0.5	0.00 (0.0)	0.20 (100.0)	0.5 (100.0)	0.0 (0.0)	0.2 (100.0)	4.0 (33.3)
0.51-1.0	2.40 (87.5)	8.40 (40.5)	4.6 (86.9)	3.7 (89.2)	1.0 (70.0)	2.3 (100.0)
1.01-1.5	1.90 (78.6)	3.10 (90.8)	4.2 (85.00)	7.3 (56.8)	5.4 (48.8)	1.3 (50.0)
1.51-2.0	7.93 (71.0)	7.90 (34.2)	7.6 (69.4)	9.4 (57.2)	7.8 (55.6)	7.5 (67.8)
2.01-3.0	60.76 (64.3)	151.14 (55.9)	13.8 (62.4)	14.1 (47.1)	16.5 (49.3)	10.5 (36.6)
>3.0	82.33 (69.1)	254.00 (55.6)	133.82 (76.7)	61.00 (54.0)	216.57 (36.7)	23.50 (39.5)

A two-way ANOVA was used to compare the percentage of viable seed between populations and between height categories (data were arcsin transformed prior to analysis) (Table 19). There was no significant difference between populations ($P = 0.4655$). However, there was a significant difference between height categories ($P = 0.0062$).

Table 19. Total number of viable seeds and mean % viable seeds (\pm standard deviation) per height category of *Dryandra serra* in each of six populations and six height categories (number of plants in each category in brackets).

Height category (m)	South Sister	Down Road	Hunwick Road	Mount Hallowell	Kordabup Road	Rose Road
Total number of viable seed/height category						
0.0-0.5	0 (0)	4 (1)	0 (0)	0 (0)	3 (1)	7 (1)
0.51-1.0	47 (4)	16 (3)	85 (8)	25 (7)	13 (3)	3 (1)
1.01-1.5	32 (7)	20 (6)	86 (8)	21 (8)	100 (3)	10 (2)
1.51-2.0	118 (10)	63 (6)	138 (7)	30 (8)	133 (3)	32 (6)
2.01-3.0	131 (9)	593 (10)	229 (9)	50 (10)	229 (6)	130 (17)
>3	78 (3)	218 (3)	632 (9)	83 (8)	194 (6)	230 (21)
Mean viability (%) / height category						
0.0-0.5	-	100.0 \pm 0.00	-	-	75.00 \pm 0.00	77.8 \pm 0.00
0.51-1.0	92.15 \pm 10.89	87.50 \pm 12.50	98.75 \pm 3.54	43.04 \pm 40.62	77.78 \pm 38.51	75.0 \pm 0.00
1.01-1.5	63.40 \pm 46.84	26.60 \pm 30.15	97.14 \pm 6.00	26.6 \pm 32.22	98.03 \pm 1.76	62.50 \pm 17.68
1.51-2.0	68.65 \pm 35.97	36.52 \pm 22.22	92.77 \pm 11.95	36.34 \pm 36.06	92.00 \pm 3.61	19.27 \pm 23.29
2.01-3.0	85.68 \pm 17.48	69.77 \pm 21.89	89.36 \pm 24.80	28.19 \pm 26.12	96.30 \pm 2.55	64.88 \pm 34.19
>3	91.77 \pm 9.42	82.00 \pm 17.62	96.79 \pm 3.88	29.98 \pm 18.23	97.37 \pm 3.24	60.70 \pm 27.19

Age of first cone production can be estimated when age is regressed against number of cones (Figure 10). Age of first cone production varied from 3.8 years for Down Road and Rose Road to 4.5 years for South Sister and Hunwick Road (Table 20). Height at first cone production varied from 0.83 m at South Sister and Rose Road to 1.02 m at Kordabup Road (Table 20, Figure 11). The variation in mean crown diameter at first cone production ranged from the smallest diameter of 0.19 m at Rose Road to the largest diameter of 0.35 m at Down Road (Table 20, Figure 12).

Table 20. Age (years), height (m) and crown diameter (m) of *Dryandra serra* in six populations at first cone production. Ages and measurements were determined by solving \times mathematically for where $Y=0$.

Population	Age at first cone production (years)	Height at first cone production (m)	Mean crown diameter at first cone production (m)
South Sister	4.71	0.83	0.32
Down Road	3.83	0.85	0.35
Hunwick Road	4.48	0.97	0.27
Mount Hallowell	3.99	0.95	0.24
Kordabup Road	4.19	1.02	0.34
Rose Road	3.75	0.83	0.19

There was a positive relationship when the number of cones of *D. serra* was regressed against plant height, crown diameter and volume and plant age (Table 21).

Table 21. Regression of number of cones of *Dryandra serra* against height, diameter, volume and age.

Attribute	<i>p</i>	r^2
Height	<0.0001	0.264
Crown diameter	<0.0001	0.583
Crown volume	<0.0001	0.624
Plant age	< 0.0001	0.315

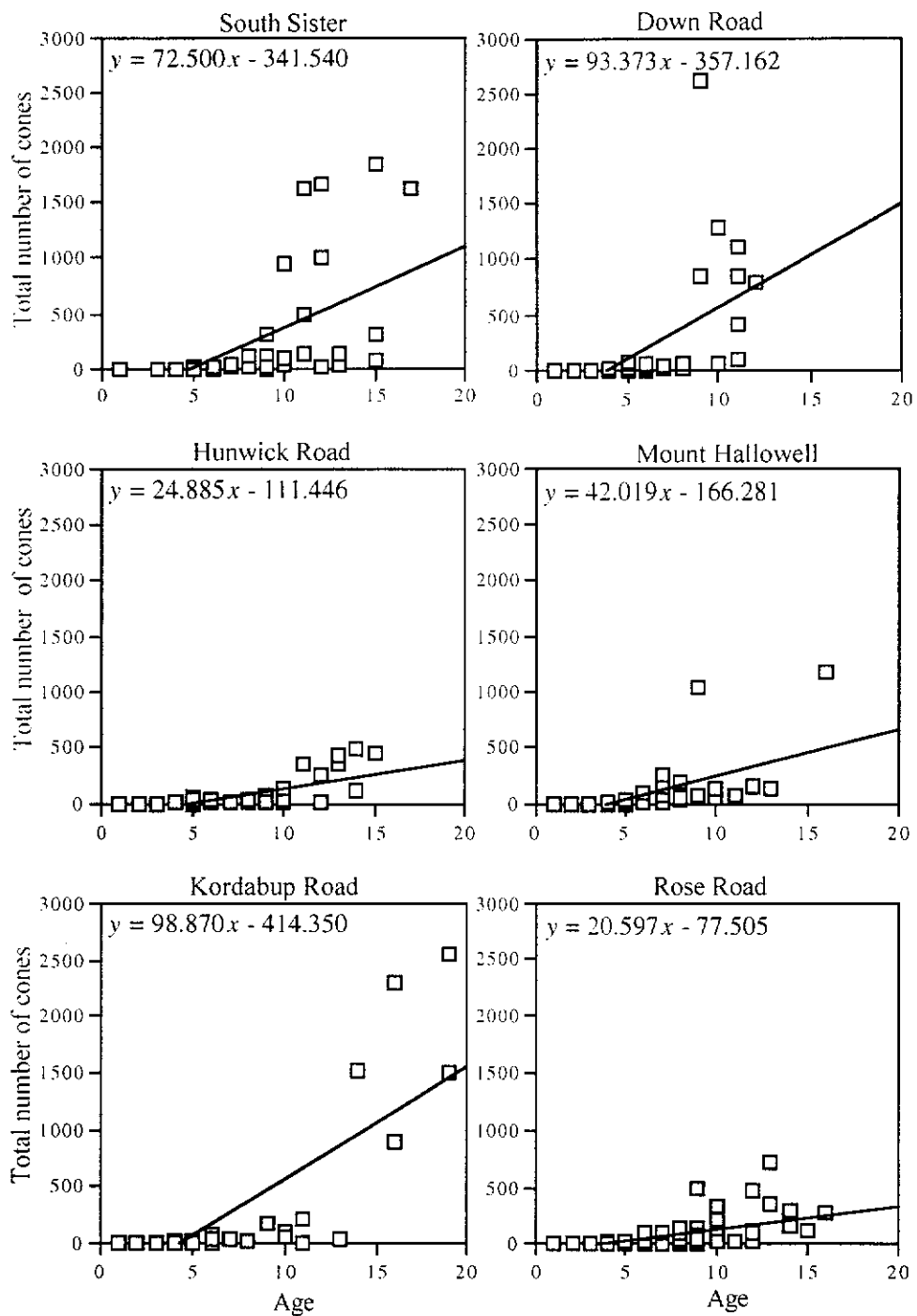


Figure 10. Regressions of age against number of cones for the six study sites of *Dryandra serra*.

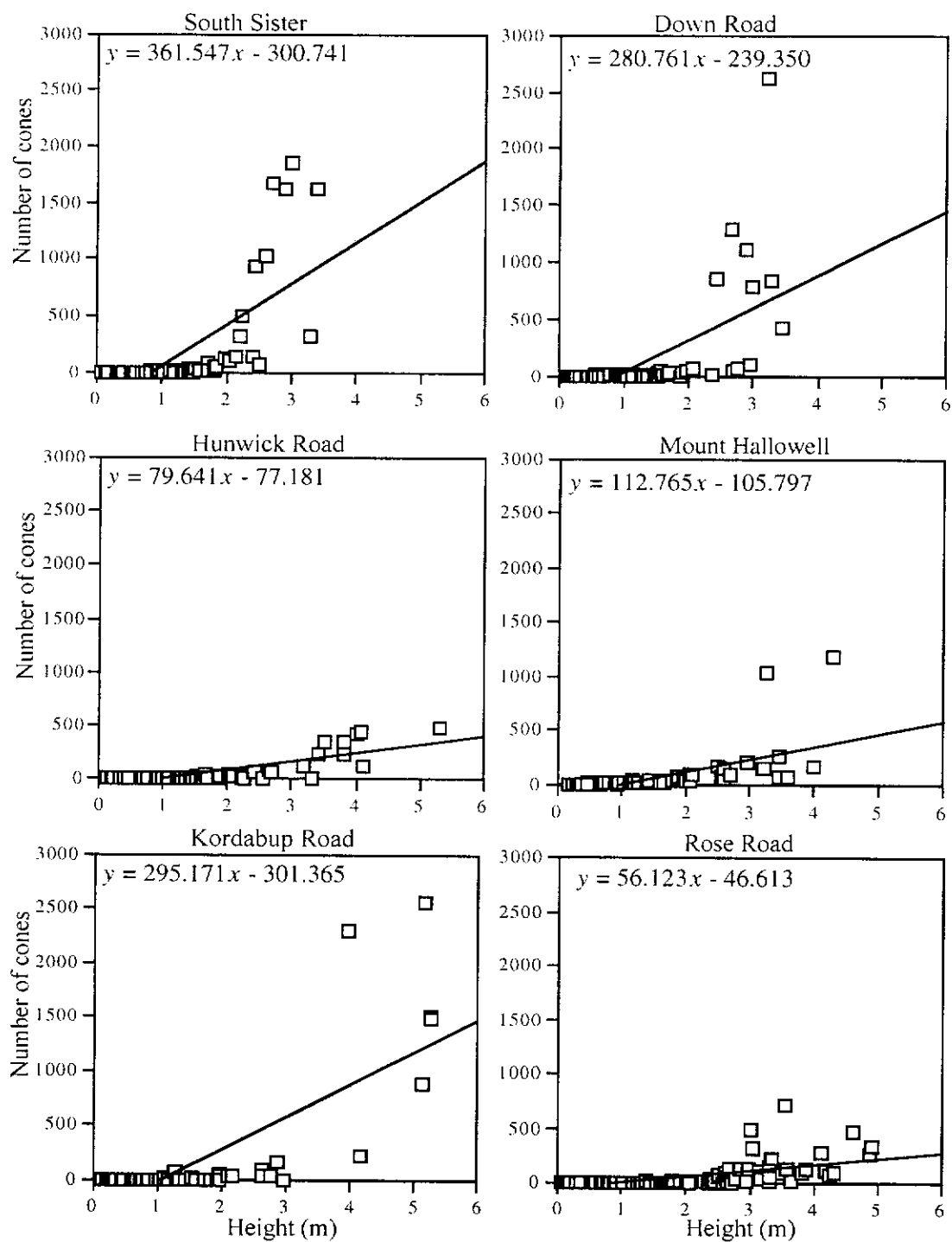


Figure 11. Regressions of height against number of cones for the six study sites of *Dryandra serra*.

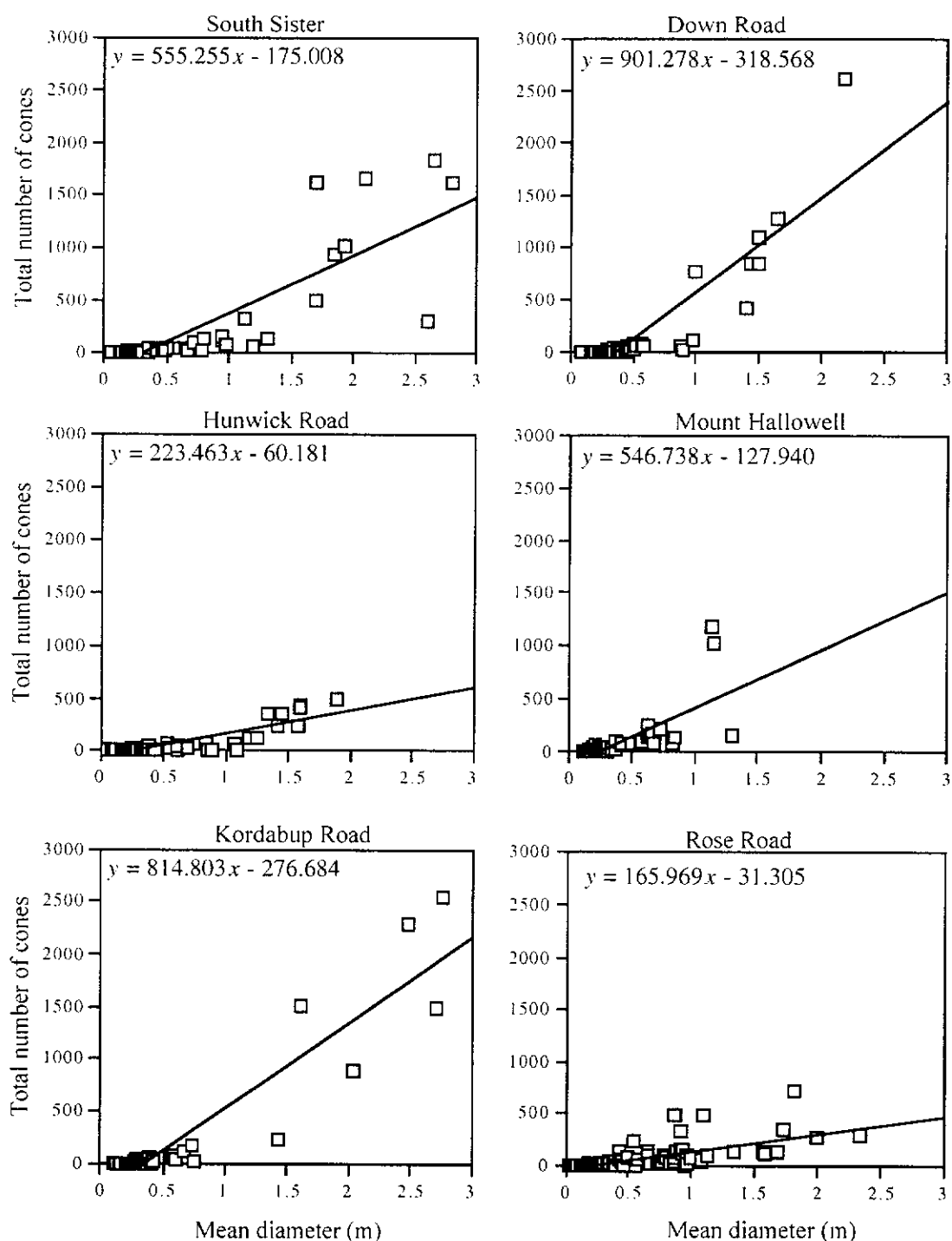


Figure 12. Regressions of mean crown diameter against number of cones for the six study sites of *Dryandra serra*.

Discussion

It is important to know the factors that affect the production of seeds and therefore control the number of seeds available for recruitment of the next generation. Two factors likely to be critical in the control of seed bank size are plant age and size (Aarssen and Taylor 1992).

There is often a correlation between increasing plant age and increasing seed production. For example, Cowling *et al.* (1987) observed a marked increase in cone production with increased plant age for the nonsprouters *Banksia leptophylla* and *B. prionotes*. There was a positive correlation between the number of cones and plant age for *D. serra*, with the number of cones increasing linearly with increasing plant age. Weiner (1988), however, suggests fecundity is best viewed as a function of size rather than age due to factors such as plant density affecting access to nutrients, light, water and therefore affecting size. The number of cones of *D. ionthocarpa*, *D. mimica* and *D. serra* were shown to increase linearly with increasing plant height or volume and therefore larger plants make a greater contribution to the seed bank.

Higher numbers of flower heads and cones were produced in older (21 year old) plants of *B. speciosa*, *B. baxteri*, and *B. coccinea* than in younger (10 year old) plants (Witkowski *et al.* 1991). However, on a percentage basis there were fewer viable seeds and greater amounts of insect damaged seeds in older plants. In contrast the percentage of intact follicles increased and the percentage of eaten follicles decreased with increasing height for *D. ionthocarpa*. This may be a form of seed predator satiation (De Steven 1982, 1983, Cowling *et al.* 1987, Janzen 1971) where larger plants produce larger seed crops and therefore the impact of seed predation is reduced overall.

Many plants must achieve a minimum size before the production of flowers and fruits can occur. Above this size there is a relatively simple relationship between plant size and seed production (Weiner 1988). A linear relationship between size and fecundity was evident for *D. ionthocarpa* and *D. mimica* once a minimum size was reached (Figure 7 and 8). The minimum height of *D. mimica* for the production of sterile cones (0.10 m) was lower than for the production of fertile cones (0.22 m), which is not uncommon among other proteaceous species (Witkowski *et al.* 1991). The minimum height for cone production by resprouting *D. mimica* plants is attained approximately 17 months after a fire (Table 23, Chapter 3). Plants of *D. serra* were almost 1 m tall (see Table 20) before first cone production began. After that a linear relationship between height and cone production was evident (Figure 11).

Fecundity has been shown to be highly correlated with plant size; however, there was variability in reproductive effort exhibited by plants of the same species growing in different environments (Aarssen and Taylor 1992). There is a clear difference between populations of *D. serra* in the age of first reproduction (Table 20) and the rate of canopy stored seed build up (Figure 10). As there is no clear pattern to these differences it is difficult to attribute them to a specific cause. It is likely that it is a combination of environmental factors, such as rainfall and temperature that contribute to these differences. In contrast there was little variation in reproductive effort between the two populations of *D. ionthocarpa*. Considering the short distance between the two populations (~ 500 m) this is not surprising, as environmental differences would be minimal.

Knowledge of the juvenile period of a species in a fire prone environment is important for management considerations (van der Moezel *et al.* 1987). The first cone production for *D. serra* was between 3.83 and 4.71 years of age (see Table 20), which is similar to other nonsprouting Dryandras (van der Moezel *et al.* 1987). Of the three species of

nonsprouting *Dryandra*, researched by van der Moezel *et al.* (1987), all had juvenile periods of between two and four years. In the absence of a reliable ageing method for *D. ionthocarpa* and *D. mimica*, height to first cone production can be substituted, as this is another frequently used measure of plant size. *D. mimica* was 0.14 metres in height at first cone production. From data in Chapter 3, this height was obtained 17 months after a fire, similar to other resprouting *Dryandras*, which have juvenile periods of approximately two years (van der Moezel *et al.* 1987). It is estimated that *D. ionthocarpa* first sets fertile cones at approximately 0.3 metres in height (see Table 2). It is not known how old seedlings of this species are before this height is attained. Seedlings planted in 1996 (see Chapter 5) appear unlikely to set seed within the next few years. If this is the case, the juvenile period for this species is at the upper end of the scale for nonsprouting *Dryandras* (van der Moezel *et al.* 1987).

