Department of Environmental Biology

Ecological study of plant species at Sandford Rocks Nature Reserve (SRNR)

Mangadas Lumban Gaol

This thesis is presented as part of the requirements for the award of
the Degree of Doctor of Philosophy of
Curtin University of Technology

April 2002

DECLARATION

I declare that all work presented in this thesis is that of myself alone unless otherwise acknowledged. The contents of this thesis have not been submitted previously, in whole or in part, in respect of any academic award.

Mangadas Lumban Gaol
Date: April 2002

COPYRIGHT

Mangadas Lumban Gaol
Date: April 2002

ABSTRACT

The ecology of plant species at Sandford Rocks Nature Reserve (SRNR) was studied. The study site is an important nature reserve that contains relatively undisturbed natural vegetation. It has a mosaic of exposed granite rocks, scrublands and woodlands. The study involved: a description of the structure and composition of the vegetation; the population characteristics of selected *Acacia* species; aspects of reproduction in *Acacia*; germination and seedling characteristics of some *Acacia* and grass species that dominate the reserve; the effect of seed size on germination and seedling characteristics; and, the relationship of seed size to seed coat thickness in selected *Acacia* species.

Five different areas were studied using the point centered quarter method to sample the woody perennial species. Thirteen *Acacia* species were examined for reproduction characteristics; and in 2 selected *Acacia* species, the effects of phyllode and/or inflorescence removal on reproduction was investigated. Germination tests were conducted to identify germination characteristics in 8 *Acacia* and 7 grass species dominant at SRNR. The possible effects of variation in seed size on germination; seedling characteristics; and, seed coat thickness were investigated in *Acacia fauntleroyi* and *Acacia prainii*.

A total of 85 species from 20 families of woody perennials were collated. All areas were dominated by the Myrtaceae, Mimosaceae and Proteaceae families. There was considerable variability in the structure and composition of vegetation. Most species were present in particular sites and the composition of communities appears to be related to the heterogeneity of the habitat within the reserve. In areas of shallow or rocky soil, vegetation types present include *Allocasuarina huegeliana* woodland, *Grevillea paradoxa* low scrubland and *Acacia neurophylla* medium shrubland. In a seasonally wet area, vegetation types present include low open grassland; *Eucalyptus capillosa* (wandoo) woodland; and, *Acacia saligna* thicket. In deep, dry sandy soil, vegetation types include *Phebalium tuberculosum* shrubland, *Acacia acuminata* and *Acacia coolgardiensis* thickets. On relatively flat areas that gain water from adjacent large granite hills, the

vegetation consists mainly of tall, open woodlands of *Eucalyptus* species. Vegetation types include: medium tall *Eucalyptus salmonophloia* woodland with *Kunzea pulchella* shrubland at the periphery of the *Eucalyptus* woodland. At rock areas, vegetation types present include dense *Leptospermum erubescens* thicket, low open *Acacia prainii* and *Dodonaea viscosa* shrubland.

Of the *Acacia* populations studied, in *A. lasiocalyx* no recent seedling establishment was observed. It is hypothesised that recruitment occurs in particular periods. As the plants are associated with rock and soils are generally shallow, it appears that recruitment depends on run-off water from the rocks in winter. Continuous recruitment seems to be the pattern in *A. prainii* with both seedlings and saplings represented. *A. fauntleroyi* forms relatively small populations; apparently long drought periods (>100 d) result in mass death and limit its population size. In *A. hemiteles,* no seedling stage was found, root competition (for water) from associated *Eucalyptus* species presumably limits its recruitment.

Reproductive success of *Acacia* is affected by rainfall. A wet winter is required to induce flowering and further rain is required after flowering to promote pod development and good seed set. All *Acacia* species suffer from drought in the reproduction season, however they differ in their degree of susceptibility. Leaflessness and tree shape also affect *Acacia* fecundity. Plants bearing more phyllodes produce more flowers and pods, and branches in the upper part of the crown bear heavier inflorescences. In 1998, all *Acacia* species at SRNR produced mature seed of low weight, with many immature and diseased seed, which gave poor germination. A late spring frost in 1998 is believed to be responsible for limited seed development. In two selected *Acacia* species, removal of phyllodes reduced the number of pods produced. Presumably, phyllode removal reduces photosynthate produced, therefore the competition among inflorescences (or pods) for resources is more intense and subsequent abortions are likely to occur.

All *Acacia* species studied showed best germination in the cool winter temperature range. Apparently, seeds are adapted to germinate in winter when seasonal moisture is more

likely to be available. The best temperature however, varied slightly between species. The grass species dominant in the reserve, except for *Aristida contorta,* also had more germination in cooler rather than warmer temperatures. The flora of SRNR is similar to typical vegetation of the Southwest. Generally, *Acacia* species are present only in particular sites, presumably were habitat moisture allows. Seedlings of *Acacia* species growing in naturally dry areas have greater root: shoot masses than those growing in seasonally wet areas. Biomass partitioning is an apparent strategy to conserve water. Of the 7 grass species, *Amphipogon strictus* appears to have fastest growth. *Eriachne ovata* has greater root than shoot mass, while in all other species, shoot mass is greater than root mass; a characteristic of species that grow well in moist habitats. The longest shoots and roots are in *Austrostipa elegantissima,* an understorey species of eucalypt woodland.

In *A. fauntleroyi,* the degree of hard-seededness varies between seed sizes. There is a higher proportion of soft seed in smaller seed. Seed of different sizes show some responses to different pre-treatments and incubation temperatures for germination. Larger seeds generally germinate in greater numbers after higher treatment temperatures. The best treatment for small seeds is pre-treatment at 75°C and incubated at 15°C. For medium and large seed, best pre-treatment is at 75°C with incubation at 30°C or soaking in boiling water and incubation at either 15 or 30°C. In *A. prainii,* seed size; pre-treatment; incubation; and, their interaction all affected germination; larger seeds are more viable. The best treatment to promote germination of *A. prainii* is soaking in boiling water and incubation at 25°C. In both *A. fauntleroyi* and *A. prainii,* larger seeds produce larger seedlings. Seedlings from large seeds have the potential for more rapid pre-photosynthetic growth. Larger, heavier seed has a thicker seed coat. The seed coat of *A. prainii* is thicker than in *A. fauntleroyi;* the difference in seed coat thickness is reflected by more soft seed in *A. fauntleroyi* (35%) than in *A. prainii* (6%).