Dryandra ionthocarpa

A small percentage of intact seeds of *D. ionthocarpa* was stored in the canopy beyond one year (between 2% and 42%). However, in the absence of any accurate ageing method it was not possible to estimate for how long these seeds were retained. From observations, the older cones that contained intact seeds were often located on the outer parts of the branches, and so it can be assumed they were only a few years older than those cones produced in the 1996 fruiting season. Therefore, this species may be considered weakly serotinous.

There were more cones and follicles produced in the 1996 fruiting season than produced in earlier seasons. This suggests that cones and follicles may disintegrate after a few years, and that there is no significant canopy stored seed bank. It is also evident that seed is not retained as a soil stored seed bank (Table 7). It therefore appears that the majority of seeds are released annually from the cones, but decay after only a short time in the soil. This has significant implications for the management of this species,

particularly where fire may be used as a management tool. These data indicate that by spring there is only a small canopy stored seed bank and no soil stored seed bank. Thus a spring or summer fire has the potential to significantly reduce the size of the populations by killing the flowers in spring or immature seed crop in summer.

There were fewer open follicles for cones produced in the 1996 season than for cones produced in earlier fruiting seasons. This means that follicles will open progressively in the absence of fire. Observations showed that almost 100% of the cones from plants burnt for the experiment in Chapter 3, opened in response to an autumn fire, releasing the follicles. Results in Chapter 3 showed that there was significant recruitment following an autumn fire. So, while seeds are released in the absence of fire, it is still the stimulus for mass follicle release and seedling recruitment, similar to other proteaceous species (Cowling *et al.* 1987).

Plant age was estimated at 24 years for the whole dead plant. Anecdotal evidence (B. Beirstow pers. comm. 1996) indicated that the last fire in the *D. ionthocarpa* populations was between 20 and 25 years ago, which corresponds with the estimated age of the whole dead plant. Due to the small variation in plant height (all plants were between 0.3 and 0.6 m) it can be assumed that there is also only a small variation in plant age. If this is the case, there has been little or no subsequent recruitment following initial recruitment after the last fire. Drought induced mortality of the adult plants (see Chapter 6) does not result in seedling recruitment. This is in contrast to findings that almost 50% of the proteaceous species studied, where mortality of the adult plants was induced by drought, resulted in seedling recruitment (Hnatiuk and Hopkins 1980). It appears that recruitment in *D. ionthocarpa* is confined to the postfire period, and population age structure is controlled by the frequency of such disturbance events. This is common for nonsprouting species (Lamont *et al.* 1991a and b).

There were no significant differences between the two populations for mean height, volume, total number of cones, number of cones produced in 1996 or in earlier fruiting seasons or in percentage viability of the seeds. However, there were significant differences between the populations in the fate of the follicles. Population 1 had significantly more open and intact follicles and fewer eaten follicles than population 2. This may be due to the greater number of plants in population 1 (~700) than in population 2 (~300). Satiation of seed predators has been recorded in years of high seed production (De Steven 1982, 1983, Cowling *et al.* 1987, Janzen 1971) and it is possible that this occurred in *D. ionthocarpa*. There may be similar levels of predation in both populations, but this has less impact in the larger population (1).

Dryandra mimica

No seedlings of *D. mimica* were observed during the course of this study. The number of fertile cones was a small percentage of the total number of cones (between 10 and 22%), and viability of the seeds was low (9.6%). In contrast, viability of seeds collected by CALM's Threatened Flora Seed Centre from the same population ranged from 25 to 100% (K. Brown pers. comm. 1997). It is difficult to explain this difference in viability as similar seed incubation conditions were used. However, very little is known about the seed biology of *Dryandra* species and there may be dormancy mechanisms or ripening periods that influence germination.

Almost two thirds of fertile cones had been attacked by insect granivores. This suggests that predation is having a significant effect on the population dynamics of this species. Anderson (1989) argues that if the number of safe sites for seedling recruitment is low, then the effect of predation is negligible, because the number of safe sites is the limiting factor. This may be true for *D. mimica* - the only safe site for seedling recruitment appears to be inside the parent plant where it is less likely to be grazed or trampled by stock or kangaroos. Therefore, there are limited opportunities for seedling recruitment

and intense competition with the adult plant for survival. In which case, predation is not an important factor in limiting seedling recruitment. However, if stock were to be removed (assuming kangaroos have only a small impact) granivory would again become a major limiting factor for recruitment.

Most cones were found to be barren - between 78 and 90% (see Table 12). This is not dissimilar to what has been shown for other resprouting species in the family Proteaceae. Between 62 and 71% of cones were barren in *Banksia menziesii* (Cowling *et al.* 1987, Whelan and Burbidge 1980), 64 and 85% in *B. grandis* (Abbott 1985, Whelan and Burbidge 1980) and 11 and 51% for *B. attenuata* (Cowling *et al.* 1987, Whelan and Burbidge 1980). 99.6% of *B. elegans* cones were found to be barren and it was suggested root suckering, a nutrient conserving strategy, has been adopted over seed production, a nutrient depleting strategy, to cope with a nutrient deficient environment (Lamont and Barrett 1988). *D. mimica* has short underground stems (George 1984), which enable plants to recover after fire, although it is unlikely to be the primary mode of reproduction. Sexual reproduction is considered to be more important for nonsprouters, which rely solely on seed production for postfire survival, than resprouters, where seed production is primarily to facilitate species dispersal (Lamont and Groom 1996). So the high percentage of barren cones for *D. mimica*, similar to other resprouting proteaceous species, may not be an important factor in the survival of this species.

Dryandra serra

The six study populations of *D. serra* were significantly different for most attributes, however, these differences showed no clear pattern. Variation in plant size is common within natural plant populations. Size differences may be due to genetic differences, age differences, environmental heterogeneity, maternal effects or differential effects of competition, herbivory or disease (Weiner 1988, Aarssen and Taylor 1992). Recruitment events for *D. serra* appear to have occurred after quarrying for gravel or clearing for

roads near the populations, and from observations in Chapter 3, a major recruitment event occurs following a fire. However, the age distribution graphs (see Figure 9) show significant interfire, or interdisturbance, establishment. It is possible that the differences in ages between the populations, and hence height, volume, and number of cones and follicles, can be explained by variations in time since the last disturbance.

In summary, the three *Dryandra* species exhibit a range of demographic characteristics. The size of the seed bank increased with increasing plant height for all three species, a common trend for many plants investigated to date (Weiner 1988). Both *D. ionthocarpa* and *D. serra* appear to be weakly serotinous, retaining a small seed bank beyond one year. However, it is difficult to conclude anything about the degree of serotiny of *D. mimica* as the seed bank is small and the plants cannot be accurately aged. No soil seed storage is evident for *D. ionthocarpa*, and this is probably the case for *D. mimica* as seeds often get caught in the half opened follicles. It is probable that soil seed storage is negligible in *D. serra* as the multi-aged structure of the populations indicates that seed release usually results in recruitment. Seed predation accounts for approximately half of the seed crop of *D. ionthocarpa* and *D. serra*. However, these species produce large quantities of seed and therefore seed predation may not be a significant factor in the seedbank dynamics, particularly in *D. ionthocarpa* during interfire periods. In contrast, *D. mimica* produces extremely small numbers of seeds and only has a low level of seed predation. It may be that negligible rewards mean that seed predators bypass this species (Wright 1994). There is scope for future research into the pollination biology of these species as well as factors that limit seed set, other than granivory (which will be discussed in a later chapter).

Chapter 3: Fire Ecology

Introduction

Recurrent fires are a feature of sclerophyllous vegetation throughout the world (Kruger 1983, Gill 1975, Bell *et al.* 1984). It is thought that fire may have become more common in Australia with the retreat of rainforests and the increase in sclerophyllous vegetation (Gill 1975). Fires were most likely to have been started by lightning strikes or volcanic activity during this time. The arrival of Aborigines, followed by Europeans, meant that the fire regime is likely to have changed, and fire frequencies probably increased markedly (Gill 1975).

The components of a fire regime (frequency, intensity, type and season of burn) are important when investigating the effect of fire on a plant species or community (Gill 1981; Kruger 1983). The immediate effects of fire depend on its intensity, but long-term effects depend on fire frequency and season of burn (Gill 1981). However, the use of a particular fire prescription over repeated cycles is thought to be hazardous because it may promote the recruitment of some species at the expense of others (Cowling *et al.* 1990).

Fire frequency is the number of fires experienced by a community within a given time period (Cary and Morrison 1995). Kruger (1983) suggested that the upper limits of fire frequency are determined by vegetation structure and productivity and the lower limits by the probability of ignition. Shorter fire intervals are associated with a reduction in the number of species and an increase in the abundance of the remaining species. Interfire periods of between one and five years result in an increase in abundance of herbaceous, fire-tolerant species. An interfire period of between one and six years may result in a reversible reduction in fire-killed species, especially those species with canopy stored

seeds and non-leguminous species with soil store seeds (Cary and Morrison 1995). Hobbs and Atkins (1990) studied vegetation development in stands of *Banksia* woodland, with time since the last fire ranging from one to 44 years. Annuals were only present in stands less than five years old. Species richness was greatest in the five year old stand and shrub species were most abundant between two and five years after fire. Lamont and Barker (1988) found that *Banksia burdettii* populations were likely to survive fire if the fire interval was at least 10 years, with an optimum at 20 years.

Season of burn is an important component of the fire regime. In some cases population size is as sensitive to season of disturbance as it is to frequency (Bond 1984). Fires naturally tend to occur in the summer half-year of mediterranean-type climates (Kruger 1983). Most management burns take place in autumn or spring in southwestern Australian, so most literature concentrates on fire effects during those seasons. Auld and Bradstock (1996) measured soil temperatures following a summer and a winter fire and in unburnt vegetation in summer. Soil temperatures did not rise above 40°C following the winter fire and in the unburnt vegetation in summer, and these temperatures were inadequate to break seed dormancy. Soil temperatures above 40°C were measured up to 4.5 cm deep in the area that was burnt by a summer wildfire, while in the top 0.5 cm temperatures in excess of 60°C were measured. These temperatures following the summer wildfire were considered adequate to break seed dormancy in some legume species.

Hobbs and Atkins (1990) studied post-fire dynamics in two stands of woodland dominated by *Banksia attenuata* and *B. menziesii*. Seedling regeneration only occurred after the autumn fire, and not after the spring fire. Resprouting was quicker and species diversity was higher after the spring burn. Introduced annuals increased significantly after the autumn fire. Thus, they concluded that spring burning was more favourable than autumn burns in *Banksia* woodlands. Bond *et al.* (1984) showed that seedling

recruitment differed significantly with season of the fire. Autumn fires produced greatest seedling establishment, while summer fires were less favourable and there was more variability in establishment from fire to fire. Winter and spring fires led to poor seedling establishment, often below replacement levels. Bond (1980) suggested that the Proteaceae in the Cape of South Africa historically had been subjected to a highly seasonal fire regime, mainly summer and autumn burns. An autumn burn allowed for maximum seed release and minimum exposure to seed predators.

Cowling *et al.* (1987) noted that the flowering time of the species is important when considering optimum season of burn. Winter-flowering species would be carrying a new crop of ripe seeds by the start of the summer season when the fire risk is high. This was considered to be important for the weakly serotinous *Banksia menziesii* and *B. prionotes*, in which the current year's crop formed a high proportion of the total viable seed reserve. For the summer flowering *B. attenuata*, summer and autumn fires would have destroyed the current year's crop. However, this species was strongly serotinous and could buffer the loss of a single year's reproductive output. Spring and winter burns consistently produced poor recruitment in *Protea* species in South Africa (Bond 1984). In contrast, Enright and Lamont (1989b) showed that the greater intensity of competition after autumn burns resulted in similar recruitment of *Banksia* species as after a spring burn.

Fire intensity is generally classified either as 'hot', 'medium' or 'cool' for management burns, whereas wildfires may cover the whole range of intensities over the duration of the fire. Siddiqi *et al.* (1976) investigated the survival of seeds of three species of *Banksia* when exposed directly to fire. Seeds of *B. serratifolia*, *B. aspleniifolia* and *B. ericifolia*, when exposed to fire for 7 minutes were killed at temperatures over 150°C, while temperatures of 100°C were not lethal. Seedling recruitment levels were similar after an intense wildfire and a patchy backburn fire in *Banksia* scrub (Lamont *et al.* 1993b).

Knowledge of the juvenile period (the age of the plant when it first sets seed) is essential for gauging the minimum fire interval allowable to ensure adequate recruitment. This is four to five years for many fire-killed species in southwestern Australia (Cowling *et al.* 1987). However, it takes about 10 years for *Banksia menziesii*, *B. attenuata*, *B. prionotes* and *B. leptophylla* to reach the capacity for substantial annual follicle production. Therefore, to maintain the population it was recommended that the scrub be burnt at intervals of no less than 10 years. Monks *et al.* (1994) showed that the geographically restricted *Banksia verticillata* had a juvenile period of between 13 and 17 years and recommended a fire regime of no less than 20 years for this species.

Plants that have evolved under the fire-prone, mediterranean-type climate of southwestern Australian usually show one of two responses to fire: resprouting or death (Bell *et al.* 1984). Those species termed resprouters generally take many years to mature and are long lived, and resprout from epicormic buds or lignotubers after fire. Those species that are killed by fire are termed nonsprouters or obligate seeders. They usually have a shorter life-cycle, often flower within four years of germinating and produce abundant seedlings after the adult plant is killed by fire. As a result, nonsprouting species usually form even-aged stands (Bond 1984; Lamont *et al.* 1991a).

Dryandra species appear to show a range of responses to fire (George 1999), similar to the related genus *Banksia*. This study sought to establish whether *D. ionthocarpa*, *D. mimica* and *D. serra* were nonsprouters or resprouters by either subjecting them to a burn (*D. ionthocarpa* and *D. mimica*) or by monitoring their recovery after a burn had taken place (*D. serra*). In addition the timing and frequency of fire and whether fire is necessary for recruitment was assessed.

Materials and Methods

Dryandra ionthocarpa

A total of 20 plants in each of the two known populations of *D. ionthocarpa* were selected for the fire ecology study. Measurements of the height and crown width in two directions were taken and the total number of cones was counted. On 2 May 1996 ten of these plants in each population were burnt. This involved burning only the individual plant. Fire was prevented from burning any surrounding vegetation. In population 2, three dead plants (one that had died the previous summer and two that had died more than a year ago) were also burnt to investigate (non-experimentally) whether dead plants were a source of recruitment. The length of time the plants burnt, flame height, fuel depth and weather conditions during the burn were recorded. Circular wire enclosures were placed around each individual burnt plant (and controls) to stop mammalian herbivores grazing on any regrowth and enclosed seedlings. The number of germinants for each plant was counted in August 1996, October 1996 and May 1997 following the first summer drought.

Two way ANOVA were used to compare plants in the fire ecology study with plants measured during the demography study. Chi-squared analysis or Fisher's exact test were used in all other cases.

Dryandra mimica

Several populations of *D. mimica* were surveyed, and two populations at Mogumber were selected for a fire ecology study. Sets of 30 plants in each of the two populations were randomly selected. Heights and crown widths in two directions were measured, and the number of cones counted (Figure 13). Fifteen of these plants in each population were burnt on 4 July 1995 (Figure 14). Only the individual plant was burnt, fire was prevented from burning any surrounding vegetation. The length of time the plants burnt,

flame height, fuel depth and weather conditions during the burn were recorded. Circular wire enclosures, closed at the top, were placed around each individual burnt plant (and controls) to prevent the stock (sheep and cattle), and native mammalian herbivores grazing on the regrowth and seedlings. Monitoring of the regrowth (Figure 15) and seedling growth was carried out in December 1995, April 1996, November 1996 and June 1997.

Repeated measures ANOVA's were used to compare height, crown volume and fecundity through time and between populations and treatments (control and burnt).



Figure 13. A *Dryandra mimica* plant just prior to being burnt (Scale: 9cm = 0.6m).



Figure 14. A *Dryandra mimica* plant being burnt (Scale: 9cm = 0.6m).



Figure 15. A regenerating plant of *Dryandra mimica*. Figure 15 shows this plant prior to burning. Almost 2 years after burning this plant has regrown to preburnt height. (Scale: 9cm = 0.6m).

Dryandra serra

A search of areas around Albany and Walpole that were to be, or had recently been, subjected to a burn was made for populations of *D. serra*. Two populations were chosen; one (an area off Beardmore Road north of Walpole) and the second (an area off Nichol Road north of Walpole).

Plants in the Beardmore Road population had height and crown width in two directions (N-S and E-W) measured and the age and number of cones and flowers counted. These data were compared with the data collected from the plants in Chapter 2, to test whether this population was representative. The burn took place on 14 November 1995. A thorough search of this area revealed all *D. serra* plants within the study site were completely consumed by the fire. To ensure that this death of *D. serra* was due to the fire, the *D. serra* plants studied in Chapter 2 were also inspected in November 1995. No widespread death of adult plants was observed. The number of germinants in the burnt site was counted in December 1996, April 1997 and October 1997. A two way ANOVA was used to compare attribute of the Beardmore Road population to the six other study sites.

The Nichol Road population had been completely burnt by a mild intensity fire on 28 November 1984. A second fire on 17 December 1990 had only burnt half of this population. A total of 100 plants in this Nichol Road population (50 in the section that had been burnt once and 50 in the section that had been burnt twice) had height and crown width in two directions (N-S and E-W) measured and the age and number of cones and flowers counted. A two way ANOVA was used to compare attributes of the two areas (once burnt compared the twice burnt) within the Nichol Road population.

Results

Dryandra ionthocarpa

Prior to the burn, all experimental and control plants in both populations had their dimensions measured and number of cones counted. To ensure representative individuals were chosen in the fire ecology experiments their attributes were compared with plants investigated in the demographic studies. This comparison showed that only the height of the plants measured in the fire ecology studies were significantly different from those plants measured in the demographic studies (Table 22). The volume and total number of cones estimated for those plants in the fire ecology experiment were not significantly different from the plants in the demographic studies. It seems likely that, despite significant difference in height between plants used in the two studies (Table 22), representative plants were chosen. This is because the most important attribute in a fire response study, the number of cones per plant, was not significantly different.

All adult plants subjected to the burn were completely consumed by the fire and no regeneration of these plants was observed over the monitoring period (369 days). No controls died over that time ($P < 0.0001$). Seedlings were first observed around plants 118 days after the burn and were not observed around unburnt plants (Table 23). Chi-squared analysis was used to Comparisons of whether burnt or control plants were more likely to have seedlings around them (combining populations) showed there was a significant difference for the presummer observations (counts 1 and 2) ($P < 0.0001$). However, there was no significant difference for the post summer observations (count 3) ($P < 0.1060$) due to their widespread death. Analysis showed no significant difference between populations ($P = 0.1409$). After one year, only 3.3% of the original 424 seedlings at population1 survived, and 8.3% of the 24 at population 2 (Table 24), however, there was no significant difference between populations ($P = 0.2222$).

Table 22. A comparison between attributes (\pm standard deviation) of *Dryandra ionthocarpa* plants in the fire ecology study, prior to the burn, and plants in the demography study.

	Fire ecology study	Demography study	<i>P</i> value
Height (m)	0.40 ± 0.05	0.44 ± 0.08	$P = 0.0043$
Volume (m ³)	0.16 ± 0.05	0.17 ± 0.1	$P = 0.8584$
Total number of cones	104.6 ± 53.7	122.9 ± 100.2	$P = 0.2723$

Comparing the highest pre-summer number with the post-summer (Table 24), there was a sharp drop in both populations. The percentage fall was greater in population 1 (where 3% of the original number of seedlings remained) than in population 2 (where 8% of the original seedlings remained).

For the three dead plants that were burnt, no regeneration of the adult plants nor any seedling recruitment was observed.

Table 23. Number of plants of *Dryandra ionthocarpa* with (+) and without (-) live seedlings around them in two populations (1 and 2) following the burning of ten live plants in each of the populations (and three previously dead plants in population 2). Counts were made 118 (count 1), 175 (count 2), and 369 (count 3) days after burning.

	Seedlings +/-	Pre-summer				Post-summer	
Count time		Count 1		Count 2		Count 3	
Population		1	2	1	2	1	2
Burn (live)	+	9	5	9	4	3	1
	-	1	5	1	6	7	9
Burn (dead)	+	-	0	-	0	-	0
	-	-	3	-	3	-	3
Control	+	0	0	0	0	0	0
	-	10	10	10	10	10	10

Table 24. Mean number of seedlings (\pm standard deviation) of *Dryandra ionthocarpa* per adult in two populations following the burning of ten plants in each of the populations (1 and 2). Counts were made 118 (count 1), 175 (count 2), and 369 (count 3) days after burning. The last column refers to the number of seedlings alive (A) and dead (D) at the final count.

	Pre-summer				Post-summer			
Count time	Count 1		Count 2		Count 3		Final	
Population	1	2	1	2	1	2	1	2
Burn (live)	34.40	2.40	42.60	1.40	1.70	0.20	14 A	2 A
	± 59.58	± 4.60	± 77.02	± 2.32	± 3.50	± 0.63	410 D	22 D
Burn (dead)	-	0.00 \pm	-	0.00 \pm	-	0.00 \pm	0 A	0 A
		0.00		0.00		0.00	0 D	0 D
Control	0.00 \pm	0.00 \pm	0.00 \pm	0.00 \pm	0.00 \pm	0.00 \pm	0 A	0 A
	0.00	0.00	0.00	0.00	0.00	0.00	0 D	0 D

Dryandra mimica

Only one plant of *D. mimica* died over the 23 months of post fire monitoring (Table 25). This was an experimental plant in population 2 that resprouted after the burn, but appeared to succumb to the summer drought (death occurred between count 2 and 3).

Table 25. Number of live and dead *Dryandra mimica* plants in two populations (1 and 2) 23 months after a burn (n = 15).

	Burnt		Control	
Population	1	2	1	2
Live	15	14	15	15
Dead	0	1	0	0

Height was shown to be significantly different between times of count ($P < 0.0001$, repeated measures anova) with the plants gaining height over time (Table 26). A comparison of heights between populations showed there was a significant difference ($P < 0.0001$), with those plants in population 1 having a greater mean height (0.3 m) than those in population 2 (0.2 m). There was also a significant difference between treatments ($P < 0.0080$), with the burnt plants showing an initial drop in height after the burn and growth over the 23 months post burn finally exceeding preburn heights. By count 5 (23 months post-burn), the height of the burnt plants had exceeded that of both the pre-burn height and the height of the control plants at count 4 and 5 (Table 26).

Crown volume was significantly different between time of counts ($P < 0.0001$), with plants in the burnt treatment showing a progressive increase in crown volume after the burn whilst those in the control treatment showed no clear pattern. There was a significant difference between populations ($P < 0.0001$), with those plants in population 1 consistently having a greater mean volume (0.071 m^3) than those plants in population 2 (0.044 m^3). Plants assigned to the burn treatment started with a greater mean volume but this was not significant ($P = 0.0611$). There was a difference between treatments when measurements were taken after the burn (count 2) (Table 26) with the burnt plants having a smaller volume than the control plants. However, by count 5, the volume of burnt plants had exceeded that of the controls (Table 26).

Table 26. Mean height and crown volume (\pm standard deviation) of *Dryandra mimica* after a burn ($n = 15$) for two populations (1 and 2). Measurements were made prior to the burn (1), 6 months post-burn (2), 10 months post-burn (3), 17 months post-burn (4) and 23 months post-burn (5). Count dates are as follows: 21 June 1995, (burnt 4 July 1995), 23 December 1995, 27 April 1996, 9 December 1996 and 7 June 1997.

Count time	Burnt		Control	
	1	2	1	2
Height (m)				
1	0.27 \pm 0.03	0.24 \pm 0.05	0.28 \pm 0.02	0.23 \pm 0.04
2	0.18 \pm 0.04	0.21 \pm 0.04	0.29 \pm 0.04	0.25 \pm 0.04
3	0.19 \pm 0.03	0.22 \pm 0.08	0.28 \pm 0.04	0.21 \pm 0.06
4	0.25 \pm 0.03	0.17 \pm 0.09	0.27 \pm 0.02	0.16 \pm 0.04
5	0.36 \pm 0.04	0.24 \pm 0.11	0.36 \pm 0.04	0.23 \pm 0.05
Crown volume (m ³)				
1	0.09 \pm 0.04	0.08 \pm 0.03	0.07 \pm 0.03	0.05 \pm 0.02
2	0.03 \pm 0.02	0.07 \pm 0.03	0.03 \pm 0.02	0.05 \pm 0.02
3	0.04 \pm 0.02	0.07 \pm 0.04	0.04 \pm 0.02	0.05 \pm 0.02
4	0.07 \pm 0.03	0.08 \pm 0.03	0.03 \pm 0.02	0.03 \pm 0.02
5	0.10 \pm 0.04	0.08 \pm 0.04	0.05 \pm 0.03	0.03 \pm 0.02

Number of flower heads and cones were significantly different between times of count (both at $P < 0.0001$) with an increase in the number of flower heads during the flowering season (count 2 and 4), and an increase in the number of cones following the flowering season (count 3 and 5) (Table 27). There was a significant difference between populations for both the number of flowers ($P < 0.0001$) and cones ($P = 0.0210$) with population 1 having more flower heads and cones on average than population 2. A

significant difference was also detected between treatments for both number of flowers and cones ($P < 0.0001$).

Table 27. Mean number of flower heads and number of cones (\pm standard deviation) of *Dryandra mimica* after a burn ($n = 15$) for two populations (1 and 2). Counts were made prior to the burn (1), 6 months post-burn (2), 10 months post-burn (3), 17 months post-burn (4) and 23 months post-burn (5). Count dates are as follows: 21 June 1995, (burnt 4 July 1995), 23 December 1995, 27 April 1996, 9 December 1996 and 7 June 1997.

Count time	Burnt		Control	
	1	2	1	2
Number of flower heads/ plant				
1	0	1.93 ± 2.40	0	0
2	0	0	9.53 ± 7.14	4.40 ± 6.36
3	0	0	0	0
4	2.93 ± 3.97	0.73 ± 1.91	16.27 ± 13.07	0.53 ± 1.06
5	0	0	0	0
Number of cones/ plant				
1	30.07 ± 15.49	27.53 ± 12.11	20.67 ± 10.93	10.47 ± 6.70
2	0	0	16.27 ± 9.79	12.07 ± 7.21
3	0	0	25.40 ± 16.00	15.20 ± 8.36
4	0	0	17.67 ± 13.46	15.20 ± 12.84
5	5.20 ± 5.09	4.60 ± 7.26	10.80 ± 9.41	2.13 ± 5.07

Dryandra serra

The attributes of the Beardmore Road population of *D. serra* measured before the burn were compared with those populations examined for the demographic studies (Table 28). If the Beardmore Road was not significantly different from the populations studied for the demographic studies an estimate of the number of viable seeds released from the Beardmore Road population could be made.

Table 28. Comparison of height, crown volume and number of cones per plant between the six demography study sites and the fire ecology study site at Beardmore Road.

Population	Height (m)	Crown volume (m ³)	Number of cones
South Sister	1.40	1.36	205.63
Down Road	1.42	0.64	160.79
Hunwick Road	1.69	0.85	57.36
Mount Hallowell	1.71	0.43	77.83
Kordabup Road	1.82	1.50	182.60
Rose Road	2.17	1.09	63.46
Beardmore Road	1.14	0.11	33.56

The height of the Beardmore Road population was significantly different from those at Hunwick Road ($P = 0.0231$), Mount Hallowell ($P = 0.0182$), Koordabup Road ($P = 0.0052$) and Rose Road ($P < 0.0001$), but was not significantly different from South Sister and Down Road. The crown volume of the Beardmore Road population was significantly different from South Sister ($P = 0.0104$), Koordabup Road ($P = 0.0033$) and Rose Road ($P = 0.0217$), but there was no significant difference from populations Down Road, Hunwick Road and Mount Hallowell. The Beardmore Road population was significantly different from South Sister ($P = 0.0128$) and Koordabup Road ($P = 0.0310$) in the number of cones per individual, but not significantly different from populations at Down Road, Hunwick Road, Mount Hallowell and Rose Road. The small crown volume of the Beardmore Road population in relation to the six other populations may have been due to the large number of young plants in the population (19 plants aged three and under compared to 20 plants aged four and over).

Table 29. Number of live and dead *Dryandra serra* plants at Beardmore Road before and after a management burn.

	Number of live plants	Number of dead plants
Preburn (24 October 95)	39	6
Postburn (4 July 1996)	0	45

No regeneration of the pre-burn adult plants was observed over the 23 months (Table 29). Adult plants in the other populations studied for Chapter 2 during that period showed no widespread death, although exact counts were not made. Possibly because of the timing of the burn (late spring - 14 November 1995), no seedlings were observed before the following summer. The number of seedlings counted peaked at 93 at 17 months after the fire (Table 30). If the number of viable seeds for the Beardmore Road population was estimated using results from Chapter 2, there should have been about 416 viable seeds in the canopy prior to the burn. This means only about 22% of viable seeds germinated after the fire.

Table 30. Number of seedlings of *Dryandra serra* after a spring (14 November 1995) burn. Seedlings resulted from 45 adult plants in an approximately 45m² area.

Date of Count	Number of seedlings	Health of seedlings
4 July 1996	0	-
15 December 1996	44	All seedlings healthy, no insect damage.
26 April 1997	93	All seedlings healthy, no insect damage.
14 October 1997	53	All seedlings healthy, no insect damage.

The height, crown volume, number of flowers and number of cones were compared between the two areas of the Nichol Road population. These areas had been burnt twice

and once respectively. All attributes were found to be significantly different between the two areas at $P < 0.0001$. Plants within the area that had been burnt twice were younger, smaller and had fewer flowers and cones than those plants that had only been burnt once. No plants in the twice burnt area were older than the last fire (Table 31).

Table 31. Mean attributes of the once burnt (28 November 1984) and twice burnt (28 November 1984 and 17 December 1990) population of *Dryandra serra* off Nichol Road.

Attribute	Once burnt	Twice burnt
Mean age (years)	6.32	2.96
Age distribution (# of plants in each category)		
>3 years	1	16
3-4 years	10	33
5-6 years	17	1
7-8 years	13	0
9-10 years	5	0
11-12 years	4	0
Height (m)	2.30	0.67
Crown volume (m ³)	0.70	0.03
Number of flower heads/ plant	29.80	0.70
Number of cones/ plant	43.50	2.10

Discussion

Plant species in southwestern Australia usually have one of two responses to fire - death of the adult plant or resprouting from the adult plant (Gill 1981). Nonsprouters should have an abundance of seedlings near the adult plants in contrast to resprouters (Enright and Lamont 1989b). Enright and Lamont 1989b noted that two nonsprouters had 23 and 86 seedlings per parent plant and three resprouters had 6, < 1 and 0 seedlings per parent

plant in the first summer after an autumn burn. Monks *et al.* (1994) observed that the rare *Banksia verticillata* was killed by fire and had 25 seedlings per parent plant; they considered this species a nonsprouter. After the first summer following an autumn burn *D. ionthocarpa* had 1.4 seedlings per parent plant in population 1 and 0.2 seedlings per parent plant in population 2. This is considerably lower than would be expected for a nonsprouter in southwestern Australia and closer to that expected for a resprouter. There were 42 seedlings per adult plant prior to the first summer, closer to the seedling ratio expected of a nonsprouter. Most seedlings appeared to succumb to the summer drought, which highlights the importance of favourable conditions following a burn for seedling survival (Lamont *et al.* 1991b). There was no seedling recruitment for *D. mimica* following a late autumn burn. The absence of seedling recruitment is characteristic of a resprouter. A total of 93 seedlings of *D. serra* were recorded from 39 parent plants. These were recorded after the second summer following a late spring burn (no seedlings were seen until the first spring after the burn). This gives 2.4 seedlings per parent plant, which is closer to the ratios expected from a resprouter. Interestingly the number of seedlings had increased between the December and April counts, probably due to a flush of germination with the beginning of cooler weather in autumn (Enright and Lamont 1989b).

Nonsprouting species often have an even-aged population structure due to a single seedling recruitment event occurring after the adult plants have been killed by fire (Bond 1984). In contrast the long-lived resprouting species often recruit in the absence of fire (Whelan and Main 1979), forming uneven-aged stands (Bradstock 1990). Of the *D. serra* plants in the area that had been burnt once at Nichol Road, none were older than when the population was last burnt. Likewise no plants in the area that had been burnt twice were older than when the second fire went through. So, all adult plants present before the fire must have been killed by the fire, and regeneration occurred through seedling recruitment. Similarly, all adult plants were killed by the fire at the Beardmore Road site.

Nearly two years after the burn, more seedlings (53) were counted at the site than the number of adult plants that were counted prior to the burn (39). These seedlings resulted from one disturbance event and it seems likely that a relatively even-aged stand would result. However, the age graphs shown in Figure 9 (see Chapter 2) show a multi-aged stand with at least one peak in ages. This lack of even-aged stands is most unusual for a non-sprouting species (Bradstock 1990). A multi-aged stand is a feature of species that take advantage of disturbed areas or gaps (Whitmore 1978). Lamont *et al.* (1991a) showed that seedling recruitment in the nonsprouter *B. cuneata* was closely linked to disturbance events, usually fire. It is common to find *D. serra* populations near roads, disused gravel pits and other disturbed areas. Recruitment, therefore, appears to be common after any disturbance event, whether it is fire, road works or quarrying for gravel, resulting in a multi-aged stand.

Dryandra ionthocarpa

Interestingly, population 2 recruited significantly fewer seedlings per burnt adult plant than population 1. It is unlikely that a difference in viability of the seeds was the cause of this difference. Percentage viability data, shown in Table 6 (Chapter 2), indicated no significant difference in seed viability between populations. If the number of cones per plant in each population are compared there is a significant difference, with population 2 having more cones than population 1.

The two populations are only about 500 m apart so it seems unlikely that any weather difference could explain this discrepancy. Variation between the sites may help explain this phenomenon. Population 2 is at the summit of a slight hill, and water might drain from this site more easily than population 1 which is located on a wide flat area. Population 1 therefore may be (and appeared) wetter in winter - encouraging greater germination, and then drier in the summer due to the shallow soils - enhancing drought related deaths, which was the pattern observed. It is also important to note that at all

translocation sites seedlings from population 2, when translocated (see Chapter 5), had significantly higher survival rates and were taller than seedlings in population 1. It may be that plants in population 2 produce fewer seeds but they are of higher quality than plants in population 1. Further research is necessary to elucidate why this pattern was observed.

Dryandra mimica

There were significant differences between the two populations for all four attributes after fire. It was noted that while cattle were present and sometimes displaced the cages in both populations, they only caused damage (by browsing or trampling) to plants in population 2. This is expressed in the consistently smaller crown volumes measured for plants in population 2.

By two years after fire, crown volume was not significantly different from crown volume prior to the burn. The burnt plants had started flowering after only a year and a half after fire. In contrast, Witkowski and Lamont (1997) found the rare, prostrate, resprouting *Banksia goodii* had a delay of three summers between fire and flowering.

There were a greater number of cones at count 5 than the number of flowers at count 4. This may be due to the difficulty in finding the buried flower heads and cones, and therefore may be a counting error. Or, flowering occurred over a wide period of time and flowers that had died or not opened at the time of count 4 were therefore missed. The cones, however, persisted on the plant and therefore were all able to be counted at time 5.

After the burn, several follicles were seen in the remains of the plants, and during count 2, several open follicles were noted near two burnt plants in population 1. However, no seedlings were found near the burnt or control plants. This could be attributed to either

no germination of seeds occurring during the time of the study, a lack of fertile seeds, release of infertile seeds from the follicles, post release seed predation, cattle trampling the young seedlings or the difficulty in finding seedlings. This species rarely produces fertile seeds as shown in Table 12 (Chapter 2), and it is likely that this lack of viable seeds is the explanation for the absence of seedlings during the course of this study. Several germinants were noted during close inspection of non-experimental individuals of this species. These were actually located within the half-buried follicles, or within the crown of the plants, highlighting the difficulty in obtaining evidence of seedlings.

Seeds of *Dryandra* are not protected within the confines of a woody follicle, and are therefore not insulated against the extreme temperatures of a fire (Bell *et al.* 1993). Because the seeds are not insulated by a woody follicle it is believed that they are able to withstand the intense heat from fire. (Bell *et al.* 1993). The inflorescences and cones of *D. mimica* were often found three quarters buried in the sand. This may insulate the seeds from the heat of the fire or decrease the likelihood of granivory; however, this needs further investigation.

Dryandra serra

Interfire establishment for nonsprouting species is not unusual. Monks *et al.* (1994) showed that the nonsprouter *B. verticillata* had a peak in the age frequency graphs that corresponded to a fire, as well as significant interfire establishment. Of the *D. serra* plants at the Nichol Road site, the plants that had been burnt once had a mean age of 6.3 years and the plants that were in the area burnt twice had a mean age of 3 years. Considering that the first fire was in 1984, 11 years ago, it was expected that the mean age would be around 11 years. The maximum age of the plants in this group was 12 years and the minimum age 2 years and the frequency distribution graph showed a population that was relatively normally distributed with the main peak between 4 and 8 years of age. As this species set seed at a relatively young age, between 3.8 and 4.5 years

(Table 20), it is possible that the peak may correspond to the second generation of plants after the fire, with a number of deaths of the first generation plants. The plants in the area that had been burnt twice had a mean age that was closer to what may have been anticipated, five years after the burn the mean age was 3 years with the oldest plant being 5 years old and the youngest 1 year old. The peak in the frequency distribution graph was between 3 and 4 years of age. Clearly, significant recruitment of *D. serra* occurs after fire. However, interfire establishment appears to play an equally important role in shaping population structure.

In summary, *D. ionthocarpa* has attributes characteristic of a nonsprouter. That is, adult plants are killed by fire and seedling recruitment occurs post-fire. In the absence of any adult regeneration and the presence of numerous seedlings post-fire, it would seem that *D. serra* is also a nonsprouter. In contrast, the low seed set of *D. mimica*, the lack of post fire seedling establishment, and the regrowth of foliage from surviving stems indicates that this species is a resprouter.

Chapter 4: Granivory

Introduction

Survival of a plant species is dependent on reproduction, and this is usually through production of seeds. An upper limit to seed set in an individual is determined by the number of ovules produced (Stephenson 1981). Factors that limit seed availability are numerous: for example, plant age and resources as they affect ovule production, rainfall, herbivory and granivory (Auld and Myerscough 1986), pollinators (Bierzychudek 1981) and resources as they affect seed production (Stock *et al.* 1989).

Predation is an important factor as it may reduce the number of viable seeds available per plant (Zammit and Hood 1986, Vaughton 1990, Scott 1982, Auld and Myerscough 1986). However, seed predators may sometimes be dispersal agents or serve to break seed dormancy (Janzen 1971). Factors that play a role in seed predation and, indirectly, seedling recruitment include the timing of invasion by the seed predators and plant defences against such an invasion.

Plant defence against seed predation is often via the production of very high numbers of seeds (Janzen 1971), or to have variable seed set through time. Cowling *et al.* (1987) suggested that satiation of predispersal predators could explain low levels of seed damage in years of high follicle production in *Banksia attenuata* and *B. leptophylla*. De Steven (1983) also observed that episodic periods of high fruiting in *Hamamelis virginiana* satiated seed predators, resulting in an average of 45% predation. In years of low fruit production seed predation averaged 80-90%. Grimm (1995) found that 41% of the pods and seeds of *Pithecellobium pallens* were damaged by seed predators and neither satiation of predators nor rapid development of seeds reduced the impact of seed predation on seed production.

Variable seed set has been identified as a defence mechanism against predation by insects. It was found to be positively correlated with seed survival and was identified as the most important factor in determining seed survival in several *Protea* species (Wright 1994). Scott (1982) suggested numerous mechanisms that *Banksia* species may employ to protect their seeds against predation. These include having long cones, widely spaced follicles, and few seeds per follicle so that insects have to travel further to locate the nutrient-rich seeds; increasing the rate of seed development, to reduce the time available for predator invasion; ceasing growth of follicles after invasion, which makes the granivore obvious to its predators, such as cockatoos; having nectar that attracts parasites and predators of the granivore; and hardening of follicles that either prevents later attacks or traps the granivore inside and prevents it attacking other seeds. However, Scott (1982) made no mention of variable seed set or high seed set causing predator satiation.