ACKNOWLEDGEMENTS

I wish to express my sincere gratitude to my supervisor, Professor John E.D. Fox, for providing invaluable assistance and guidance throughout this research work. His encouragement, patience, friendship and diligence in reviewing my drafts is greatly appreciated. I also wish to thank Dr. Christina Cox (Mulga Research Centre) for her advice in reviewing some of my drafts. Staff of the Department of Environmental Biology, Curtin University, Professor Jonathan Majer and Assoc Professor Jacob John gave moral support during my research.

I thank the technical staff at the Department of Environmental Biology, particularly Peter Mioduszewski, Ian Abercombie and Lydia Kupsky, for helping me in the field or lab. Special thanks also go to Department secretaries Jean and Enid, computer technician Charles La Coste and financial officer Kathy. Assistance in the field by volunteers was invaluable and my thanks go to all those who helped, particularly Kazuo Iiyama, G.C. Clark, Li Khim Teh and B. Sharples.

I would like to thank the rector of Nusa Cendana University (UNDANA), West Timor, Indonesia, for his facilitation of my study. Moral support from my colleagues in the Department of Biology, UNDANA is also appreciated. This project was funded by DUE project UNDANA scholarship (1998-2001). Thanks to all DUE project staff for their kindness in preparing my scholarship.

Fellow research students, Roy, Dylan, Lara, Markus, Maze and Kacung are thanked for their friendship. Finally, I would like to thank my wife and both my daughters for their encouragement, and God for all support and help.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

GENERAL INTRODUCTION

1.1. Introduction

In this chapter, I present a general introduction to the study. A theoretical background, general methods and aims are given. This chapter draws attention to a set of target species of importance in a particular area of vegetation selected for study. A description is provided of the general habitat and distribution of selected species. The study area is an important nature reserve that has more or less undisturbed natural vegetation. Data collection comprises 3 groups: collected from field (natural); at the Field Trial Area (FTA) of Curtin University in Bentley (cultivated plants); and in the glasshouse or laboratory. Data from the FTA were taken for the same species as found at Sandford Rocks Nature Reserve (SRNR), because it was not possible to apply treatments (phyllode and inflorescence removal) at SRNR, as it is natural vegetation.

In the first part (Chapter 2) of the thesis I investigated the structure and composition of vegetation at Sandford Rocks Nature Reserve (SRNR). Population characteristics of four selected *Acacia* species (*A. lasiocalyx* C.R.P Andrews, *A. prainii* Maiden, *A. fauntleroyi* (Maiden) Maiden & Blakely and *A. hemiteles* Benth.) and their associated species were investigated in chapter 3. Chapter 4 deals with aspects of reproduction in *Acacia* species. The main objectives were to investigate variation between years and effect of leafiness and tree shape on reproduction in *Acacia*. The effects of phyllode and inflorescence removal on reproduction in two selected *Acacia* species (*A. saligna* (Labill.) H. Wendl. and *A. lasiocalyx*) are reported.

In the next part (Chapter 5), germination and seedling characteristics of *Acacia* and the common grass species at SRNR were studied. The main subjects were the effect of temperature on germination and variation in seedling characteristics between the species. Chapter 6 deals with the effects of seed size on germination and seedling characteristics in two selected *Acacia* species (*A. fauntleroyi* and *A. prainii*). Seed coat thickness was measured to determine the effect of seed size on seed coat thickness. In the final part (Chapter 7), I present some general conclusions relating to the ecology of the species in this part of the Western Australia wheatbelt.

1.2. Description of study area

The town of Westonia is approximately 316 km east of Perth and 52 km east of Merredin, in the wheatbelt of Western Australia (Figure 1). My study site (Sandford Rocks Nature Reserve) is located 11 km northeast of Westonia (31° 18′ S, 118° 42′ E). It is 360 m above sea level. The reserve has an area of 805.9 ha with a perimeter of 12.2 km. It is the third largest reserve in the district, with a complex mosaic of exposed granite rock, shrublands and woodlands (Muir 1979). The reserve is one of a number of significant granite outcrops within the Western Australian wheatbelt. Some species of plants and animals are only found on granite outcrops. The reserve is a relatively undisturbed area of natural vegetation.

The reserve is managed for nature conservation. The Department of Conservation and Land Management (CALM) of Western Australia is responsible for actively supporting, promoting and protecting the natural values of the reserve. As the most developed of all the reserves in the Westonia shire, SRNR currently attracts a large number of tourists.

Fire has not affected the reserve for over 72 years (Gow 1997), except for a very small part that was burnt in 1999. However, this form of disturbance can be discounted as having influenced the vegetation in recent times. The reserve also contains stands, which lie at a distance far enough from farmed land to allow some confidence to be placed in the integrity of ecosystems as they are now (Hobbs & Atkins 1988). The reserve is in very good condition (Muir 1979).