The timing of invasion can occur either prior to seed formation or dispersal, or after dispersal of the seeds (Janzen 1971). Insect damage may occur before anthesis in some banksias (Zammit and Hood 1986). Zammit and Westoby (1987) also noted that seed predation increased with cone age for *Banksia oblongifolia* and cone age and follicle position for *B. ericifolia*. Scott (1982) suggested that the timing of attack by seed predators is limited to the first year of seed development when the follicles are relatively soft. However, Cowling *et al.* (1987) showed that follicle attack increased with cone age for the weakly serotinous *B. menziesii* and *B. prionotes*. Lamont and Barker (1988) also observed that predation levels in canopy stored seed of *B. burdettii* increased with increasing cone age.

Percentage seed loss is directly related to predator dynamics (Auld and Myerscough 1986), and seed predation does not approach 100% regardless of the size of the seed

crop. Therefore, a factor associated with the predator population dynamics plays a role to limit the percentage of seed crop damaged. However, Gill (1975) showed that larvae of the moth *Hyaletis latro* may consume the entire seed crop within a 12 month period.

Seed predation alone is only one of a complex interaction of factors affecting seed production. Wallace and O'Dowd (1989) showed that it was the interaction of the factors of insect predation and nutrient availability that limited seed set in *Banksia spinulosa*. Only the addition of nutrients in conjunction with the exclusion of seed predators increased fruit set. The relationship between seed predation in the geographically restricted *Banksia tricuspis* and cockatoo predation on the flower heads was investigated (van Leeuwen and Lamont 1996). They found that about 60% of the heads were eaten by moth larvae and 20% were damaged by parrots. The cockatoos were 88% accurate in finding inflorescences containing moth larvae, and therefore in keeping the moth larvae numbers down. Without cockatoo predation on the moth larvae, negligible seeds would be produced. Scott and Black (1981) also investigated the interactions between seed production on a *Banksia* species, seed predators and cockatoos. They found that cockatoos attacked a higher proportion of inflorescences containing moth larvae than those that did not contain larvae. However, if larvae were absent the birds still destroyed the follicles and cone.

On inspection of the two *D. ionthocarpa* populations in September 1995 it was noticed that a large number of cones (infructescences) had been subjected to insect attack. This study sought to investigate the effect of seed predation on the seed bank of *D. ionthocarpa* and *D. serra*. Seed predator exclusion experiments were used to quantify the level of seed damage by insects. No investigation into the effect of granivory on the seed bank of *D. mimica* was undertaken due to the low level of fruit set and the difficulty in locating fertile cones.

Materials and Methods

Dryandra ionthocarpa

My investigation of the extent of insect granivory on the seed bank was based on the experimental designs used by Auld and Myerscough (1986), Wallace and O'Dowd (1989), Vaughton (1990) and Zammit and Hood (1986).

Experiment 1

A total of 40 inflorescences and cones in each population were randomly selected. Ten were sprayed with approximately 50 mL of water, 10 sprayed with 50 mL of Maverick®, a broad spectrum contact synthetic pyrethroid, 10 bagged with nylon stockings and 10 both bagged and sprayed with approximately 50 mL of the insecticide. It was not known at which developmental stage of the inflorescence or cone that granivory commenced. Three developmental stages were targeted: inflorescences that had just been pollinated (young flower) (this was tested by running a finger over the stamens, if no pollen was present on the finger the inflorescence was considered to have been pollinated), inflorescences with dehiscent florets (old flower) and young cones (young fruit) (Figures 16, 17 and 18). Thus, totals of 80 inflorescences and 40 cones in each population were included in the design. A repeat spraying of all inflorescences and cones was carried out 28 days after initial spraying. All experimental cones were collected in March 1996 and the number of cones with damaged follicles and the number follicles damaged or intact was counted for each cone. Because it was unlikely decay would have been a factor, due to the short duration of the experiment, all follicles that were not intact were counted as damaged.



Figure 16. Young flower stage of *Dryandra ionthocarpa* - inflorescences that have just been pollinated (Scale 2cm = 0.04m).



Figure 17. Old flower stage of *Dryandra ionthocarpa* - inflorescences with dehiscent florets (Scale 2cm = 0.04m).

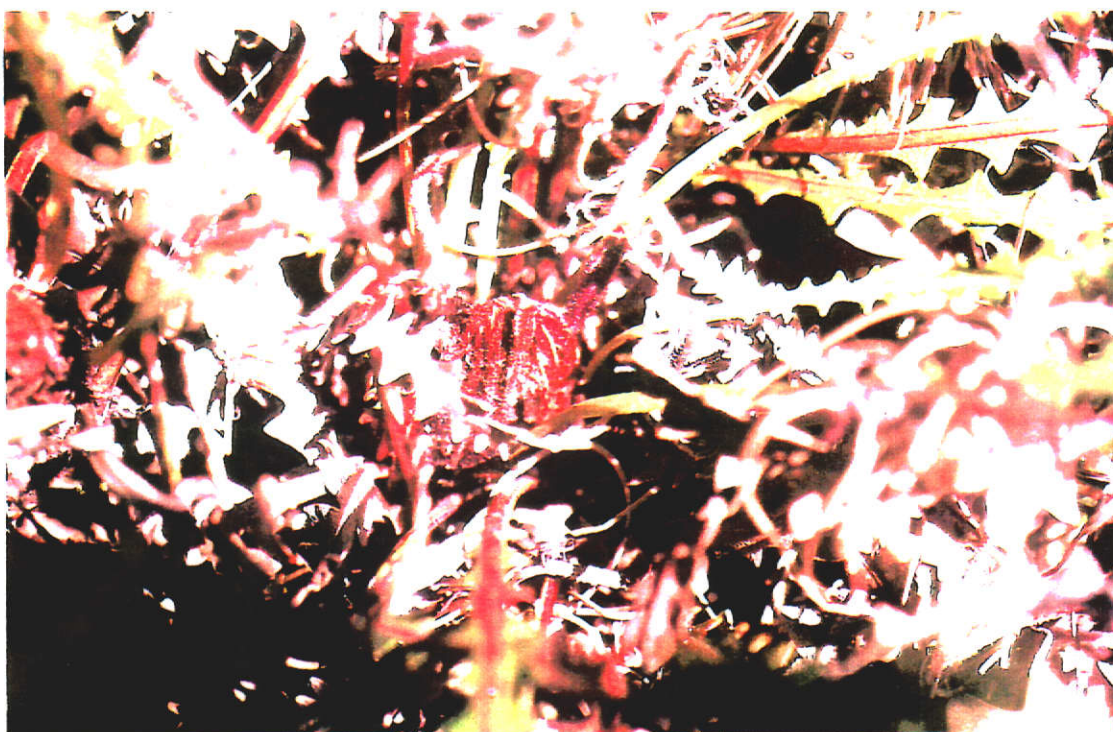


Figure 18. Young fruit stage of *Dryandra ionthocarpa* (Scale 2cm = 0.04m).

A *t*-test was used to compare the percentage of damaged cones between the two populations. A three-way ANOVA was used to compare the effects of cone age, bagging and insecticide for percentage of damaged cones. A four-way ANOVA was used to compare populations, cone age, bagging and insecticide for the percentage of damaged follicles. The post-hoc test Fisher's PLSD, was used for further analysis where necessary.

Experiment 2

As the stockings were found to be an inadequate way of excluding herbivores (due to the dehiscing florets pushing the stocking bags off the developing cone), the experiment was modified for the 1996 flowering season and repeated.

A total of 50 pollinated inflorescences were selected from each of the two populations (Figure 16). An inflorescence was deemed to have been pollinated, if after running a

finger over the stamens, no pollen was present on the finger. The 25 control inflorescences were sprayed with 50 mL of water and the 25 treatment inflorescences in each population were sprayed with 50 mL of Maverick®. Sprayings were repeated at approximately 14 day intervals for a period of ten weeks (this was when the cones were considered to be developing, and likely to be the target of attack by granivores).

T-tests were used to compare between populations and treatments for the percentage of damaged cones. A two-way ANOVA was used to compare between populations and treatment for the percentage of damaged follicles. Percentage data were arcsin transformed prior to analysis.

Opportunistic collection of any insects that were on the inflorescences of *D. ionthocarpa* were made throughout the time of the study. These were identified and assessed as to whether they may be potential seed predators.

Dryandra serra

A total of 20 plants were randomly selected in the Down Road population of *D. serra*. Ten plants were assigned to the control group and 10 were assigned to the experimental group. For each plant, a branch segment containing about five just pollinated inflorescences was sprayed (pollination was tested for using the same method described for *D. ionthocarpa*). The control plants were sprayed with 25 mL of distilled water, and the experimental plants were sprayed with 25 mL of the broad spectrum synthetic pyrethroid, Maverick®. Sprayings were repeated at about 14 day intervals on two further occasions.

T-tests were used to analyse the number of damaged, intact and percentage damaged follicles for *D. serra*. Percentage data were arcsin transformed prior to analysis.

Opportunistic collection of any insects that were on the inflorescences of *D. serra* were made throughout the time of the study. These were identified and assessed as to whether they may be potential seed predators.

Results

Dryandra ionthocarpa

From the opportunistic collections of insects several types were identified. These were adults and juveniles of a species of Caddis fly (Order: Trichoptera) which are not known as seed predators. Two species of moth larvae, which are potentially seed and leaf predators and one species of weevil (Order: Coleoptera, Family: Curculionide) where the adult is not a seed predator (T. Burbidge, pers. comm). All damage could be attributed to the boring activities of insect larvae. Scott (1982) observed that it was the juveniles of a species of weevil (Order: Coleoptera, family: Curculionide, genus: *Myositta*) that feed on the developing inflorescence of several *Banksia* species. It is possible that the juvenile form of the insects found in *D. ionthocarpa* cones are seed predators.

Experiment 1

There was no significant difference in the percentage of damaged cones between the two populations ($P = 0.7210$). Granivore exclusion using insecticide had a significant effect ($P = 0.0113$), with those cones sprayed with insecticide having fewer damaged cones than those not damaged (Table 32). There was no significant difference between time of treatment ($P = 0.3381$), with slightly more cones damaged at the old flower stage (Table 32). Granivore exclusion using bagging had no significant effect ($P = 0.5930$) (Table 32).

Table 32. Number of intact, damaged and % damaged cones of *Dryandra ionthocarpa* after bagging, treating with insecticide or both for two populations (1 and 2) and treated at three stages.

Stage of treatment	Treatment	Intact		Damaged		% damaged	
		1	2	1	2	1	2
Young flower	Control	4	3	6	7	60	70
	Bagged	8	0	2	9	20	100
	Insecticide	4	7	5	3	56	30
	Bagged and insecticide	7	6	2	3	22	33
Old flower	Control	2	4	8	6	80	60
	Bagged	1	0	8	10	89	100
	Insecticide	4	6	6	4	60	40
	Bagged and insecticide	4	5	6	5	60	50
Young fruit	Control	2	4	6	6	75	60
	Bagged	2	3	8	6	80	67
	Insecticide	3	6	5	5	62	45
	Bagged and insecticide	6	5	4	5	40	50

Table 33. Numbers of follicles per cone (\pm standard deviation) of *Dryandra ionthocarpa* intact, damaged and % damaged after bagging, treatment with insecticide or both for two populations (1 and 2).

Stage of treatment	Treatment	Intact		Damaged		% damaged	
		1	2	1	2	1	2
Young flower	Control	6.40 \pm 5.10	6.10 \pm 8.35	3.86 \pm 4.78	8.38 \pm 6.15	38	58
	Bagged	7.80 \pm 4.08	0.22 \pm 0.67	1.42 \pm 3.15	11.16 \pm 3.22	15	98
	Insecticide	5.22 \pm 5.85	11.90 \pm 6.64	4.51 \pm 4.41	2.86 \pm 4.99	46	19
	Bagged + insecticide	6.67 \pm 5.66	9.00 \pm 6.45	1.24 \pm 3.06	2.58 \pm 4.58	16	22
Old flower	Control	2.60 \pm 4.03	3.80 \pm 6.07	6.40 \pm 5.20	6.70 \pm 5.88	71	64
	Bagged	2.00 \pm 4.09	1.70 \pm 2.98	8.18 \pm 3.07	10.78 \pm 4.28	80	86
	Insecticide	3.60 \pm 5.42	7.10 \pm 6.19	5.00 \pm 4.58	4.44 \pm 6.28	58	38
	Bagged + insecticide	4.40 \pm 5.25	8.70 \pm 6.11	4.70 \pm 4.75	3.38 \pm 4.84	52	28
Young fruit	Control	5.12 \pm 6.01	4.70 \pm 6.41	6.45 \pm 4.55	6.40 \pm 6.21	56	58
	Bagged	2.80 \pm 4.21	4.11 \pm 5.99	5.92 \pm 4.39	6.58 \pm 5.50	68	62
	Insecticide	4.89 \pm 5.25	7.10 \pm 7.95	3.38 \pm 3.82	4.54 \pm 5.47	41	39
	Bagged + insecticide	5.60 \pm 5.23	8.10 \pm 8.02	2.96 \pm 4.35	3.8 0 \pm 5.57	35	32

No significant difference was evident between populations ($P = 0.8423$) for the percentage of damaged follicles. Granivore exclusion using bagging had no significant effect ($P = 0.8278$) on the percentage of damaged follicles (Table 33). However, granivore exclusion using insecticide did have a significant effect ($P < 0.0001$). This was independent of time of application, with those cones sprayed with insecticide having

fewer damaged follicles than those not sprayed (Table 33). There was a significant difference between time of treatment ($P = 0.0488$), with fewer follicles damaged at the young flower stage (Table 33). The significant difference was between the young and old flower stage ($P = 0.0127$), with no significant difference between the young flower and young fruit ($P = 0.2026$), and old flower and young fruit ($P = 0.2276$).

Experiment 2

Analysis of the percentage of damaged cones showed that there was no significant difference between populations ($P = 0.6809$). There was no significant difference between treatments ($P = 0.3033$). However, there was a clear decrease in the number of damaged cones after application of insecticide in population 1 (Table 34).

Table 34. Numbers of cones of *Dryandra ionthocarpa* damaged or intact after treatment with insecticide for two populations (1 and 2).

	Control		Treatment	
	1	2	1	2
Intact	8	10	22	12
Damaged	18	12	3	13
% damaged	69	55	12	52

The data in Table 35 show that those flower heads sprayed with insecticide had more intact follicles than those flower heads not sprayed. There was a significant difference between populations ($P = 0.0184$) and treatments ($P = 0.0120$) for the number of damaged follicles in experiment 2, with no significant interaction effect ($P = 0.0640$). There was a significant difference between treatments ($P = 0.0088$) for number of intact follicles; however, there was no significant difference between populations ($P = 0.3381$). There was a significant interaction effect ($P = 0.0500$) for the number of intact follicles. There was no significant difference between populations for percentage damaged follicles

($P = 0.2332$). However, there was a significant difference between treatments for percentage damaged follicles ($P = 0.0016$) with treated cones having more intact and fewer damaged follicles than control cones (Table 35). The interaction effect for percentage damaged follicles was significant ($P = 0.0204$).

Table 35. Numbers of follicles, intact, damaged (\pm standard deviation) and % damaged for *Dryandra ionthocarpa* cones that were sprayed with insecticide for two populations (1 and 2).

	Control		Treatment	
	1	2	1	2
Intact	4.46 \pm 5.76	8.83 \pm 9.50	11.36 \pm 5.57	9.85 \pm 8.22
Damaged	6.94 \pm 5.66	7.58 \pm 7.49	1.45 \pm 4.01	6.74 \pm 7.04
% damaged	60	46	11	41

Dryandra serra

Opportunistic collections of insects that were on the *D. serra* inflorescence resulted in the identification of a species of weevil (Order: Coleoptera, family: Curculionide). The adult was not considered to be a seed predator (T. Burbidge, pers. comm.). A juvenile of a species of weevil (Order: Coleoptera, family: Curculionide, genus: *Myositta*) has been observed (Scott 1982) feeding on the developing inflorescence of several *Banksia* species. It is possible that the juvenile form of the insects found in *D. serra* cones are seed predators.

Treatment with insecticide had no significant effect on the number of follicles damaged ($P = 0.0768$) or intact ($P = 0.2433$) (Table 36). However, from Table 36, it is clear that there is some effect, as those plants sprayed with insecticide had 4 times fewer follicles damaged by insects and 1.7 times more intact follicles. This is also shown in a significant difference in the percentage of damaged follicles ($P = 0.0347$) (Table 36).

Table 36. Mean number of damaged, intact and % damaged follicles (\pm standard deviation) for nine control plants and ten plants sprayed with insecticide of *Dryandra serra* at the Down Road population. The total number of cones for each treatment is listed also.

	Control	Insecticide
Mean number of follicles		
- Damaged	3.22 \pm 3.70	0.80 \pm 1.62
- Intact	3.67 \pm 3.71	5.90 \pm 4.28
- % damaged	49.77 \pm 37.94	15.05 \pm 22.71
Total number of cones	61	69

Discussion

Granivory is known to be an important factor in limiting seed bank size (Auld and Myerscough 1986). The extent to which granivores can consume the seed crop is in turn limited by timing of attack and plant defences against such attack (Janzen 1971). The timing of insect attack on two species of *Banksia*, *B. ericifolia* and *B. oblongifolia* was investigated by Zammit and Hood (1986). They concluded that two suites of predators were supported: those that fed on the young flower heads and those that were considered seed predators. Scott (1982) also noted that on six species of *Banksia* there were two groups of predators. *B. attenuata*, *B. littoralis*, *B. menziesii*, *B. telmatiaea*, *B. grandis* and *B. ilicifolia* were all attacked at the flower head stage, and the first four species were also attacked at the cone stage. The timing of insect attack on cones of *D. ionthocarpa* appears to be very early in inflorescence development. Treatment just after pollination increased the number of intact cones and decreased the number of damaged cones. However, an insecticide effect was still recorded at the young fruit stage, indicating that larvae were slow to hatch or develop. Some invaded cones were not fully consumed, with some follicles remaining intact. Although the seed predator is present

early in cone development, it appears that consumption of the follicles does not occur until after the cone is almost fully developed.

Vaughton's (1990) study of *Banksia spinulosa* var. *neoanglica* showed that the exclusion of insects increased the number of inflorescences that produced seeds and increased the number of seeds per cones by 45%. Insects were found to destroy up to 60% of the follicles of six *Banksia* species that contained one or more seeds (Scott 1982). Similarly insects destroyed between 46% (in population 2) and 60% (in population 1) of follicles in *D. ionthocarpa*. Interestingly, use of the insecticide had the effect of increasing the number of intact follicles in population 1 by 49%, but only by 5% in population 2. This implies there are differences in insect activity between the two populations. Although there are notable difference between the populations in reproductive and habitat attributes as shown in chapter 1 and 2, as these differences may be compounding the differences in levels of granivory.

In most cases, the upper level of fruit production is limited by resources and nutrient availability (Stephenson 1981, Wallace and O'Dowd 1989). However, variation in other factors, such as the level of insect damage, may determine proximate levels of fruit set (Wallace and O'Dowd 1989). The level of natural abortion of seed was shown to match that of the effect of seed predators when seed predators were excluded (Auld and Myerscough 1986). Seed predators were therefore taking excess fruits that, probably due to resource limitations, would not have matured. Aborted follicles were not observed in *D. ionthocarpa*. There are several possible reasons for this. Either low nutrient availability is not a factor limiting seed set; abortion occurs on a whole cone basis and, by coincidence, these cones were not selected for this study; there is a lack of pollinator success and therefore no competition between developing embryos for scarce resources or pollinator limitation. Seed granivores appear to be having a major effect on the seed bank of *D. serra* (Table 18, chapter 2). There is a net positive increase in the number of

intact follicles after spraying with insecticide (Table 36). The only natural abortion in the follicles tagged during the experiment were those on a branch ripped off, probably by cockatoos or parrots. Therefore, it seems more likely that seed granivory, rather than resource limitations, is playing the larger role in limiting the size of the seed bank in this species.