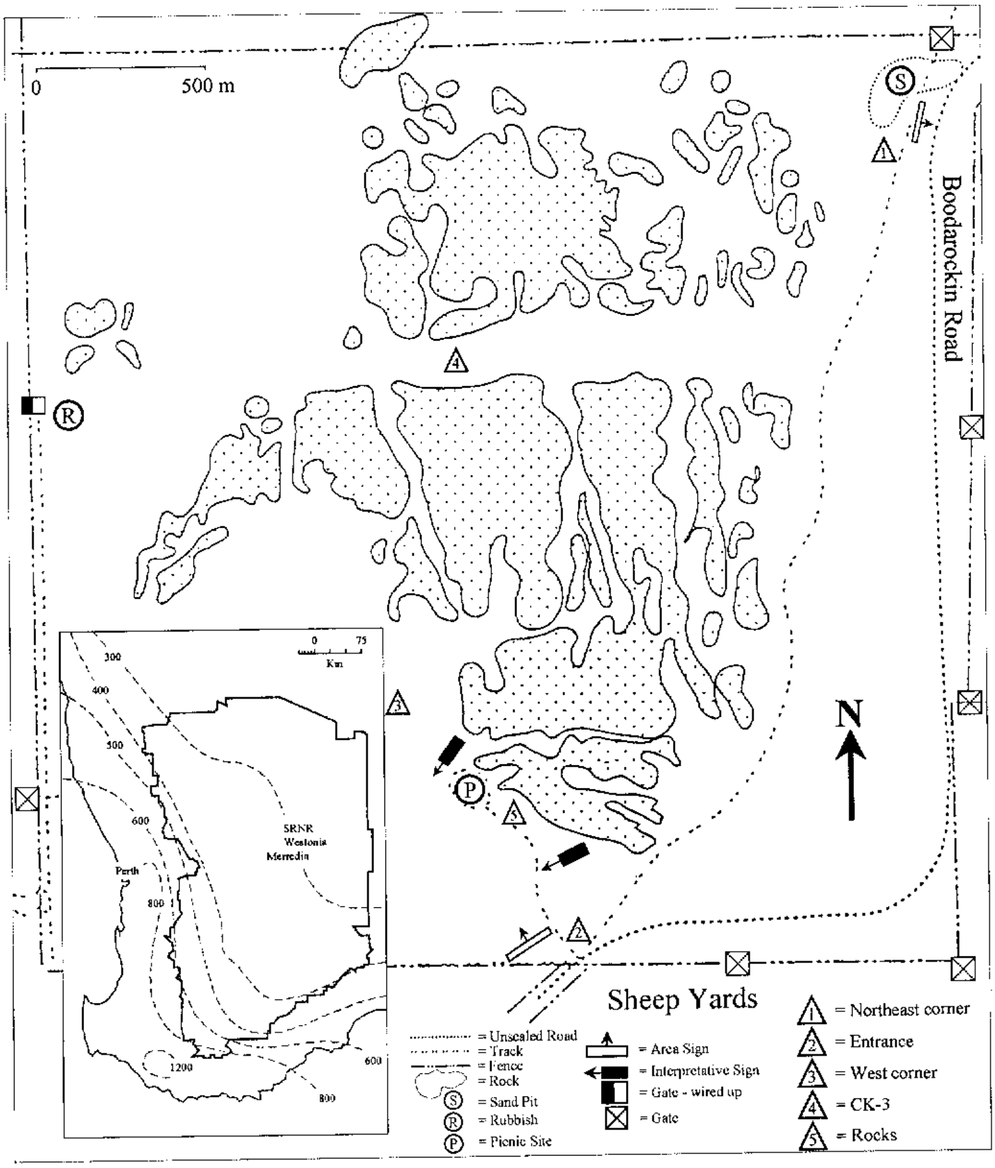

Figure 1. Plan of Sandford Rocks Nature Reserve (SRNR). Adapted from Wallace and Morre (1987).

1.3. Climate at Westonia/Sandford Rocks Nature Reserve (SRNR)

Westonia experiences a Mediterranean climate with summer temperatures ranging from 35-45°C and winter temperatures of 0–27°C. The climate is moderate with cool wet winters and occasional frosts; and the summers are dry and warm. The mean annual rainfall for the period 1980-2000 is 344 mm with most falling in winter, between

May and August (Figure 2a). The climate is characterised by long (7-8 months) hot, dry summers with short, wet winters. As a result, water is scarce for much of the year. Occasional summer thunderstorms and spring frosts may occur and are unpredictable. During the period 1980-2000, rainfall has been higher from 1995 than in the first part of this period (Figure 2b). In 1999 the total was 597.2 mm (Table 1), the highest rainfall in the last 20 years. Severe drought occurred in 1994 (214.8 mm) and in 1980 (232.6 mm). In calender year 1917, 543.1 mm fell and in 1963 the total was 607.5 mm. All other years from 1915 were less than 550 mm.

Table 1. Rainfall Westonia Calendar Years 1980-2000.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Σ
1980	16.6	22.4	0	22.4	39.3	60.1	30.0	8.6	4.0	19.0	5.8	4.4	232.6
1981	21.8	9.2	1.8	22.2	82.0	43.4	37.8	43.8	10.6	18.6	44.8	16.0	352.0
1982	17.0	0	5.8	1.0	44.4	58.2	20.2	45.0	22.0	50.6	6.8	36.2	307.2
1983	3.2	0.6	0.2	2.2	3.6	53.4	54.6	29.4	43.0	0	47.4	70.0	307.6
1984	12.6	17.6	32.6	62.4	103.6	19.8	34.0	17.0	15.8	11.2	9.2	1.0	328.8
1985	0	36.0	63.0	6.4	12.4	16.8	55.4	45.2	23.8	9.2	9.8	1.8	289.8
1986	19.2	16.6	7.6	11.6	49.2	73.0	33.6	33.6	16.4	14.2	18.4	13.2	306.6
1987	2.0	0	3.4	33.0	42.8	31.0	30.6	54.3	9.7	19.1	23.4	74.3	323.6
1988	0.1	0	3.6	31.2	83.4	40.5	42.3	55.5	14.9	9.7	21.9	13.0	316.1
1989	17.6	32.0	5.0	34.5	79.6	60.1	32.8	17.2	7.8	6.3	2.0	8.2	303.1
1990	43.4	11.5	46.9	34.4	16.3	25.8	66.0	37.1	23.6	23.2	0	1.0	329.2
1991	18.3	0	0	12.2	35.1	53.0	58.0	26.3	22.6	5.0	12.6	25.1	268.2
1992	0.4	21.5	53.6	23.2	8.9	73.8	25.4	94.5	36.5	7.1	8.8	17.6	371.3
1993	0	6.4	18.4	8.9	86.0	80.2	26.5	73.9	15.7	9.1	49.0	2.2	376.3
1994	11.9	19.3	1.3	0	31.7	36.1	21.3	50.2	20.0	4.9	0.4	17.7	214.8
1995	17.5	36.1	42.8	19.7	56.3	38.5	104.2	14.5	23.3	24.2	1.4	36.8	415.3
1996	0	3.5	10.0	40.9	20.3	64.5	93.4	58.5	57.3	6.0	43.7	0.5	398.6
1997	0	61.3	51.1	42.8	42.3	23.2	43.4	48.1	37.8	12.8	20.4	1.9	385.1
1998	3.5	0	13.6	79.7	56.2	99.3	61.7	45.2	26.1	11.3	6.3	7.2	410.1
1999	26.8	36.2	110.8	29.1	112.5	40.0	75.3	50.5	35.0	17.4	39.7	23.9	597.2
2000	103.2	18.7	95.3	32.5	4.5	17.6	51.6	42.6	19.6	0	2.9	1.0	389.5