The conclusions of most studies on seed bank dynamics (Vaughton 1990, Scott 1982, Abbott 1985, van Leeuwen and Lamont 1996) are that seed predation by insects cannot fully account for low seed set. Instead it is an interaction of factors. Wallace and O'Dowd (1989) showed application of insecticide to *Banksia spinulosa* var. *cunninghamii* did not significantly increase fruit set. Instead, they showed that it was the application of both insecticide and nutrients that raised fruit set. Clearly, insect predation has a negative effect on the seed bank size of *D. ionthocarpa*. As it is a nonsprouter and dependent on seeds for regeneration, further studies, such as whether pollination is limited, are needed to fully determine what other factors, if any, are limiting the seed bank of *D. ionthocarpa*. These studies may included whether pollination

Zammit and Hood (1986) showed that exclusion of seed predators increased the number of *Banksia ericifolia* flower heads that set seeds, and increased the number of seeds per cone. However, it had no effect on the seed set of the co-occurring *B. oblongifolia*. They attributed this lack of change for *B. oblongifolia* to the possibility of predators already being present when the experiment began. There is a possibility that this occurred in these experiments on *D. ionthocarpa* and *D. serra* as well. Care was taken to select only undamaged pollinated inflorescences but, in the absence of any indication of when the granivores attacked the follicles of *D. serra*, the possibility that granivores were already present cannot be excluded. In the absence of any aborted seeds it seems more likely that either the insecticide degraded quicker than expected between repeat sprayings, allowing

attack to occur, or attack occurred after spraying had ceased. The developing fruits were not investigated, because of the possibility of damaging the fruit. As a result, any of the above are just as likely to be the reason that there was no significant difference in the number of damaged follicles between the control and the treatment in *D. serra*. Further investigations are needed to fully determine what effect granivores, along with other factors are having in determining the size of the seed bank of *D. serra*.

Chapter 5: Translocation Studies

Introduction

Many rare plant species in Western Australia are present in marginal habitats, such as rugged upland terrain that is often gravely rock or deep sands (Hopper *et al.* 1990). These areas are mostly unsuitable for agriculture and have been set aside as a network of small reserves. These reserves, along with road reserves, provide an invaluable network of habitats containing many rare and endangered species. However, these reserves are vulnerable to any disturbance due to their isolation from other reserves and their small size. It is important to know why rare species are restricted to a particular habitat, and whether they may grow in other habitats, in case translocation to a secure area becomes an essential action for the species' recovery. Transplant experiments are a useful tool for obtaining this information (Pavlik *et al.* 1992, Schemske *et al.* 1994, Pavlik 1995).

A transplant (or translocation) is the removal of a part of a plant that can be propagated, from its original site with the intention of re-establishing it in the same or a new locality (Hall 1987). Transplant experiments were initially used to investigate whether genotype or environment played the most important role in phenotypic development (Briggs and Walters 1984). Clausen *et al.* (1939) undertook numerous transplant experiments to different climates and to a standard garden and measured the responses of these plants to these different climates. They used these experiments as a tool to investigate the species concept. Reciprocal transplantation of *Plantago lanceolata* by Antonovics and Primack (1982) was used to test the importance of genotype and environment in accounting for differences in life history. Using the characters of mortality, growth rate and fecundity they showed that environmental differences played an important role in determining life history. Reciprocal transplants of *Eucalyptus viminalis* (Ladiges and Ashton 1974) showed

that, although environmental conditions played a major role, genetically determined differences also affected phenotypic characteristics. Reciprocal transplant experiments by Chapin and Chapin (1981) on *Carex aquatilis* investigated the interactions between genotype and environment in controlling growth parameters. The experiment showed that this species had differentiated genetically in response to distinct environments through changes in several growth processes.

Reciprocal transplant experiments often address the view that individual populations of the same species are adapted to local conditions. This could be important if it is necessary to transplant rare species to another locality. If they are adapted to local conditions this has implications for the establishment of new populations and which parent seed stock may be used. Microsites for new populations must be selected carefully because natural selection in atypical habitats is likely to be severe, especially on genetically depauperate species, a characteristic of many rare species (Pavlik *et al.* 1993). Transplant experiments on *Coreopsis lanceolata*, where the levels of nutrients and competition were manipulated, showed that this species grew, survived and reproduced better in areas where it does not occur naturally, provided competition was reduced (Folgate and Scheiner 1992). This suggests that there is a trade off between competitive ability and growth attributes, and this may account for the distribution of *C. lanceolata*.

Silander (1984, 1985) and Silander and Antonovics (1979) undertook a series of experiments to investigate the genetic basis for the ecological amplitude of *Spartina patens*. One of these experiments (Silander 1985) involved the reciprocal transplantation of *S. patens* from adjacent salt marsh, swale and dune habitats. Individuals at their original site tended to show greater relative fitness than alien individuals. Reciprocal transplant experiments on *Plantago lanceolata* showed no difference in survival between populations (Antonovics and Primack 1982). The significant differences between populations were in growth and flowering, with differences in growth rates between populations favouring those populations growing

at their original locality. Reciprocal transplant studies by Chapin and Chapin (1981) among five populations of *Carex aquatilis* used plant size, growth rate, reproduction and survival to compare ecotypic differences between populations. They found that, in general, populations fared best at their original locality, and in two sites the locally evolved populations were the only survivors after three years.

Reciprocal transplant experiments of the winter annual *Phlox drummondii* showed that individuals native to a site left more progeny, had a greater survival rate, a greater seed survivorship and a greater fitness, relative to individuals introduced to the site (Schmidt and Levin 1985). Reciprocal transplant experiments by Mustart and Cowling (1993) over two summers tested whether the distribution of four closely related proteaceous species was explained by edaphic requirements at the seedling stage. *Protea obtusifolia* and *Leucadendron meridianum* were shown to fare better on their original limestone type soil. *P. susannae* and *L. coniferum* had a higher seedling mortality and lower survivorship overall on their own colluvial sands soil type, but were larger than the other two species. All four species preferred limestone soil. Mustart and Cowling (1993) suggested that competitive exclusion from limestone soils may account for the existence of *P. susannae* and *L. coniferum* on colluvial sands.

Lately, the focus of transplant experiments has shifted to that of conservation, and recovery of rare species. It is becoming more common that recovery of a rare species requires the creation of new populations in secure areas so that the risk of the species becoming extinct is reduced (Pavlik *et al.* 1992). There are several different types of transplant experiments that are undertaken for conservation purposes (Translocation Working Group 1997). *Restocking* translocations involve the addition of new individuals to known sites. *Reintroduction* translocations usually involve the moving of individuals to areas where they do not occur now but where they were previously known to occur. *Introduction* translocations involve the moving of individuals to area where they do not occur now, and were not previously known, but is within the

taxon's known range and habitat type. A *conservation introduction* translocation involves the moving of individuals to areas outside the known range of the taxon, for the purpose of conservation.

These transplant experiments often address the question of why species are geographically restricted or have specific habitat requirements. Reciprocal transplant experiments along a topographic gradient on the geographically restricted *Banksia hookeriana* were used to determine why this species only occurred at the midrange of the gradient (Lamont *et al.* 1989). Negative interactions between certain habitats and co-occurring species, as well as the additional pressure of summer drought, appeared to account for the restricted distribution of this species. Witkowski and Lamont (1997) used transplant studies to investigate whether the rarity of *Banksia goodii* could be explained by climatic factors. They transplanted *B. goodii* and the closely related, common species, *B. gardneri*, along a climatic gradient. Although there was 100% death in the two driest sites, they showed that *B. goodii* could survive at drier and wetter sites than its present distribution suggests.

Translocations of several rare plant species in South Australia identified numerous techniques that increased translocation survival (Jusaitis and Sorensen 1998, Jusaitis *et al.* 1998). Translocated seedlings of *Acacia whibleyana* were shown to have a survival of 55% after two years in the absence of weeds, although, no seedlings survived after 55 weeks in the presence of weeds (Jusaitis and Sorensen 1998). The translocation of the endangered *Amsinckia grandiflora* focused on evaluating demographic factors to investigate whether the new population was self-sustaining (Pavlik *et al.* 1992). Olwell *et al.* (1987) transplanted 150 plants grown from cuttings of the rare *Pediocactus knowltonii* into similar habitats, but where this species does not presently grow. A survival rate of 95% after one year was recorded. Further monitoring after three years (Olwell *et al.* 1990) showed a survival rate of 83%. Flowering and fruiting were occurring, indicating pollinators were present, however,

they reserved their judgement as to whether the transplanting was a success until juveniles were recorded.

This study involved the translocation of two rare and geographically restricted species, *D. serra*, and *D. ionthocarpa*. *D. mimica* was excluded because insufficient seed was available and cutting material could not be successfully propagated in the time available. *D. ionthocarpa* was transplanted to two other soil types as well as to its original soil type. In addition two sites were established in a nearby nature reserve with similar spongolite soils and vegetation, but where this species had never before been recorded. The aim was to investigate whether *D. ionthocarpa* would establish in different soil types, or other areas with similar soil. The reciprocal translocation study of *D. serra* aimed to investigate whether individuals would survive and grow better in their own localities, or whether they would perform better in alien localities. This species occurs across a geographic range from Mount Manypeaks to Walpole. Six sites across the range of this species were chosen, these are the same sites investigated in chapter 2. Seedlings from every site were planted back into their original locality and into every other study site.

Materials and Methods

Dryandra ionthocarpa

Eight sites were selected as transplant study sites for *D. ionthocarpa*. Two sites were within the two known populations (sites 1 and 2), two sites were in areas on lower parts of a slope with dark brown heavy clay soil (sites 3 and 4), two sites were in an area of the Kamballup Reserve (where *D. ionthocarpa* presently grows) that had been burnt in autumn 1996 and that had light coloured sandy loam soils (sites 5 and 6) (Figure 19a). The other two sites were in the spongolite soil of the nearby Kalgan Plains Nature Reserve (sites 7 and 8) (Figure 19b). The transplants commenced on the 27 August 1996.

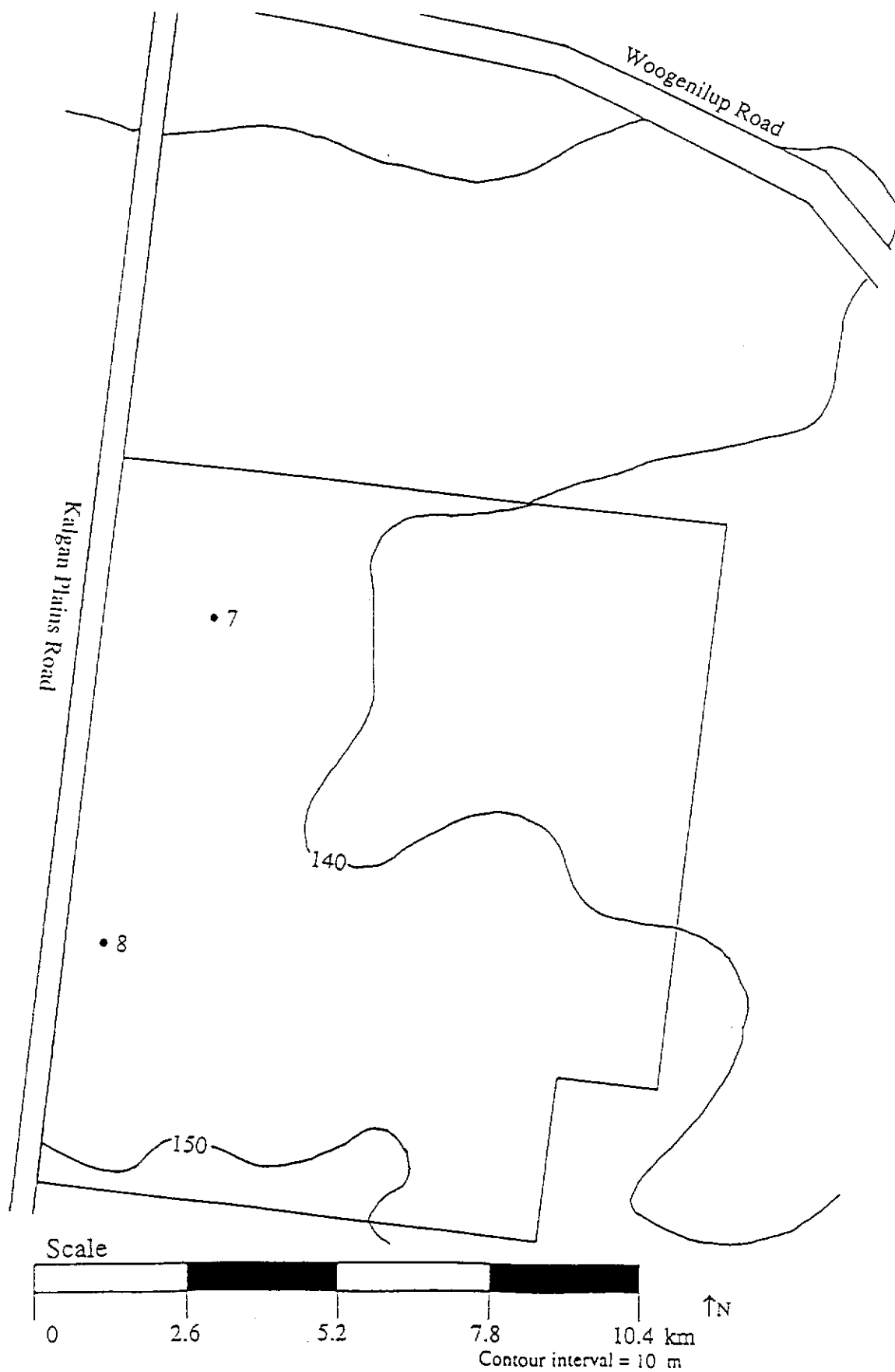


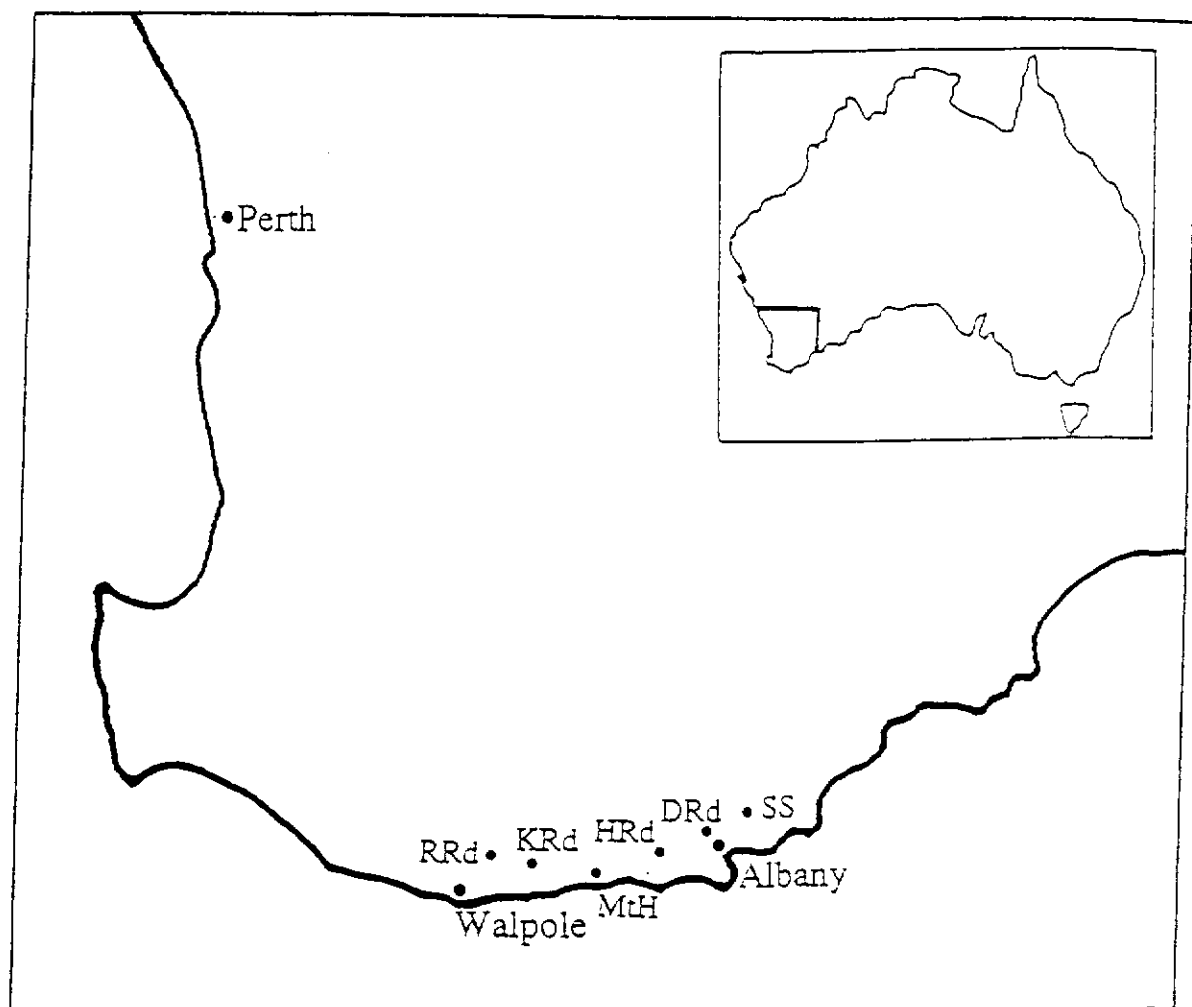
Figure 19b. Map showing the localities of the two *Dryandra ionthocarpa* transplant study sites (•) within the Kalgan Plains Nature Reserve.

Seeds were collected from the two populations. Seeds were germinated on agar plates containing 10 mg/L gibberellic acid at a temperature of 15°C. At each of the sites an area of 2.6×1.6 metres was cleared of vegetation down to ground level and divided into two subplots. Each subplot was planted with germinants from both seed sources in alternating rows, so that there was a total of seven germinants from population 1 and 15 germinants from population 2. The different number of germinants from each population was due to a lower germination from seeds of population 1. The plots were covered with white 70% shade shade-cloth, which was supported 50cm above the plots by 5 wooden stakes, to exclude mammalian herbivores. Sites were monitored for initial survival of the germinants, survival over the first summer drought and growth (using height as a measure) over a nine month period. Data were analysed using two way ANOVA. Fishers PLSD test was used if further analysis was needed. Percentage data were arcsin transformed prior to analysis.

Dryandra serra

Six populations across the range of *D. serra* were selected as sites for the transplant study (these were the same study sites as for the Demography Study in Chapter 1) (Figure 20). At each of these populations, follicles were collected and the seeds were removed. Most follicles were subjected to wet-dry cycles to remove all the seeds (Cowling and Lamont 1985).

Seeds of *D. serra* were placed on agar plates with 10 mg/L of gibberellic acid at a temperature of 15°C to germinate. At each of the six populations an area of 3.1×1.9 metres was cleared of vegetation down to ground level. The cleared site was divided into three subplots, allowing for a boarder of 0.4 m around the subplots. Each of the subplots was planted with germinants from the six populations so that each subplot contained germinants from all six populations. Each subplot was planted with six germinants from Rose Road, nine from Kordabup Road, four from Mount Hallowell, 12 from Hunwick Road, seven from Down Road and one from South Sister. The number of germinants was determined by the percentage germination of the seeds collected.



Key

SS =	South Sister
DRd =	Down Road
HRd =	Hunwick Road
MtH =	Mount Halowell
KRd =	Kordabup Road
RRd =	Rose Road

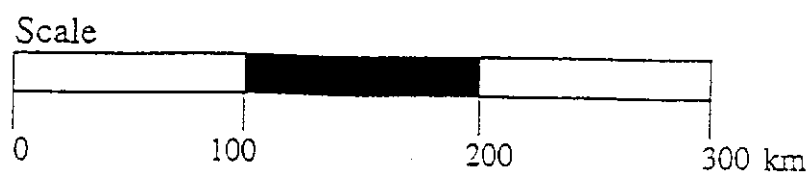


Figure 22. Map showing the localities of the six *D. serra* translocation sites in south-western Australia.

Sites were monitored for initial survival of the germinants, survival over the summer drought and growth (height) over a nine-month period. Data were analysed using two-way analysis of variance, and where necessary Fisher's PLSD post-hoc test. Percentage data were arcsin transformed prior to analysis.

Results

Dryandra ionthocarpa

Analysis of the initial survival of *D. ionthocarpa* at the eight translocation sites showed that there was a significant difference between populations with respect to seedling source ($P = 0.0011$), with those seedlings originating from population 2 clearly having superior survival over those seedlings from population 1 (Table 37). There was a significant difference between the site localities ($P = 0.0002$) with those seedlings grown in the spongolite soil types (site 1, 2, 7 and 8) having a greater initial survival than those grown in the clay (site 3 and 4) and sandy loam (5 and 6) soil types (Table 37).