In contrast, some observations (Chapter 4) were made at the FTA of Curtin University (32° 00′ S, 115° 88′ E). The mean annual rainfall at the FTA is similar to the Perth city at 791.9 mm. The FTA has summer temperatures of 14-32°C and winter temperatures of 8-18°C (Bureau of Meterology 2002).

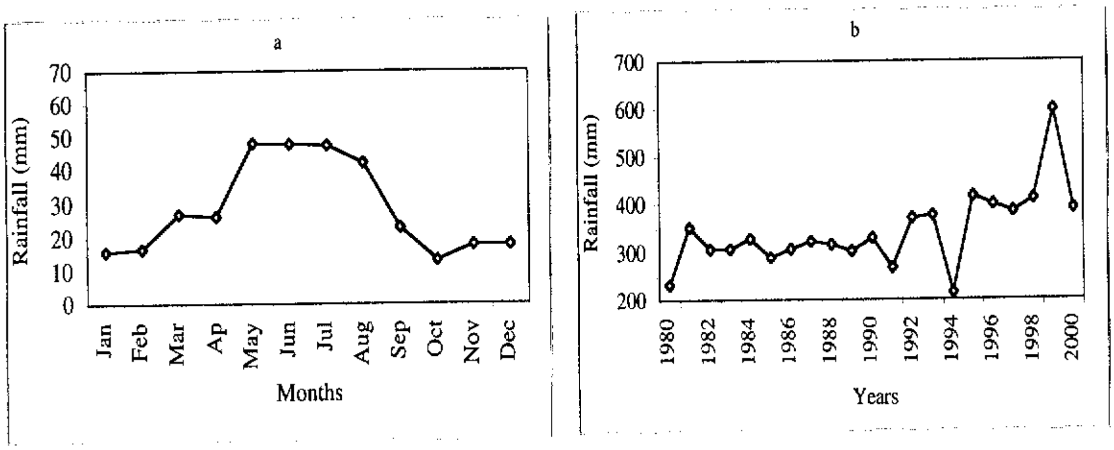

Figure 2. Rainfall at Westonia. a. Mean monthly rainfall (1980-2000). b. Total annual rainfall by calendar years 1980-2000. Source: Westonia post office.

1.4. Vegetation and *Acacia* population of Sandford Rocks Nature Reserve (SRNR)

A preliminary inspection of vegetation at SRNR revealed some patterns. The vegetation consists of a mosaic of patches of various species. These occupy fairly distinct zones in which some species are dominant. Some associations are related to the large granite outcrop. This has been extensively eroded, particularly by wind, rain, lichen and mosses. These forces have exposed and shaped the granite outcrop, contributing to the formation of the surrounding soils and the assemblage of distinct vegetation types (Hopper, Brown & Marchant 1997). The tallest vegetation stratum is dominated by tree species of *Eucalyptus*. In several areas the tall tree *Eucalyptus salmonophloia* F. Muell. (Salmon gum) is present in an open woodland. This is accompanied by *Acacia hemiteles* as an understorey species. *Acacia* species are locally abundant, present in various associations of eucalypt woodland, melaleuca thicket and scrub. Many *Acacia* spp. appear to occupy distinctive habitats. For example, *A. prainii* occupies winter-wet soils adjacent to an ephemeral creek. *A. fauntleroyi* and *A. lasiocalyx* occur on shallow soils near granite rocks that receive additional run-off in winter. A number of grass species also occur and some of these appear to dominate particular parts of the reserve. *Spartochloa scirpoidea* (Steud.) C.E. Hubb is a large perennial hummock grass that is found in clefts among rock areas.

This project involved a study of the composition and structure of vegetation at SRNR. After several visits to the area, five sites were selected based on vegetation appearance and habitat properties, representing the environmental variation across the reserve. The five areas chosen are the northeast corner; entrance; west corner; CK-3; and rocks respectively (Figure 1). At each area, 100 m transects were set up and the point centred quarter method was employed (Mueller-Dombois & Ellenberg 1974) to sample the woody perennial species. For areas of rock, where the vegetation was scattered in small patches among the granite rocks, a modification of the point quarter method was applied. Sampling points in the centred quarter method were replaced by a point where selected *Acacia* species (*A. lasiocalyx*, *A. prainii* and *A. fauntleroyi*) were present. Density, dominance (crown cover), and importance values of each species were calculated. In addition, stem diameter and plant heights were measured.

At SRNR, about 18 species of *Acacia* were found to occur. They are locally abundant, occupy particular habitats, and clearly play important roles in the associations present. The population characteristics of four selected *Acacia* species (1.1. Introduction) and their associated species were investigated (Chapter 3). The modification of the point centred quarter method was employed. The aims were to investigate the natural regeneration of these species as population characteristics; and to investigate associated species.

1.5. Aspects of reproduction in *Acacia* species

In plant conservation, reproductive potential or capacity of a plant is of practical concern as it has an impact on the natural regeneration of plants. For *Acacia* species, reproduction in a particular period can be summarised as dependant on: the number of inflorescences initiated; the number of flowers per inflorescence; the number of pollinated flowers; the number of fertilised ovules; the extent of pod and seed predation; weather conditions; and, the availability of resources for development. Reproduction may vary within a reproductive episode. Factors that may reduce reproduction include a short growing season; low or high temperature, low nutrient and moisture availability; herbivore activity; wind at the time of pollination; competition; disease, and scarcity of pollinators. These factors may reduce the possibility of flowering and seed set (Stephenson 1981).

The resources available to a given flower or fruit depend on the total resources of the individual or branches and the number of reproductive structures drawing upon those resources (Lloyd 1979). Plants usually match their reproductive output to the resources available by flower and juvenile fruit abscission. Many species produce mature fruits from only a small portion of the flowers. These species regularly abort flowers and immature fruits (Stephenson 1979).

The concerns were to discover how rainfall variation between years affects reproduction of *Acacia;* and the effects of phyllode number and tree shape on reproduction. In 1999-2000, eight *Acacia* species were examined (Chapter 4 section 4.2.3.1 and 4.2.3.2). Parameters recorded were numbers of phyllodes and inflorescences per branch. After all the pods had matured, or nearly so, the number of pods per branch and number of pods per inflorescence were measured. Calculations were made on the number of inflorescences that set pods and number of pods per inflorescence.

In December 1998, pods from 13 species were harvested to investigate the reproduction capacity of the species. Number of seeds and aborted seeds per pod, together with dimensions of pods, were recorded (Chapter 4 section 4.2.3.3). Seeds were then germinated to obtain a measure of viability (percentage germination).

As resources available to reproduction depend on the total resources of the individual and the number of reproductive structures drawing upon those resources, it is interesting to examine the effects of phyllode and inflorescence removal on reproduction of *Acacia*. The concerns were to investigate: does removal of phyllodes restrict pod development? Does reduction of inflorescences increase the probability of remaining inflorescences producing a pod? Two selected *Acacia* species (*A. saligna* and *A. lasiocalyx*) were investigated (Chapter 4 section 4.3.3.1 and 4.3.3.2). The treatments were 0, 50 and 100% (phyllodes) and 0 or 50% (inflorescences) removed, from individual branches.

1.6. Germination and seedling characteristics of *Acacia* and grass species of Sandford Rocks Nature Reserve (SRNR)

The germination of seeds is affected by a number of factors. These are conveniently considered as either internal (maturity at harvest, age of seeds and seed dormancy) or external (water availability, temperature, light and oxygen) factors. The optimum temperature for seed of particular species to germinate is specific to the type of seed. Optimal condition varies considerably between species. The experimentation required to determine these optimum temperatures for most Australian species has not been completed (Peterson 1985).

Seed germination or seedling establishment is the first phase in the establishment of a new plant. The second phase is seedling growth and survival. Under natural conditions, only few seedlings survive to maturity. A germination test was conducted under various conditions of incubation temperature to find: under what temperature regime do most *Acacia* seeds germinate. Eight *Acacia* species were examined (Chapter 5 section 5.2). Incubation treatments were 15, 20, 25 and 30°C. Any germinants were recorded and planted. Seedlings of each species were also harvested at 14 d after transplanting, to examine variation of seedling characteristics between species in early growth. Root and shoot were separated, dried and weighed, then root and shoot ratios were determined.

At SRNR, a number of grass species occur and some of them appear to dominate particular parts of the landscape. A series of germination tests was conducted (Chapter 5 section 5.3) to identify germination characteristics of the most dominant grass species at SRNR. The aims were to investigate: Does pre-treatment improve germination of these species? Under what temperature regime do most seeds germinate? The effect of hot water pre-treatment was investigated in 7 species. Pre-treatment was soaking seeds in hot water (40°C) or at ambient temperature (~20°C) for 20 minutes. The effects of incubation temperature were also investigated in 5 species. The treatments were incubation at 15, 20, 25 and 30°C. Seedlings of the 7 grass species were also grown in pots with a mixture containing 1:1:1 coarse sand: fine sand: peat moss, with no fertiliser applied. At the age of 14 d, eight seedlings of each species were harvested, to investigate variation in early seedling characteristics between the species.

1.7. Effect of seed size on germination and seedling characteristics in *Acacia* species

The seed of most *Acacia* species is characterised by a thick or "hard" seed coat (Clements, Jones & Gilbert 1977; Cavanagh 1980; Doran *et al.* 1983). This is responsible for seed coat-imposed dormancy that must be broken to enable the embryo to obtain water needed to reactivate its metabolism and start growing. The seed coat (testa) that provides the barrier to water penetration is a continuous layer of tightly packed, elongate Malpighian cells, directly below the water permeable cuticle (Cavanagh 1985). The Malpighian zone varies in thickness both within and between species. Numerous techniques have been used to render *Acacia* seeds permeable. Of all techniques, boiling water treatments give better results for Australian *Acacia* whereas pre-treatment with concentrated sulfuric acid is frequently more effective for African *Acacia* (Doran *et al.* 1983). Placing *Acacia* seeds in boiling water damages the cuticle and sometimes parts of the palisade layers of the seed coat, thus effectively breaking dormancy.

The nature of the hard seed coat is species specific. Some species are sensitive to prolonged heating but have given enhanced germination with a moderate heat pre-treatment. There are several *Acacia* species, which have soft seed coats and pre-treatment before sowing is unnecessary or even lethal (Doran *et al.* 1983). Different responses may be obtained if seeds are divided into different size classes (Moffett 1952). The direct and indirect effect of seed size on seed coat thickness, seed coat permeability and the surface volume ratio may determine both the speed and probability of successful germination (Wulff 1986). Seed size may affect seed water relations, germination and the size of the resulting seedling (Salisbury 1974). Seed size variability, however small, may have a large impact on seedling establishment and survival. Thus, through effects on seed size, the establishment requirements of a plant may affect many aspects of its reproductive biology.