When initial survival was used as a baseline for survival after nine months there was a significant difference between seedling origin ($P = 0.0488$), again with those seedlings from population 2 having consistently greater survival than those from population 1 (Table 37). There was also a significant difference between site localities ($P = 0.0329$). Further analysis shows that site 1 and 7 ($P = 0.0115$), 2 and 7 ($P = 0.0111$), 4 and 7 ($P = 0.0137$), 5 and 8 ($P = 0.0471$), 6 and 7 ($P = 0.0115$), and 7 and 8 ($P = 0.0093$) were all significantly different from each other with site 7 having lower survival than most of the other sites (0 and 6%) (Table 37).

When the number of seedlings was used as the baseline for calculating percentage survival after the first summer, seedling origin was significantly different ($P < 0.0001$), again with population 2 showing superior survival than population 1 (Table 37). Site localities were significantly different from each other ($P < 0.0001$).

Table 37. Survival of *Dryandra ionthocarpa* seedlings from two populations (1 and 2) planted at eight sites. Percentages are for survival after two and nine months respectively. Sites 1 and 2 are within the confines of the known populations.

Site locality	Initial survival (%) (after 2 months)		Survival after 9 months using initial survival as the baseline (%)		Survival after 9 months using number of seedlings planted as the baseline (%)	
	1	2	1	2	1	2
1	28	26	50	100	7	27
2	50	74	75	86	36	67
3	14	37	0	52	0	20
4	22	86	75	79	14	67
5	0	10	0	50	0	10
6	28	46	50	100	7	53
7	36	36	0	6	0	3
8	57	100	80	86	50	87

Heights of the seedlings were also measured during the post-summer (9 months) monitoring. For analysis, sites 3, 5 and 7 were excluded due to too few data points, though they are shown in Table 38 for comparison. There was no significant difference between heights of seedlings from different origins ($P = 0.8132$) although seedlings from population 2 had a mean height that was 7 mm greater than for seedlings from population 1. There was no overall significant site effect ($P = 0.0545$) (Table 38). However, all pairwise comparisons were significant except sites 1 and 8 ($P = 0.8366$), and 2 and 4 ($P = 0.9537$). Those plants in site 6 (the recently burnt, sandy loam site) had the greatest mean height, despite having one of the lowest initial survivals and total survival levels (Table 37 and 38).

Table 38. Mean height (\pm standard deviation) in mm of surviving seedlings of *Dryandra ionthocarpa* at the eight translocation sites 9 months after transplanting. In brackets are numbers of surviving seedlings measured.

Site	Population 1	Population 2
1	58 (1)	34 \pm 7 (8)
2	42 \pm 14 (5)	48 \pm 8 (20)
3	.*	3 \pm 1 (6)
4	38 \pm 2 (2)	48 \pm 11 (20)
5	.*	50 \pm 25 (3)
6	51 (1)	58 \pm 14 (16)
7	.*	45 (1)
8	39 \pm 13 (7)	36 \pm 9 (26)

* no seedlings survived

Dryandra serra

Comparison of initial percentage survival of the *D. serra* seedlings showed that there was a significant difference between the site localities ($P < 0.0001$) and between the seedling origins ($P = 0.0068$). South Sister, Down Road and Hunwick Road clearly had the greatest initial survival rates (Table 39), and these were shown to be significantly different from the other sites. Mount Hallowell had a significantly lower initial percentage survival than all other sites except for Kordabup Road. However, when seedling origins were compared, South Sister had a significantly lower initial survival than all other populations ($P < 0.0001$ in all cases), and at three sites no plants from South Sister survived at all (Table 39).

Table 39. Initial survival (%) after two months of transplanted *Dryandra serra*. Each of the six populations studied was planted at its own site and at every other site. Results were merged for the three subsites.

Site locality	Seedling origin					
	South Sister	Down Road	Hunwick Road	Mount Hallowell	Kordabup Road	Rose Road
South Sister	67	43	83	92	52	67
Down Road	67	38	56	50	78	61
Hunwick Road	0	43	75	100	85	67
Mount Hallowell	33	5	6	8	4	11
Kordabup Rd	0	38	14	25	41	6
Rose Road	0	38	53	58	30	33

Table 40. Total % survival after the first summer of transplanted *Dryandra serra*, using number of seedlings planted as the baseline. Each of the six populations studied was planted at its own site and at every other site. Results were merged for the three subsites.

Site locality	Seedling origin					
	South Sister	Down Road	Hunwick Road	Mount Hallowell	Kordabup Road	Rose Road
South Sister	0	19	14	17	11	44
Down Road	67	14	44	42	59	50
Hunwick Road	0	24	42	42	22	11
Mount Hallowell	33	5	6	0	7	0
Kordabup Road	0	19	8	17	26	6
Rose Road	0	24	39	33	30	39

When survival after the first summer was calculated as a percentage of the total number of seedlings planted, the site localities were significantly different from each other ($P = 0.0024$), with Down Road often having the greatest percentage survival

and Mount Hallowell, again often having the lowest percentage survival (Table 40). However, the seedling origins were not significantly different ($P = 0.1200$) from each other. Further analysis showed that South Sister still had significantly fewer surviving seedlings than all other populations except Down Road. This is clear from Table 40, where the seedlings from South Sister did not survive at four of the six sites.

To avoid including the possible high number of deaths due to transplanting shock the initial percentage survival can be used as the starting number of seedlings. Using this baseline the analysis of the post summer data shows that there is a significant difference between sites ($P = 0.0045$), with Hunwick Road and Kordabup Road having significantly greater percentage survival than all other sites (Table 41).

Seedling origin was also shown to be significantly different ($P = 0.0054$), again with South Sister having a lower overall survival than all other seedling origins (Table 41), and surviving at only two sites.

Table 41. Total % survival after the first summer of transplanted *Dryandra serra*, using initial % survival as the baseline data. Each of the six populations studied was planted at its own site and at every other site. Results were merged for the three subsites.

Site locality	Seedling origin					
	South Sister	Down Road	Hunwick Road	Mount Hallowell	Kordabup Road	Rose Road
South Sister	0	44	17	18	21	67
Down Road	50	38	80	83	76	82
Hunwick Road	0	50	56	42	26	17
Mount Hallowell	100	100	67	0	100	0
Kordabup Road	0	50	60	67	64	14
Rose Road	0	62	74	57	100	100

There was a significant site locality effect ($P < 0.0001$), with all pairwise comparisons significant except South Sister and Down Road ($P = 0.5365$), Down Road and Rose Rd ($P = 0.4846$), and Mount Hallowell and Kordabup Road ($P = 0.1286$). Seedlings were taller on average at Down Road and smaller on average at Mount Hallowell (Table 42). A significant difference between the sites where the seedlings originated was found ($P < 0.0001$), with seedlings originally from Hunwick Road having the tallest mean height overall and those from South Sister having the lowest overall.

The seedlings from Mount Hallowell planted at Down Road attained the greatest mean height, although its significance was not determined (Table 42). At no site did the seedlings at their resident site have a greater mean height than those seedlings alien to the site (Table 42). Seedlings originating from South Sister consistently fared poorly at all sites. Seedlings from all localities generally fared poorly at the Mount Hallowell site.

Table 42. Mean height (mm) (\pm standard deviation) of surviving seedlings of *Dryandra serra* at the six translocation sites seven months after being planted. Results were merged for the three subsites.

Site locality	Seedling origin					
	South Sister	Down Road	Hunwick Road	Mount Hallowell	Kordabup Road	Rose Road
South Sister	-*	65 \pm 39	91 \pm 28	45 \pm 52	40 \pm 27	90 \pm 20
Down Road	15 \pm 26	56 \pm 38	74 \pm 16	92 \pm 17	60 \pm 15	82 \pm 22
Hunwick Road	-*	75 \pm 20	56 \pm 21	63 \pm 36	51 \pm 38	22 \pm 26
Mount Hallowell	28 \pm 48	25 \pm 43	35 \pm 32	-*	48 \pm 44	-*
Kordabup Road	-*	51 \pm 32	20 \pm 19	34 \pm 40	52 \pm 14	23 \pm 40
Rose Road	-*	58 \pm 22	76 \pm 26	65 \pm 15	51 \pm 14	85 \pm 20

* no surviving seedlings

Discussion

Dryandra ionthocarpa

Initial survival was greatest for those seedlings growing in spongolite soils (sites 1, 2, 7 and 8). By the second count, those in the spongolite soils were still performing better overall, whether initial or total survival were used as the baseline. However, the site with the lowest overall survival was site 7. *D. ionthocarpa* may survive and grow, for at least 9 months in soil types other than spongolite (Table 37). However, this study also shows that this species survives and grows better in its native soil. Similar results were shown by Goldberg (1985) for *Quercus albocincta* and *Lysiloma divaricata* and Mustart and Cowling (1993) for *Protea obtusifolia*, *P. susannae*, *Leucadendron meridianum* and *L. coniferum*. This would suggest a need to find other suitable spongolite areas if translocation becomes a necessity.

The poor results in site 7 (a spongolite soil site) in comparison with site 8 (another spongolite soil site) also highlights the need to match habitat type as well as soil type (Pavlik *et al.* 1992, Hall 1987). Site 7 was planted in a relatively cleared, open area, which was more exposed and it appears that this area was once cleared and that soil compaction may have had a detrimental impact on survival. Site 8 was surrounded by dense vegetation that was 0.5 - 1 metre tall and was very similar to sites 1 and 2 (which were located in the known *D. ionthocarpa* populations).

In Hall's (1987) review of 15 translocations she considered that most failed with respect to monitoring and maintenance. Olwell *et al.* (1987, 1990) showed that the ongoing monitoring of a translocation is important. They reserved judgement on the success of their translocation of *Pediocactus knowltonii* as new seedlings from the translocated plants had not yet been recorded. It is not known for how long the juvenile period of *D. ionthocarpa* lasts. Thus, the translocation of *D. ionthocarpa* should be monitored until flowering and fruiting, and the recruitment of seedlings

occurs, before it is decided whether the translocations have been successful. Demographic data (Chapter 2) can also be used to assess the success of the translocation (Pavlik 1995). The use of data, including number of flowers, fruit or seeds, is particularly important in assessing the success of translocations of species, such as *D. ionthocarpa*, that have no interfire recruitment.

Due to the large number of viable seeds produced by this species in its native habitat it is probable that pollinators are abundant. It may be small mammals, as for other *Dryandras* with a similar habit (Lamont *et al.* 1998), as the species has drab, inconspicuous hidden inflorescences which are located very close to the base of the plant (common traits of mammal pollinated species (Hopper 1980)), but this has not been studied. It is not known whether these pollinators occur in Kalgan Plains Nature Reserve. It is recommended that further studies into what pollinates this species are undertaken.

On both occasions when counts of survival were made, seedlings from population 2 had superior survival than those from population 1, and in almost every case seedlings from population 2 had a greater mean height than those seedlings from population 1. It appears that seedlings from population 2 are more vigorous than those from population 1 under a wider range of growing conditions. There was no obvious reason for this difference.

Dryandra serra

Numerous authors have focused on the question of whether individual populations of the same species are best adapted to local conditions. Folgate and Scheiner (1992), Silander (1985), Chapin and Chapin (1981) and Schmidt and Levin (1985) all showed that individuals in their original site tended to show greater relative fitness than alien individuals. They measured fitness by measuring survival, growth and reproductive effort.

The proportion of surviving ramets of *Spartina patens* over two years was recorded as being high at all sites (Silander 1985), with only the dune plants having a higher survival at their own site. *D. serra* also did not have a clear pattern for survival. In initial survival, only South Sister germinants had equal greatest survival in their original locality. After the first summer, no population had the greatest total survival at its original locality. However, if survival after the first summer was calculated, using initial survival as the baseline, then Rose Road had greatest survival in its original locality.

Growth of reciprocally transplanted *Plantago* species was generally greater and faster at the original site than at alien sites (Antonovics and Primack 1982). At no site was *D. serra* shown to have greater growth at its original site than at an alien site.

Reciprocal transplant experiments on *Plantago lanceolata* by Antonovics and Primack (1982) showed no difference in survival between populations, whether they were planted at their original site or at an alien site. Instead the variation between populations was in growth and flowering, with differences in growth rates between populations favouring those populations growing at their original locality. It was not possible to measure the fecundity of *D. serra* during the course of this study, as the juvenile period is around four years. It may be that differences between the relative fitness of *D. serra* populations will become clearer after growth and survival have been measured over several seasons or after reproduction has occurred. It is recommended that the reciprocal translocation sites of *D. serra* continue to be monitored over several seasons to observe whether a clearer pattern emerges.

D. serra seedlings from South Sister consistently had lower survival and growth, but this may be due to the small numbers of seedlings planted initially. The Mount Hallowell site had the lowest overall seedling survival and growth. However, when initial survival was used as the baseline for calculating survival after the first summer (see Table 41) then survival at that site is similar on average to all other sites. It may

be that planting shock was greatest at this site, or that some other factor (eg. frost, invertebrate grazing) was greatest at this site.

It is worth noting that a large percentage of the literature on reciprocal translocations deals with short-lived annuals or herbaceous perennial (see Folgate and Scheiner 1992; Silander 1985; Chapin and Chapin 1981; Schmidt and Levin 1985; Antonovics and Primack 1982) where it is possible to collect data for several generations over just a few years. Very few studies dealt with long-lived woody perennials (see Ladiges and Ashton 1974 for an exception). The long juvenile periods for most woody perennials, compared with annuals, means data must be collected over a long period of time before any differences in flowering or seed set will emerge. In addition the survival or growth of the translocated plants may be low due to unexpected events such as damage by foraging animals (Monks *et al.* 1994), insect attack (Schmidt and Levin 1985), adverse climatic conditions or even vandalism (Ladiges and Ashton 1974).

Chapter 6: Drought Stress Study of *Dryandra ionthocarpa*

Introduction

Biological stress may be defined as any change in environmental conditions that might reduce or adversely change a plant's development or the ability of a plant to cope with an unfavourable environment (Salisbury and Ross 1992, Taiz and Zeiger 1991). Stress may result from high or low temperatures, frost, high salt concentrations, or high or low water levels.

There are several mechanisms plants may employ to cope with water stress where water is limited. They might escape the stress by completing their life cycle in a period of the year when water is not limiting and the species exists as dormant seeds during the dry period. They may develop a deep taproot and utilise water stored in the soil. They may store water in succulent tissues. They may utilise several strategies to reduce water loss, such as small leaves, sunken stomates, hairs on the leaf surface, or shedding of leaves. Or they may tolerate dehydration and have an ability to rehydrate and function after water stress is alleviated (Salisbury and Ross 1992, Taiz and Zeiger 1991).

There are two main ways of investigating whether water stress is occurring within a plant. One is to monitor the change in water potential of the plant and the other is to monitor the changes in photosynthetic pigments.

Water potential is the tendency of water to move across membranes and therefore is a measure of the water status of the plant (Taiz and Zeiger 1991). As the soil dries, the ability of water to move via soil particles is reduced. Plants may only continue to absorb water as long as their water potential is below that of the source of the water. When water stress starts, plants may reduce their water potential by accumulating solutes in

the cell. This decrease in water potential (osmotic adjustment) can therefore be used as an indication of a response to water stress.

Photosynthetic pigments are vital in photosynthesis as they absorb certain wavelengths of light and transfer this energy to the reaction centres. There are two main groups of pigments: chlorophylls which are green because they reflect green light and strongly absorb violet, blue, orange and red light, and carotenoids (Beta-carotene and xanthophyll) which absorb only blue and violet light, and reflect green, yellow, orange and red light which give a yellow-orange colour to the pigments. Carotenes have a dual function. Not only are they light absorbing pigments which contribute to the photosynthetic process, but they also protect chlorophyll against oxidation under high light conditions. Therefore, in environments where hot dry conditions with high light intensities are experienced, the phenomenon of orange leaves may be an indication that a response to drought stress is occurring (Salisbury and Ross 1992, Taiz and Zeiger 1991). This change in the relative composition of the photosynthetic pigments may therefore be used as an indication of a response to water stress.

The resurrection plant, *Selaginella lepidophylla*, was shown to exhibit a change in pigment content within the leaf even under low light conditions (Casper *et al.* 1993). The rise in xanthophyll pigment was considered to be a photoprotection mechanism. Stem curling and self-shading were also thought to be a photoprotection mechanism. On a leaf area basis, the carotenoid, chlorophyll *a* and chlorophyll *b* contents of *Digitalis lanata* remained almost constant throughout the range of water potentials investigated (-0.7 to -2.5 MPa) (Stuhlfauth *et al.* 1990). However, the Beta-carotene content at a water potential of -2.5 MPa increased by about 25%, compared with the unstressed controls at -0.7 MPa. This increase was attributed to a response that protects against photosynthetic pigment breakdown under high light conditions.

Drought is a common occurrence in the Western Australian heathlands (Hnatiuk and Hopkins 1980). A total of 36% of vascular plants studied by Hnatiuk and Hopkins (1980) in the northern sandplains were found with dead individuals following two consecutive years of below average rainfall. Individuals from the family Proteaceae were affected the most with 47% recorded as having died from drought. Orange leaves and associated plant deaths observed in the two *D. ionthocarpa* populations were initially thought to be caused by *Phytophthora cinnamomi* (see Chapter 1: Threats To Rare Species In Western Australia). However, tests for the fungus were negative (M. Grant pers. comm.). This study sought to investigate whether the bright orange colour of some plants of *D. ionthocarpa* during the dry summer months was due to drought stress and whether these plants recovered from this condition. It was expected that colour change from orange to green could be used as an index of water stress and the likelihood of plant death in future studies.

Materials and Methods

Eleven green, 11 orange and 14 intermediate coloured plants were randomly selected in autumn 1995 and tagged (Figure 21 and 22). A total of six green, six orange and eight intermediate coloured plants were tagged in population 1 and five green, five orange and six intermediate coloured plants in population 2. Pre-dawn recording of water potential (xylem tension) of one individual leaf from each tagged plant was carried out in autumn, winter and spring over two years. A true summer reading of water potential was not taken in the summer of 1995/1996 or 1996/1997 as plants did not show the characteristic orange colours until autumn. Mean monthly rainfall compared with the average during the length of the study are shown in Table 43. Tensions were recorded with a Scholander-type pressure chamber (Nk 3005, Soil Moisture Equipment Company, Santa Barbara, California). Tensions were measured over two successive mornings, usually with tagged plants in population 1 measured on the first morning and tagged plants in

population 2 measured on the second morning. At all times the colour of the 36 plants was described using Royal Horticultural Society Colour Charts and the colour class of green, orange, intermediate or brown (dead) was recorded for 275 plants in each of the two populations. Chlorophyll was extracted from a sample of a representative leaf of each tagged plant using N,N-dimethylformamide (DMF) (Moran and Porath 1980). Chlorophyll levels were determined using a spectrophotometer and the formulas given by Inskeep and Bloom (1985).

Table 43. Total monthly rainfall (mm) for Mount Barker (the nearest weather station to Kamballup) over the period when drought stress readings were recorded, compared with average monthly rainfall. Figures shown in bold are months when drought stress readings were recorded.

Month	Average	1994	1995	1996
January	23.3	-	15	9
February	23.9	-	28	6
March	35.5	-	23	23
April	53.5	-	20	16
May	86.6	-	88	50
June	96.5	-	86	69
July	106.9	-	90	129
August	90.6	-	58	86
September	79.3	-	64	144
October	71.4	-	73	58
November	43.0	-	62	32
December	28.8	2	77	43



Figure 21. Green coloured plant of *Dryandra ionthocarpa* (Scale 13 cm = 0.6 m).