The possible effects of variation in seed size on germination and seedling size were investigated in *A. fauntleroyi* and *A. prainii* (Chapter 6 section 6.2 and 6.3). The aim was to investigate: to what extent are germination and seedling characteristics affected by seed size? Three seed size classes (small, medium and large) were chosen in each species. Germinated seeds from small and large size classes were also planted, and root and shoot ratios determined. Seed coat thickness in these species was examined (Chapter 6 section 6.4). Seeds representing each size class were sectioned and examined microscopically. The aims were to investigate the possible effects of variation in seed size on seed-coat thickness: does seed coat thickness differ among seed of different size?

1.8. Study species

In this chapter, I also present a general introduction to some of the more important species selected for study. A brief description is provided of general habitat and distribution. There were 9 of the 14 *Acacia* species and all 7 grass species are included here.

1.8.1. *Acacia* species

Of the *Acacia* species described here, all 9 were generally flowering in July-September with seed becoming mature in December. This review of the species generally follows the Flora of Australia volume 11 A and B, Mimosaceae, *Acacia* part 1 and 2, ABRS/CSIRO, Publishing (Orchard & Wilson 2001ab).

1.8.1.1. *Acacia neurophylla* W. Fitzg.

A. neurophylla is a tall shrub or small tree growing to around 4-6 m tall by 3-4 m wide and erect or low spreading in shape. Phyllodes are stiff, glossy and dark green with distinctive veins. Flowers are golden yellow; flower heads are cylindrical. Bark is dark grey and smooth. It is both drought and frost tolerant, requiring well drained, light to medium soil, with partial or full sun (Elliot & Jones 1990). Germination usually occurs after rains. It occurs in semi-arid to arid areas of Western Australia. Distribution is disjunct, occurring from Morawa to Cunderdin, with a southern variant occurring near Beacon (55 km E of Koorda) and from the Lake Johnston area to Norseman and Moir Rock. Northern populations grow in sand and laterite, and southern populations in sandy loam, often near granite, in scrub and shrubland. At SRNR, *A. neurophylla* is found only at the northeast corner site, growing on yellow shallow-dry sand.

1.8.1.2. *Acacia fauntleroyi* (Maiden) Maiden & Blakely

A. fauntleroyi is an erect shrub, 1.8-5 m tall. The bark is red and fibrous, stringy and shaggy. Plants are sometimes single stemmed but commonly have more than one stem, at 20 cm above ground level. Phyllodes are several-nerved, grey-green or yellowish-green, more or less resinous and aromatic. Distribution occurs from Wongan Hills and Bonnie Rock to Hyden, in inland southwestern Western Australia. It grows on or around granite outcrops, in scrub and shrubland. At SRNR, it generally flowers in September and seed becomes mature in December. Plants are mainly found at the base of the main granite rock, in shallow well-drained, coarse granitic sandy soil. Populations are low in number. It is sometimes present with *A. lasiocalyx* and commonly found with large clumps of the perennial grass *S. scirpoidea.*

1.8.1.3. *Acacia lasiocalyx* C. R. P Andrews

A. lasiocalyx is commonly called the silver wattle because of the silvery appearance of its bark. It is a shrub or tree, 2-3.5 m tall but it can grow to a height of 10 m. *A. lasiocalyx* is widely distributed in south western W.A, from near Eneabba and Kalgoorlie to Bremer Bay and Mt. Heywood. It grows in sand, gravelly and loamy sand, clayey sand and loam. It is common on slopes of granite hills and granite outcrops but is also found in heath and open heath. Plants growing at the base of granite rocks are often in dense colonies and attain an arborescent habit. The main trunk is more erect and straight than those of plants occurring elsewhere. The distribution of *A. lasiocalyx* at SRNR was relatively sparse, in small clusters in pockets of soil on the edges of the main rock.

1.8.1.4. *Acacia prainii* Maiden

A. prainii or prain's wattle is a shrub or compact shrub, 2-4 m tall. Bark is dark gray or red-brown and fibrous on the main trunk and branches. Branching occurs at ground level. Phyllodes are narrow, erect, dark yellowish green or light green. Distribution: scattered in arid and semi-arid areas from Morawa and Holt Rock, WA to Amadeus, N.T and Everard, S.A. It grows in sand or sandy clay in open scrub, mallee communities, *Eucalyptus* woodland or spinifex (*Triodia* spp.) country. At SRNR, *A. prainii* are mainly found at a winter-wet area, around the base of granite rock. It is commonly present with the swamp grass species *Eriachne ovata* Nees.

1.8.1.5. *Acacia hemiteles* Benth.

A. hemiteles (Tan Wattle) is a dense, many stemmed, spreading shrub to 0.5-2 m tall. In favourable conditions it may attain 4 m tall. Branchlets are angular, flattened and often bloom covered. *A. hemiteles* has a yellowish appearance. It is often found in dense populations from around Kalgoorlie, stretching to the north of Albany and all the way to Geraldton. It is often locally common, grows in sand, loam or clay, in woodland or shrubland, sometimes on lateritic or granite rock. At SRNR, it is common as an understorey species of *Eucalyptus* woodland where it has a big population and quite wide distribution.

1.8.1.6. *Acacia saligna* (Labill.) H. Wendl.

A. saligna (golden wreath or orange wattle) is a dense shrub or small tree, 2-8 m tall, with spreading crown. Bark is grey, phyllodes often pendulous, variable in shape and size. *A. saligna* is a fast growing, drought tolerant species that is easy to coppice and spreads both by root or sucker and seed. It is used extensively in semi-arid areas of North Africa and the Middle East as wind breaks, for coastal sand dune fixation, fuel wood and fodder production. In South Africa it is a major environmental weed. Common in south Western Australia, extending from Wilgiania (Kalbarri) to Ponier Rock (Balladonia). It is naturalised in Queensland, Victoria and Tasmania. In Western Australia, it grows in a variety of habitats, including poor sandy soils of the coastal plain, clayey soil around Geraldton, the sand plains north of Gingin and the Great Southern region. It grows in deep sands, associated with watercourses and the base of granite boulders in the wheatbelt. At SRNR, it generally grows in seasonally wet areas and soil pockets on the rock. *A. saligna* regenerates after fire by both resprouting from sub-cortical-buds and from persistent soil-stored seed banks. Seeds are dispersed by ants, which move the seeds only a few meters, resulting in slow lateral spread of stands.

1.8.1.7. *Acacia steedmanii* Maiden & Blakely

A. steedmanii is a moderately open, glabrous shrub or tree, to 4 m tall. It grows in sand, sandy loam, rocky loam and gravelly clay. It is frequent on or near granite rocks but also on lateritic gravelly rises and sand plains among mallee eucalypts, tall heath and low scrub. It occurs from Pigeon Rocks to Bruce Rock and Bulla Bulling (30 km west of Coolgardie). At SRNR, it is found only at the northeast corner site and the population is very small.

1.8.1.8. *Acacia acuminata* Benth.

A. acuminata is a shrub or tree to 12 m tall. Bark is smooth to slightly rough and grey. Phyllodes are linear to narrowly elliptic and flat. It occurs widely in southern Australia, from South-western WA to the western plains of NSW. It is often locally abundant. At SRNR, there are two varieties found (small and large phyllode type). It has a wide distribution and large population.

1.8.1.9. *Acacia stereophylla* Meisn.

A. stereophylla is a shrub, 2-4 m tall. Phyllodes are linear, flat, mostly 10-17 cm long, 3-6.5 mm wide with distinct marginal nerves. It occurs from Nerren Nerren to Tammin and Boorabbin, Southwest WA. It grows in sand, gravelly sand and loam, mostly on plains, in shrubland, shrub, mallee and woodlands. At SRNR it occurs in the northeast and west corner sites. It is present in only very small numbers (small population).

1.8.2. Grass species

There are about 140 genera and some 860 species of grass present in Australia. Of these, about 31 genera are endemic to Australia. About 44 genera of the remainder are widespread in the tropics and subtropics as well as occurring in Australia (Beadle 1981), while another 65 genera are introduced into Australia, and the majority have become naturalised. At SRNR, a number of grass species occur and some of these appear to dominate particular parts of the reserve. Here I describe the 7 grass species chosen for the study. These species are well distributed, naturally occurring in the reserve and are often dominant in the areas in which they occur.

1.8.2.1. *Austrodanthonia caespitosa* (Gaudich.) H. P. Linder

A. caespitose, formerly known as *Danthonia caespitosa* (Gaudich.), is commonly known as Wallaby grass or White top. *A. caespitosa* is an erect, tufted perennial grass in the sub-family *Arundinoidea*. It grows to around 0.2-0.9 m tall. The grass is bisexual with spikelets and hermaphroditic florets. The inflorescence is few-spikelet, paniculate (some times in a raceme) or open. A fruit is borne from both lemma and palea with a golden brown coloration. Seedlings usually feature a long mesocotyl and the first sprout has a well-developed narrow lamina. It is widespread through the South-West and Goldfields areas of Western Australia as well as SA, Victoria and New South Wales (Marchant *et al.* 1987). It is found from mesophytic-xerophytic areas and is a species of open habitats, found in areas of grass and woodlands and regularly in hill regions. *A. caespitosa* flowers in October and November; seed germination occurs after extended rain periods. Being a natural pasture grass, it is important in grazing systems.

1.8.2.2. *Austrostipa elegantissima* (Labill.) S. W. L. Jacobs & J. Everett

A. elegantissima (also of sub-family *Arundinoidea*) is a large, tussock perennial grass. It can grow up to 1 m tall and has finely scabrous or smooth leaves. Its glumes are 10-12 mm long with hair on the pedicels and branches up to 3 mm. The seed are borne in florets and arranged into seed heads (spikelets), often many to a tussock. The awns are feathery and easily broken, releasing the seeds on maturity. *A. elegantissima* is widespread thorough the Eremean and southwestern botanical provinces, extending from Carnarvon in the north to Esperance in the south (Mitchell & Wilcox 1994).

1.8.2.3. *Amphipogon strictus* R. Br.

A. strictus (Greybeard grass) is an Australian perennial grass. Its stems arise from a horizontal rhizome. The grass forms dense tussocks that range from 0.3-0.8 m tall. The stems are covered with pale overlapping scales. The narrow leaf blades of the plant are hairy when they are young but eventually become stiff and erect with age. It is endemic to mainland Australia. Spikelets of *A. strictus* are bisexual with some mixed bisexual spikelets and hermaphroditic spikelets. The inflorescence is in the form of a single spike. The wiry stems of *A. strictus* are generally avoided by grazing stock, although leafy plants grown in wetter areas may be grazed and occasionally used for fodder. The seed head is less than 3 cm long and spikelets are closely arranged. The outer husks are dark gray or purplish in colour, but eventually fade to a straw colour with age. *A. strictus* flowers from October to December; flowering time however depends on the area of Australia in which the grass is growing. It can be propagated either by seed or by division. *A. strictus* is generally restricted to heathlands and low woodlands and commonly grows on sands and sandy loams. It is widely spread in the temperate parts of southern Australia, except in Tasmania. Within the Perth region, *A. strictus* has been collected from Gingin, Maddington and Helena Valley. It also occurs from Northampton in the north to Ravensthorpe in the south. *A. strictus* also occurs in New South Wales and Queensland.

1.8.2.4. *Aristida contorta* F. Muell.

A. contorta is a tufted annual or perennial (short-lived) grass-like or herb, 0.12-0.44 m tall. Flowers brown, flowering in February-June. Occurs on white or yellow sand; red or brown clay, loam; brown sandy clay; grey sand over clay, on edge of wetland and sandy soil. Mott (1974b) describes *A. contorta* as a summer growing grass.