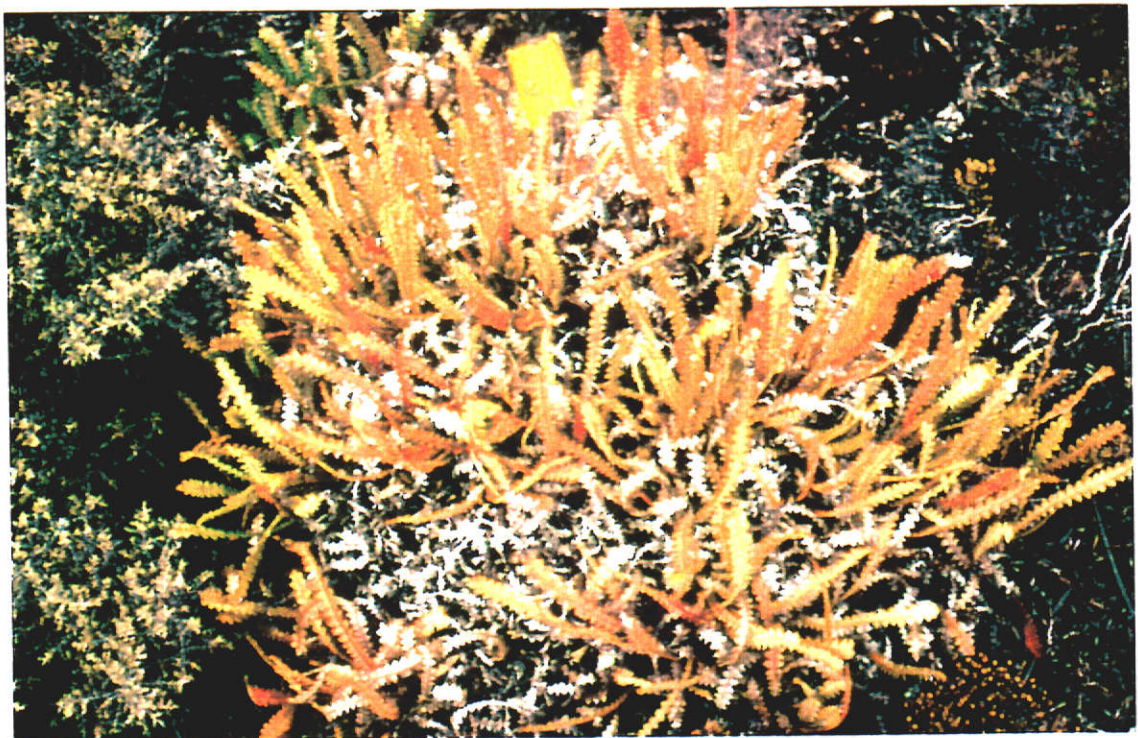


Figure 22. Orange coloured plant of *Dryandra ionthocarpa* (Scale 13 cm = 0.6 m).

Chi-squared analysis or Fisher's exact test were used to compare the number of green, intermediate and orange plants counted each season between each populations. A four way analysis of variance was used to compare the different levels of chlorophyll and xylem tensions for *D. ionthocarpa* over two populations, two years, three seasons and for three plant colour types. Fisher's PLSD test was used where further analysis was needed.

Results

The colour of the green plants tended to remain fairly constant across all seasons (Table 44). Intermediate and orange coloured plants, however, had a constantly changing colour scheme (Table 44).

When the number of green, intermediate and orange plants each season were compared between each populations, there was no significant difference between populations for autumn 1995 ($P = 0.1784$), winter 1995 ($P = 0.0631$), winter 1996 ($P = 0.0604$) and spring 1996 ($P = 0.0660$). There was a significant difference between populations for spring 1995 ($P = 0.0047$) and autumn 1996 ($P < 0.0001$). In both cases there were more intermediate coloured plants in population 1 than in population 2 (see Figure 23). When only the number of green plants were compared between populations for all seasons, there was a significant difference ($P < 0.0001$), with more green plants overall in population 2. When intermediate coloured plants were compared between populations for all seasons there was a significant difference ($P = 0.0022$), with a greater number of intermediate coloured plants in population 1. There was no significant difference between populations for orange ($P = 0.1553$) and dead plants ($P = 0.7105$), and in both cases there were more plants of these colours in population 1. When the number of green plants was compared between years there was a significant difference ($P = 0.0032$), with more green plants counted in the second year (1996). A similar significant difference was

found between years for both intermediate ($P < 0.0001$) and orange ($P = 0.0457$) coloured plants, with more intermediate coloured plants in the first year 1995, and more orange colour plants in the second year, 1996. There was no significant difference between years for the number of dead plants ($P = 0.5614$). When the number of plants of different colours were compared for each season there was a significant difference during autumn ($P < 0.0001$), winter ($P = 0.0066$) and spring ($P < 0.0001$).

The results of the comparison between the different levels of chlorophyll for *D. ionthocarpa* over two populations, two years, three seasons and for three plant colour types are shown in Table 45. There was no significant difference between populations for chl *a* ($P = 0.2609$), chl *b* ($P = 0.2527$) or total chl ($P = 0.9170$). No significant difference was shown between years for chl *a* ($P = 0.2059$), chl *b* ($P = 0.1921$) or total chl ($P = 0.4910$). There was a significant difference between seasons for chl *a* ($P = 0.0129$), chl *b* ($P = 0.0159$) and total chl ($P < 0.0001$). Further analysis showed for chl *a* that autumn and winter were significantly different from each other ($P = 0.0091$) and autumn and spring were significantly different ($P = 0.0079$). However, winter and spring were not significantly different ($P = 0.9625$). The pattern was repeated for chl *b* with autumn and winter significantly different ($P = 0.0094$), autumn and spring significantly different ($P = 0.0110$), and winter and spring not significantly different ($P = 0.9564$). All seasons were significantly different for total chl: autumn and winter were significantly different at $P < 0.0001$, autumn and spring were significantly different at $P < 0.0001$, and winter and spring were significantly different at $P = 0.0019$.

There was a highly significant difference between leaf colours for chl *a*, chl *b* and total chl ($P < 0.0001$). Further analysis showed that for chl *a*, green and orange were significantly different ($P < 0.0001$), green and intermediate were significantly different ($P = 0.0002$), and orange and intermediate were significantly different ($P = 0.0019$). For chl *b*, green and orange were significantly different ($P < 0.0001$), green and intermediate were

significantly different ($P = 0.0002$) and orange and intermediate were significantly different ($P = 0.0022$). All colours were highly significantly different ($P < 0.0001$) for total chl.

There was no significant difference between populations ($P = 0.0558$) for predawn xylem tension. There was a significant difference between years ($P < 0.0001$) with a higher mean tension for 1995 (996 kPa) than for 1996 (411 kPa) (Table 46). There was a significant difference between seasons ($P < 0.0001$) with mean tension higher for autumn (1470 kPa) than winter (291 kPa) or spring (335 kPa) (Table 46). Further analysis showed both spring and winter were significantly different from autumn ($P < 0.0001$). However, spring and winter were not significantly different ($P = 0.4646$). There was a significant difference between colours ($P < 0.0001$), with orange plants having a higher mean tension (1264 kPa) than intermediate (527 kPa), or green (376 kPa) plants (Table 46). These significant differences were found, using Fisher's PLSD test, to be between green and orange and orange and intermediate ($P < 0.0001$) and between green and intermediate ($P = 0.0109$).

Table 44. Summary table of plant colours for initially green, intermediate and orange coloured *Dryandra ionthocarpa* plants over three seasons and two years. Colour codes are from the Royal Horticultural Society Colour Charts. The number of plants in each group is shown in parentheses.

Year	Season	Green	Intermediate	Orange
1995	Autumn	137B G	144 A YG	17A YO
		143A YG	151A YG	22A YO
		144A YG	152B YG	23A YO
		146A YG	152C YG	24A O
		146 B YG (10)	152D YG	25A O
			153A YG (12)	26A O (11)
1995	Winter	137A G	137B G	25A O
		137B G	137C G	137B G
		146A YG (11)	146A YG	144A YG
			146 B YG	146B YG
			152A YG (14)	152A YG
				152B YG
1995	Spring			152C YG (11)
		146A YG	146A YG (14)	146A YG
		147A YG (11)		146C YG
				152A YG
				152B YG (9)

Table 44 (continued). Summary table of plant colours for initially green, intermediate and orange coloured *Dryandra ionthocarpa* plants over three seasons and two years. Colour codes are from the Royal Horticultural Society Colour Charts.

Year	Season	Green	Intermediate	Orange
1996	Autumn	146A YG	146A YG	22A YO
		146B YG	146B YG	152A YG
		152A YG	152A YG	152B YG
		152C YG (11)	152B YG	152C YG (11)
			152C YG	
			153A YG (14)	
1996	Winter	146A YG	146A YG	22A YO
		147A YG	152A YG (14)	46A R
		152A YG (11)		146A YG
				146B YG
				147A YG
				152B YG (11)
1996	Spring	146A YG	146A YG (14)	146A YG
		147A YG (11)		146B YG
				147A YG (10)

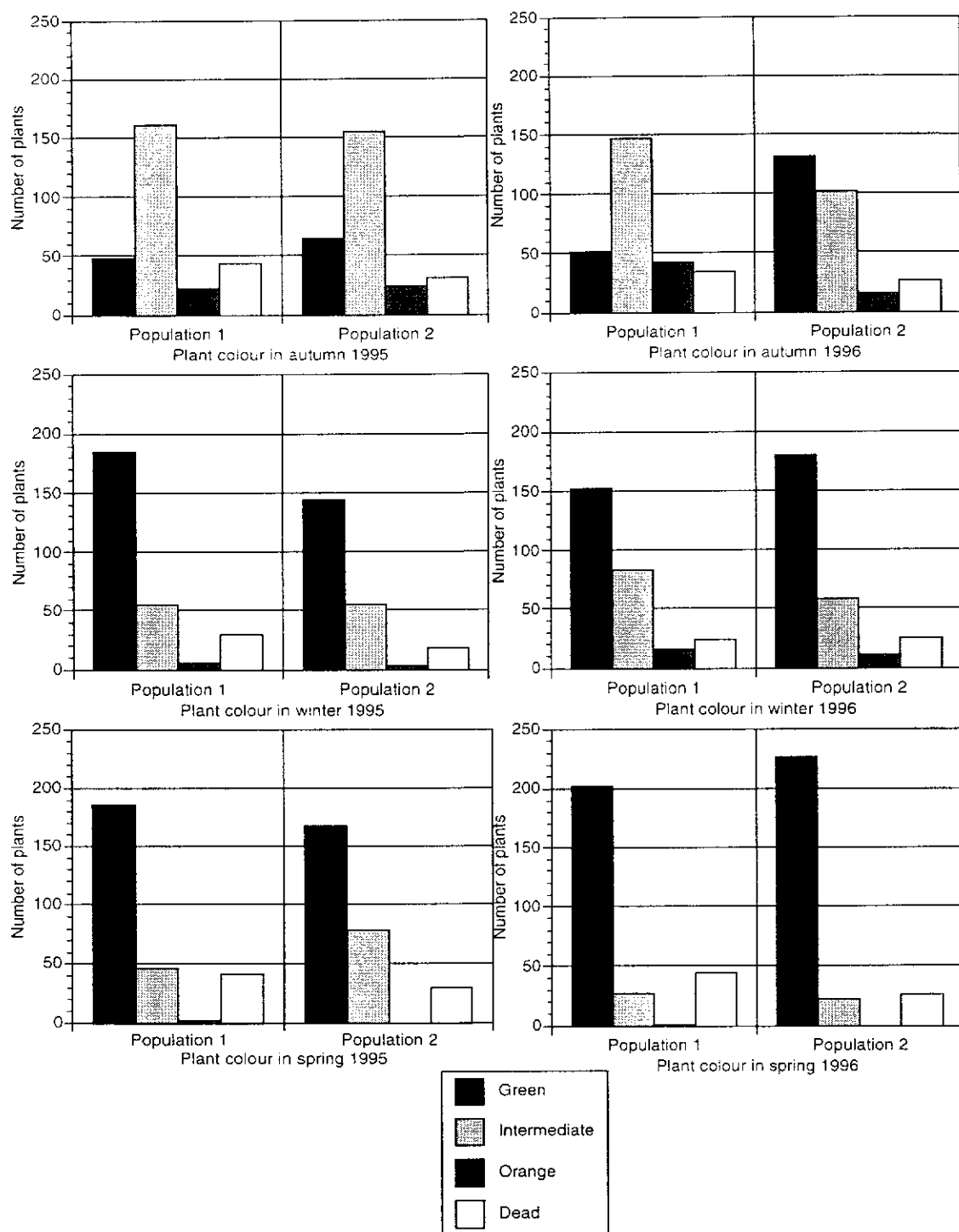


Figure 23. The number of different coloured plants of *Dryandra ionthocarpa*, from a total of 275 plants, counted each season. Plants were classified as green, intermediate, orange or dead.

Table 45. Mean chlorophyll *a* (chl *a*), chlorophyll *b* (chl *b*) and total chlorophyll (total chl) (mg chl/g dry wt) (\pm standard deviation) of leaves for green, intermediate and orange coloured *Dryandra ionthocarpa* plants over autumn, winter and spring in 1995 and 1996.

Year	Season	Population	Colour	Chl <i>a</i>	Chl <i>b</i>	Total Chl
1995	autumn	1	green	0.13 \pm 0.04	0.20 \pm 0.06	0.57 \pm 0.13
			intermediate	0.09 \pm 0.03	0.14 \pm 0.04	0.44 \pm 0.13
			orange	0.06 \pm 0.03	0.09 \pm 0.05	0.23 \pm 0.13
		2	green	0.10 \pm 0.05	0.16 \pm 0.08	0.56 \pm 0.29
			intermediate	0.04 \pm 0.01	0.07 \pm 0.02	0.23 \pm 0.04
			orange	0.03 \pm 0.01	0.05 \pm 0.02	0.17 \pm 0.04
	winter	1	green	*	*	*
			intermediate	0.12 \pm 0.03	0.20 \pm 0.05	0.67 \pm 0.18
			orange	0.07 \pm 0.04	0.11 \pm 0.07	0.35 \pm 0.23
		2	green	0.16 \pm 0.08	0.25 \pm 0.14	0.90 \pm 0.40
			intermediate	0.10 \pm 0.03	0.16 \pm 0.05	0.58 \pm 0.17
			orange	0.05 \pm 0.03	0.08 \pm 0.05	0.27 \pm 0.16
1995	spring	1	green	0.17 \pm 0.02	0.28 \pm 0.04	1.27 \pm 0.15
			intermediate	0.09 \pm 0.07	0.15 \pm 0.11	0.81 \pm 0.35
			orange	0.07 \pm 0.06	0.10 \pm 0.10	0.48 \pm 0.42
		2	green	0.17 \pm 0.03	0.27 \pm 0.05	1.13 \pm 0.27
			intermediate	0.12 \pm 0.04	0.18 \pm 0.06	0.79 \pm 0.27
			orange	0.06 \pm 0.04	0.09 \pm 0.07	0.35 \pm 0.25

* Data missing

Table 45 (continued). Mean chlorophyll *a* (chl *a*), chlorophyll *b* (chl *b*) and total chlorophyll (total chl) (mg chl/g dry wt) (\pm standard deviation) of leaves for green, intermediate and orange coloured *Dryandra ionthocarpa* plants over autumn, winter and spring in 1995 and 1996.

Year	Season	Population	Colour	Chl <i>a</i>	Chl <i>b</i>	Total Chl
1996	autumn	1	green	0.10 ± 0.02	0.15 ± 0.04	0.67 ± 0.14
			intermediate	0.06 ± 0.02	0.10 ± 0.03	0.43 ± 0.11
			orange	0.06 ± 0.04	0.09 ± 0.07	0.35 ± 0.27
		2	green	0.09 ± 0.03	0.14 ± 0.05	0.56 ± 0.15
			intermediate	0.07 ± 0.02	0.12 ± 0.03	0.43 ± 0.13
			orange	0.08 ± 0.03	0.13 ± 0.05	0.45 ± 0.14
1996	winter	1	green	0.12 ± 0.07	0.18 ± 0.11	0.87 ± 0.42
			intermediate	0.08 ± 0.02	0.13 ± 0.03	0.54 ± 0.15
			orange	0.08 ± 0.05	0.13 ± 0.08	0.45 ± 0.29
		2	green	0.12 ± 0.06	0.19 ± 0.10	0.61 ± 0.29
			intermediate	0.10 ± 0.05	0.16 ± 0.08	0.58 ± 0.21
			orange	0.12 ± 0.03	0.19 ± 0.04	0.60 ± 0.10
1996	spring	1	green	0.10 ± 0.01	0.17 ± 0.22	0.86 ± 0.11
			intermediate	0.07 ± 0.01	0.11 ± 0.02	0.62 ± 0.10
			orange	0.04 ± 0.03	0.07 ± 0.05	0.36 ± 0.23
		2	green	0.07 ± 0.02	0.12 ± 0.03	0.60 ± 0.14
			intermediate	0.07 ± 0.02	0.11 ± 0.03	0.60 ± 0.13
			orange	0.07 ± 0.02	0.11 ± 0.03	0.62 ± 0.16

Table 46. Mean predawn xylem tension (kPa) (\pm standard deviation) for leaves of green, intermediate and orange coloured *Dryandra ionthocarpa* plants over autumn, winter and spring in 1995 and in 1996.

Year	Season	Population	Colour	Tension
1995	autumn	1	green	670 \pm 374
			intermediate	2617 \pm 1488
			orange	6020 \pm 455
		2	green	655 \pm 495
			intermediate	808 \pm 577
			orange	5310 \pm 347
1995	winter	1	green	147 \pm 32
			intermediate	162 \pm 46
			orange	174 \pm 86
		2	green	132 \pm 26
			intermediate	146 \pm 60
			orange	162 \pm 58
1995	spring	1	green	300 \pm 91
			intermediate	287 \pm 131
			orange	318 \pm 52
		2	green	310 \pm 167
			intermediate	338 \pm 67
			orange	319 \pm 111

Table 46 (continued). Mean predawn xylem tension (kPa) (\pm standard deviation) for leaves of green, intermediate and orange coloured *Dryandra ionthocarpa* plants over autumn, winter and spring in 1995 and in 1996.

Year	Season	Population	Colour	Tension
1996	autumn	1	green	343 \pm 116
			intermediate	285 \pm 137
			orange	527 \pm 271
		2	green	380 \pm 148
			intermediate	483 \pm 342
			orange	774 \pm 695
1996	winter	1	green	494 \pm 202
			intermediate	491 \pm 259
			orange	438 \pm 312
		2	green	420 \pm 227
			intermediate	329 \pm 191
			orange	315 \pm 106
1996	spring	1	green	242 \pm 86
			intermediate	256 \pm 68
			orange	280 \pm 130
		2	green	490 \pm 182
			intermediate	508 \pm 235
			orange	440 \pm 96

Discussion

A feature of the Mediterranean-type climate in south-western Australia is drought (Hnatiuk and Hopkins 1980), and this is known to play a large role in the fluctuation of population sizes of numerous species (Hopper *et al.* 1990). Measurements of changes in xylem tension and chlorophyll can give an indication of whether drought stress is occurring.

An increase in xylem tension is known to be a drought response (Taiz and Zieger 1991, Lamont and Bergl 1991), as is the phenomenon of orange foliage under hot, dry conditions (Sailsbury and Ross 1992, Taiz and Zeiger 1991). Plants of *D. ionthocarpa* that are orange during the autumn readings had consistently higher xylem tensions than plants that were intermediate or green (see Table 46). This indicates that these orange coloured individuals are under greater water stress than green or intermediate coloured plants. It therefore seems likely that the presence of orange plants of *D. ionthocarpa* during the summer drought is an indication that a response to drought stress has occurred.

Stuhlfauth *et al.* (1990) showed that over a range of water potentials (-0.7 to -2.5 MPa) the chlorophyll content of *Digitalis lanata* remained fairly constant. However, there was a corresponding increase in carotenoids. They attributed this rise in carotenoids to a rise in water stress. There was less chlorophyll in plants of *D. ionthocarpa* in autumn than in winter and spring. This suggests that chlorophyll may have been broken down under the high light conditions of summer and autumn. It is not known whether the orange colour is the result of this decrease in chlorophyll, or due to a concurrent rise in carotenoids and decrease in chlorophylls. The levels of carotenoids would need to be measured over several seasons before the orange colour of some plants during summer could be attributed solely to a response to drought. However, the loss of chlorophyll, and the

greater water stress these orange plants endure indicates that the orange colour of some *D. ionthocarpa* plants during summer may be a drought response.

Lamont and Bergl (1991) found that dawn xylem pressure potentials decreased almost three fold from early summer to mid-autumn for three species of *Banksia* from the northern sandplains of Western Australia. These measurements were made when water was in limited supply and were attributed to a response to water stress. A similar change in xylem tension was observed for all different coloured plants of *D. ionthocarpa* from the spring 1995 reading to the autumn 1996 reading, indicating that all plants were under some level of water stress during the 1995/96 summer drought.

The results from Table 45 show that there is more chlorophyll in green plants than in orange or intermediate coloured plants, but that this difference was smaller in the winter and spring readings. Tagged orange and intermediate plants became green during the winter and spring. In addition, the number of dead plants, from the results shown in Figure 12, remained relatively steady, whereas the number of green plants was relatively low in autumn compared with a winter and spring high. This supports the idea that orange and intermediate coloured plants do recover from drought stress, and that orange and intermediate coloured plants were more likely to recover from water stress than die.

Although no experimental data were collected on whether orange plants were more likely to die than intermediate or green plants, this does seem to be the case. Of eleven orange plants tagged, two died during the course of the study, and one died after the study was completed. No green or intermediate plants died during or after the study.

Chlorophyll measurements showed that, overall, green plants had more chlorophyll than orange or intermediate plants, and that orange plants of *D. ionthocarpa* almost consistently had lower chlorophyll amounts than green and intermediate plants. In

addition plants that were tagged as intermediate or orange at the start of the study, while becoming green in winter and spring, became orange and intermediate again at the onset of the next period of summer drought. It might be that plants with naturally lower chlorophyll levels are more prone to drought stress and are therefore more likely to become orange during the summer drought. Or, plants which produced the drought response of orange coloured leaves never fully recovered their chlorophyll levels to pre-stress levels and are therefore more likely to succumb to the next summer drought.

In conclusion the leaf colour of *D. ionthocarpa* during dry periods of the year may be used as an indication of the general health of the plants, and has scope for use by managers as an indication of the vegetative health of the populations.

Chapter 7: General Discussion

Essential for the conservation of a species is a sound knowledge of the factors influencing populations (Pavlik and Manning 1993, Schemske *et al.* 1994). In the absence of resources or time it is sometimes necessary to extrapolate from information available for the management of species which have not been carefully researched, but may be under immediate threat. *D. ionthocarpa*, *D. mimica* and *D. serra* were chosen as study species as they are representative of the different habits, fire responses and demographic patterns of the genus (Table 45). The attributes of these three species, shown during the course of this study, can therefore be considered representative of the various life forms of this genus and the information can be used, with caution, for the management of other biologically similar *Dryandra* species.

Table 47. Summary table of the genus *Dryandra*, where the total number of upright, prostrate, nonsprouting and resprouting species, subspecies and varieties are shown (A. George pers. comm. 1999). The genus consists of 92 named species.

Fire response	Habit	
	Prostrate	Upright
Resprouter	26	16
Nonsprouter	20	67

The assessment of the demography of a population is necessary to determine whether the population is increasing, decreasing or stable (Schemske *et al.* 1994). This can then provide a basis for determining the critical limiting factors in the management and conservation of the population. Several aspects of the ecology of the three threatened *Dryandra* species considered important for assessing population stability were studied. These included the ratio of fecundity to size, seed fate, response to fire and the level of seed granivory.

The pattern of seed bank build-up was similar for all three study species. In each case a minimum size was attained before reproduction began (based on presence of cones). However, the minimum size (height) to first reproduction was smaller for the

two prostrate species, which intuitively was to be expected. Once the minimum size at first reproduction had been reached, there was a positive linear relationship between increasing plant height and increasing cone production for all three species. This is a common pattern among many flowering plant species (Weiner 1988).

The production of large amounts of viable seeds by the nonsprouters *D. ionthocarpa* and *D. serra* (both per plant and per m³) in comparison with the resprouter *D. mimica* can be attributed to their mode of regeneration after fire (Bell *et al.* 1984). However, per unit area, *D. ionthocarpa* produced far larger quantities of viable seeds than both *D. mimica* and *D. serra*. Both *D. ionthocarpa* and *D. mimica* have similar numbers of cones per m³ (Table 48); however, *D. ionthocarpa* produces some 375 times more viable seeds per m³. Most cones of *D. mimica* were found to be barren (between 78 and 90%), which is common for resprouting species (Cowling *et al.* 1987, Whelan and Burbidge 1980). *D. ionthocarpa* produces almost 12 times as many viable seeds per m³ as *D. serra*. *D. ionthocarpa* appears to disperse most of its seed crop as it ripens, and in the absence of fire this viable seed disintegrates instead of germinating. It may be that large quantities of seeds are produced 'just in case' a disturbance event, such as fire, occurs. *D. serra* also appears to release viable seeds as it ripens; however, many seeds germinate in the absence of fire.

The effect of granivory on the size of the seed bank of nonsprouting species, such as *D. ionthocarpa* and *D. serra*, is important as these species are solely reliant on seed for post-fire regeneration (Lamont and Groom 1996). In the case of *D. ionthocarpa*, because recruitment is confined to the post-fire period, and there is very little storage of seeds (either canopy or soil), the effect of granivory only becomes important in the year a fire occurs. The percentage of follicles eaten in *D. serra* never exceeded 50% (see Table 18, Chapter 2, and Table 36, Chapter 4). As this was only assessed for one year it is not certain whether this level of seed predation was due to the production of high numbers of seeds, variable seed set through time (Janzen 1971, Wright 1994), or related to predator dynamics (Auld and Myerscough 1986). However, while there is a reduction in the size of the seed bank due to predation, the graphs of the age distributions (Figure 9, Chapter 2) show recruitment is occurring each year, and therefore sufficient seeds are escaping predation to survive to germination.

Seed dispersal may be fairly restricted for the two prostrate species. The seeds of *D. ionthocarpa* do not have a wing; instead, the follicle appears to act as the wing. This indicates that wind is the primary mode of seed dispersal. However, following high winds after the experimental burn (described in Chapter 3) most seeds were still retained around the parent plant. The follicles of *D. mimica* are retained within the half-buried cones of the adult plants. Seeds released from these follicles would have remained trapped within the canopy of the adult plant indeed; in several cases, seeds were observed germinating within the half-open follicles. Seeds of the taller species, *D. serra*, may be dispersed over several meters. The follicles open fully and the winged seeds may be caught by the wind as they fall to the ground.

Both modes of regeneration post-fire were present among the three species: *D. ionthocarpa* and *D. serra* were shown to be nonsprouters while *D. mimica* was confirmed as a resprouter. The fire regime is therefore likely to be much more critical for the survival of *D. ionthocarpa* and *D. serra* than for *D. mimica* (Cowling *et al.* 1990).

The recruitment of *D. ionthocarpa* appears to be limited to the post-fire period. Mortality of the adult plants through drought did not lead to seedling recruitment (see Chapter 6). Therefore, it seems likely that *D. ionthocarpa* exists as even-aged stands. In contrast, *D. serra* has multi-aged stands with peaks in recruitment which probably correspond to a disturbance event, such as a fire, quarrying for gravel, or road maintenance. *D. mimica* has the potential to recruit seedlings post-fire, as follicles opened and some seeds were released after the experimental burn. However, it is difficult to conclude anything about the age structure, as plant age and size are not necessarily correlated for resprouting species (Bradstock 1990).

The number of seedlings per parent plant, 12 months after a fire, was similar for the two nonsprouters (Table 48). However, it is considerably lower than the 12.2 seedlings per parent plant noted for the nonsprouter, *Banksia burdettii* (Lamont and Barker 1988), and the 25.2 seedlings per parent plant for the nonsprouter, *B. verticillata* (Monks *et al.* 1994). For *D. serra* this difference may be attributed to significant interfire establishment, which would reduce the amount of seed available

for post-fire germination. For *D. ionthocarpa*, it is possible that the annual release of seeds accounts for this difference. If not released after fire, the seeds disintegrate in the soil and therefore only one year's seed crop, and a small proportion of previous years crops, are available for post-fire recruitment. In addition, the harsh summer drought conditions of the spongolite soils accounts for significant seedling death. The low number of seedlings per parent plant after fire is of concern as it indicates that there is a lack of self replacement particularly for *D. ionthocarpa*. *D. mimica* did not recruit any seedlings after fire - this is common for resprouting species (Bell *et al.* 1984, Witkowski and Lamont 1997).

The two prostrate species, *D. ionthocarpa* and *D. mimica*, are likely to be pollinated by both honey possums and honeyeaters. Honey possums are attracted to drab, hidden inflorescences, which are located on low or prostrate species (Hopper 1980). However, honeyeaters are also known to utilise these flower types (V. Saffer, pers. comm.) and therefore are also likely to be pollinators of these species. It is also likely that honeyeaters are the pollinators of *D. serra*. It has yellow, exposed, terminal inflorescences, on a tall upright plant, common traits of bird pollinated species (Hopper 1980). Insects have also been observed (pers. obs.) crawling over inflorescences of *D. serra*, and therefore they may also be pollinators. It is not known whether pollinator availability currently limits seed set in these species. While honey possum numbers can be expected to fall with continuing clearing for agriculture, all current populations are sufficiently large to continue attracting generalist pollinators such as honeyeaters, thus avoiding the problem of the 'Allee' effect (Lamont *et al.* 1993a).

The orange colour of some plants of *D. ionthocarpa* during summer was investigated, to assess whether this is a response to water stress. It was concluded that this was the case, and consequently this colour change may be used as an indication of the vegetative health within populations. Clearly summer drought is also a factor that plays a vital role in whether a population is increasing, decreasing or stabilised.

Translocations were used to assess the ability of *D. ionthocarpa* to survive and grow in edaphic conditions other than spongolite, and whether the widely distributed

populations of *D. serra* show any adaptation to localized conditions. Translocations are rapidly becoming a commonly used tool in assisting in the recovery of a rare or threatened species (Guerrant and Pavlik 1997). The use of small-scale experimental translocations has been recommended to examine factors essential to establishment prior to full-scale translocation (Jusaitis and Sorensen 1998, Jusaitis *et al.* 1998). Experimental translocations undertaken during this study assessed several factors important to establishment. *D. ionthocarpa* was shown to survive and grow in soil types other than spongolite and in other spongolite areas, indicating edaphic conditions are not the primary factor in limiting the species distribution. In addition a suitable area with similar edaphic and vegetative characteristic to the original populations was located for future, full-scale translocations. *D. serra*, reciprocally translocated across its range showed no clear pattern of survival or growth, indicating that at this stage there is no adaptation to localised conditions. Longer term monitoring of these study sites, which should encompass flowering, fruiting and second-generation plants, may reveal a clearer pattern.

Assessing the success of translocations is a contentious issue (Guerrant and Pavlik 1997, Hall 1987, Olwell *et al.* 1990). For most species, particularly ones like *D. ionthocarpa* where seedling recruitment is unlikely to occur in the absence of fire and seed is only stored for a short period of time (see Chapter 2 and 3), demographic characteristics must be used (Pavlik 1995). The baseline demographic data collected during this study will therefore be useful in determining the success of any future full-scale translocations. For example in a successful translocation of *D. ionthocarpa* we can expect to observe flowering when the plants are 30cm tall and 50cm in diameter and an average of between 117 and 132 cones per adult plant (Table 48). This information is easily assessed and not linked to episodic recruitment events.

Table 48. A summary of the conservation status, general biology and population attributes of the three *Dryandra* species studied in this project. Values are means unless otherwise indicated.

Attribute	<i>Dryandra ionthocarpa</i>	<i>Dryandra mimica</i>	<i>Dryandra serra</i>
Conservation status			
CALM conservation ranking ¹	Declared rare flora - critically endangered	Declared rare flora - endangered	Priority four
Form of rarity ²	Locally abundant in a specific habitat but restricted geographically	Constantly sparse and over a large range and in several habitats	Locally abundant over a large range in a specific habitat
Distribution ¹	Kamballup	Mogumber, Welshpool, Whicher Range	South Sister to Walpole
Number of populations ¹	2	5	≈ 20
Threats ¹	Disease Too frequent fires Weed invasion Chemical drift	Disease Too frequent fires Weed invasion Clearing Trampling and grazing by stock	Disease Too frequent disturbance from recreational activities, roads and fires
Estimated number of Plants ¹	980	450	10,000
General biology			
Habit ³	Prostrate	Prostrate	Upright
Response to fire	Non-sprouter	Resprouter	Non-sprouter
Flowering Period ³	September-October	December-February	July-October

Table 48 (continued). A summary of the conservation status, general biology and population attributes of the three *Dryandra* species studied in this project. Values are means unless otherwise indicated.

Attribute	<i>Dryandra ionthocarpa</i>	<i>Dryandra mimica</i>	<i>Dryandra serra</i>
General biology, continued.			
Likely pollinators	Honey possums, honeyeaters	Honey possums, honeyeaters	Honeyeaters, insects
Associated vegetation	Heathland	Shrubland, eucalypt woodland	Eucalypt woodland
Landscape	Elevated flats, often poorly drained	Sandplains	Undulating lateritic hills on upslope
Substrate ³	Spongolite	Deep white sand	Lateritic soils
Annual temperature (C°) (min-max) ⁴	9.3 - 20.1	11.6 - 25.1, 11.9 - 24.8, 10.4 - 21.9	9.6 - 20.7 to 9.8 - 20.4
Annual rainfall (mm) ⁴	739	462, 864, 823	602 to 1000
Population attributes			
Estimated population size	Pop 1 = 500 Pop 2 = 300	Pop 1 = 200	South Sister = 1000 Down Road = 200 Hunwick Road = 1000 Mount Hallowell = 200 Kordabup Road = 300 Rose Road = 500
Plant height (m)	Pop 1 = 0.4 Pop 2 = 0.4	Pop 1 = 0.3	South Sister = 1.4 Down Road = 1.4 Hunwick Road = 1.7 Mount Hallowell = 1.7 Kordabup Road = 1.8 Rose Road = 2.2

Table 48 (continued). A summary of the conservation status, general biology and population attributes of the three *Dryandra* species, studied in this project. Values means unless otherwise indicated.

Population attributes, continued			
Height at first cone production (m)	Pop 1 = 0.3 Pop 2 = 0.3	Pop 1 = 0.1	0.8 - 1.0
Diameter at first cone production (m)	Pop 1 = 0.5 Pop 2 = 0.5	Pop 1 = 0.3	0.2 - 0.4
Age at first cone production (y)	Unknown	Unknown	4 -5
Plant age (y): youngest (mean) oldest	Unknown (Last fire 20–25 years ago)	Unknown (Last fire 25–30 years ago)	South Sister = 1(5.7)17 Down Road = 1(3.1)12 Hunwick Road = 1(5.1)15 Mount Hallowell = 1(6.2)16 Kordabup Road = 1(5.7)19 Rose Road = 1(7.4)17
Total number cones/ plant	Pop 1 = 132 Pop 2 = 117	Pop = 90	South Sister = 329 Down Road = 293 Hunwick Road = 57 Mount Hallowell = 88 Kordabup Road = 264 Rose Road = 49
Number cones/ m ³ of crown	Pop 1 = 778 Pop 2 = 700	Pop 1 = 597	South Sister = 152 Down Road = 254 Hunwick Road = 67 Mount Hallowell = 206 Kordabup Road = 176 Rose Road = 74
Number follicles/ m ³ of crown	Pop 1 = 12,946 Pop 2 = 15,749	Pop 1 = 32	South Sister = 18 Down Road = 108 Hunwick Road = 39 Mount Hallowell = 70 Kordabup Road = 71 Rose Road = 24

Table 48 (continued). A summary of the conservation status, general biology and population attributes of the three *Dryandra* species, studied in this project. Values means unless otherwise indicated.

Population attributes, continued			
Number intact seeds/ m ³ of crown	Pop 1 = 2,478 Pop 2 = 1,640	Pop 1= 32	South Sister = 12 Down Road = 61 Hunwick Road = 32 Mount Hallowell = 38 Kordabup Road =29 Rose Road = 13
Total number viable seeds/ plant	Pop 1 = 322 Pop 2 = 213	Pop 1= 0.2	South Sister = 21 Down Road = 47 Hunwick Road = 26 Mount Hallowell = 5 Kordabup Road = 39 Rose Road = 5
Number viable seeds/ m ³	Pop 1 = 1,892 Pop 2 = 1,279	Pop 1= 1	South Sister = 10 Down Road = 41 Hunwick Road = 31 Mount Hallowell = 12 Kordabup Road = 26 Rose Road = 8
Seed release	Gradually over Time, completely After fire	After fire	Gradually over time, completely after fire
Seed dispersal distance, method	A few meters, Follicle acts as Wing	Negligible, seed with brittle wing	Several meters, winged seed
Recruitment potential	Rare, restricted to Post-fire	Extremely rare	High, both inter- and post-fire
Seedling establishment	Post-fire	Post-fire	Inter- and post-fire
Number of seedlings/ parent plant 12 months post-fire	0.8	0	1.0
Age structure of population	Even	Appears even	Multi-aged

- 1 Information from the Department of Conservation and Land Management, Declared Endangered Flora Database
 - 2 Information from Rabinowitz (1981)
 - 3 Information from George (1984), George (1996) and George (unpublished)
 - 4 Data from the Bureau of Meteorology
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Management recommendations

1. *D. ionthocarpa* is currently only known from two sites separated by 500 m. These sites could be considered a single metapopulation. Both sites face possible threats due to mining and habitat degradation associated with weed invasion. Establishment of other populations on more secure sites, such as nature reserves, provides an important conservation option for ensuring the survival of this species. Site 8 of the preliminary translocations described in Chapter 5 should be considered such a secure site. This site is located in a nearby nature reserve on the same soil type and in similar vegetation, and had the highest survival after nine months of all the translocation sites. Other sites should be located and assessed for their suitability as translocation sites for *D. ionthocarpa*.
2. Fire is likely to be an important management tool for *D. ionthocarpa*. It is recommended that small patch fires, covering about 20 individuals, be rotated through the populations in autumn every second year. This would spread the risk of unfavourable recruitment conditions following these burns. Further, it is recommended that seedlings recruited post-fire, be watered over the first summer to increase survival (see Lamont *et al.* 1991b) and that weed control be implemented at the same time.
3. *D. ionthocarpa* does not store a significant seed bank in its crown beyond one year and the seed is not retained in the soil. By spring there is only a small canopy-stored seed bank and no soil stored seed bank, and any spring or summer fire could result in the elimination of the seed bank and adult plants. It is therefore recommended that any burning of *D. ionthocarpa* take place in autumn. This burning time has the added benefit of allowing any seedlings a full six months to establish before the

onset of summer drought. Priority should be given to control of any spring or summer fire in the reserve where this species occurs.

4. Granivory was shown to have a negative impact on the size of the seed bank in *D. ionthocarpa*. However, significant numbers of seeds escape predation so that this is not of concern in years when no fire occurs within the population. Granivores can be adequately controlled using an 'off-the-shelf' brand of contact insecticide, and it is recommended that in the flowering period preceding any proposed burn that insecticide be used to increase the size of the seed bank. Further research is needed to fully determine what factors other than granivory are limiting the seed bank of *D. ionthocarpa*.

5. The bright orange-coloured foliage of *D. ionthocarpa* observed in the summer months was found to be a result of drought stress and was a prelude to death. This is an interesting finding considering that this species is confined to a spongolite soil type, which is winter wet and the conclusion would be that this species has evolved to cope with extremes of soil moisture. This species needs to be closely monitored (involving regular counts of the numbers of plants and their health) so that in the event of high numbers of individuals being killed by drought some action can be taken. This can be anticipated by counting the number of plants turning orange over summer and autumn. Action may involve watering to encourage plant survival through the dry months, translocations to a different soil type which has a higher moisture holding capacity, or small controlled fires of some individuals to encourage recruitment to replace dead plants.

6. *D. mimica* appears to be fire tolerant. Therefore, it is not necessary to continue with the present management practice of excluding this species from controlled burns or wildfires. In addition, in the case of the Whicher Range population only, these plants may benefit from having the deep layer of leaf litter removed to prevent the plants becoming buried (Witkowski and Lamont 1997). However, the Welshpool and Mogumber populations, do not require regular burning, as this is unlikely to increase population sizes, or improve their health. It is also likely to enhance weed invasion.

7. The *D. mimica* population at Welshpool and some of the populations at Mogumber are in poor condition. This is due to weed invasion at the Welshpool site, and grazing and trampling by stock at the Mogumber populations. There is, therefore, a case for locating matched sites on nearby nature reserves in which seedlings can be established (as long as the Welshpool and Mogumber populations are not mixed or reciprocally translocated). This would require careful management, including watering, exclusion of fire for at least 10 years (to allow the recruits to become fire tolerant) and weed control.

8. *D. serra* is known from several large populations over a relatively wide distribution. Most of these populations are contained within State Forest or conservation reserves. Recruitment appears to be adequate for replacement. No active management is considered necessary for this species. However, population numbers and health should continue to be monitored on a regular basis, as dieback (*P. cinnamomi*) is a threat to the species.

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