Caryopses of *A. contorta* appear just to penetrate the soil surface before losing their long, three-partite awns and remain partially uncovered until germination. *A. contorta* will germinate after winter rains, if insufficient rain for germination has fallen during the previous summer. *A. contorta* had maximum germination at 30°C, with much less and slower germination at lower temperatures. Seed of *A. contorta* has been found to have an obligate requirement for light in germination. The autumn seed of *A. contorta* would remain dormant during the cool winter before a short period of the high soil surface during the summer rains.

1.8.2.5. *Spartochloa scirpoidea* (Steud.) C. E. Hubb.

S. scirpoidea is a perennial caespitose grass, 0.3-1.5 m high or clumped caespitose grass forming hummocks with rather glaucous stems. New stems and inflorescences grow up among the old leaves. It has long cylindrical leaves, blue-green in colour, florets are creamy yellow, with stigmas and anthers purple. Plants grow in red lateritic clay sand, exposed granite and shallow gritty soils in hollows, brown clayey sand over granite flat, on red soil over green-stone rocks. Flowers in September to October or February. Distribution: Eremaean and Southwest, botanical districts Coolgardie and, Avon wheatbelt, Esperance Plains, Jarrah Forest, Mallee and Swan coastal plain. At SRNR, commonly found at the base of granite rock.

1.8.2.6. *Eriachne ovata* Nees

E. ovata is a semi-aquatic, short-awned perennial or tussocky perennial, 10-18 cm tall. It is associated with sand plain or granite; it grows in seasonally wet areas of heavy-textured clay, with poor awn development. It is also common on granitic sandy loam, rock crevices and granite outcrops. It is frequent in open scrub, red-brown sandy clay with granite domes. The species is widely distributed over Australia but not in Victoria. *E. ovata* is however, well-distributed in Western and South Australia. *E. ovata* is one of the few native grasses still seen in the wheatbelt *Eucalyptus* woodland. It is a strong competitor in the woodland environment. Flowers are green, purple; flowering in August-November. It will flower more than once in its lifetime ensuring a supply of seed from one year to the next.

1.8.2.7. *Neurachne alopecuroidea* R. Br.

N. alopecuroidea is a perennial grass, commonly referred to as the "foxtail mulga grass". It is densely clumped in nature, with 15-50 cm erect stems, arising from a stocky underground rhizome (Marchant *et al.* 1987). Growth is primarily during summer. Flowers are green, gray with white hairs. It flowers from July to November. Widespread over the temperate southwest Botanical Province of Western Australia. Inhabiting a wide variety of soils, it typically prefers sandplains, hill slopes and outcrops. Despite being heavily grazed, it is one of the few native grasses still commonly seen in eucalypt woodlands in the wheatbelt. Records exist furthermore of its presence in Victoria and SA.

CHAPTER 2

STRUCTURE AND COMPOSITION OF VEGETATION AT SANDFORD ROCKS NATURE RESERVE (SRNR)

2.1. Introduction

Natural vegetation has an intrinsic value, as a source of genetic resources and in maintaining biodiversity. Recently, there has been an increased interest in the conservation of native vegetation, coupled with a substantial increase in deforestation and land degradation due to agricultural practices and other human uses. Fragmentation of natural ecosystems is one of the major threats to biodiversity worldwide. The fragmentation process reduces the area of native ecosystems and leaves isolated remnants, which are subject to species loss, and invasion by non-native species and changes in population and ecosystem processes (Hobbs 1987). The fragmentation process also leads to many physical and biological changes, such as altered microclimatic, nutrient and hydrologic regimes; altered pollinator behaviour; a reduction in available habitat and isolation from surrounding areas (Hobbs 1987; Saunders, Hobbs & Margules 1991; Brothers 1992; Goverde *et al.* 2002).

Australia is one of the most biologically diverse countries, with a large portion of its species found nowhere else in the world. Australia's native vegetation is one of the richest and most fundamental elements of natural heritage. The depletion and degradation of native vegetation communities threaten the long term health and productive capacity of the Australian landscape. Destruction of native vegetation is the single biggest cause of biodiversity loss. It is a primary cause of land degradation; salinity and declining water quality; and it is one of the biggest contributors to net green-house gas emissions.

One of the most diverse floras in the world is found in the native vegetation of the wheatbelt of Western Australia. However, some 80% of this region has been cleared for agriculture (Saunders *et al.* 1987). The Western Australian wheatbelt now contains only scattered remnants of native vegetation, surrounded by agricultural land. Most remnants are very small, < 400 ha (Kitchener *et al.* 1980). Prior histories of fencing, felling, presence of rabbits and grazing of livestock all influence present-day condition. Prior to clearing, the vegetation existed as a mosaic of communities closely associated with the soil type. Woodlands dominated by *Eucalyptus* species occupied heavier textured loam and clay soils in the valleys, while shrub-heath and thicket were found on lateritic sands and duplex soils higher in the landscape. The association between vegetation and soil was recognized by early settlers, and vegetation type was subsequently used to classify land in terms of its suitability for agriculture (Keenan 1993). Woodlands were considered the most suitable, while areas with large amounts of scrub were considered the least suitable, consequently woodlands are very poorly represented in the wheatbelt today.

Sandford Rocks Nature Reserve (SRNR) is a remnant of the native vegetation that remains in the Western Australia wheatbelt (Chapter 1, Figure 1). The reserve has an area of 805.9 ha, with a complex mosaic of exposed granite rock, shrubland and woodland (Muir 1979). Granite outcrops are distinctive, natural features of the wheatbelt landscape (Hopper *et al.* 1997). Some species of plants and animals are only found on granite outcrops. Away from the outcrops, the landscape of the areas is gently undulating, with very little relief between valley floor and the ridges between major drainage lines. The main soils of the area include earthy sands, podsolics, lithosols, red brown earths or calcareous clay sub-soil and a hard-setting surface soil, and solonized brown soil. Soils are low in phosphorus, iron and aluminium oxides and high in potassium, with generally much organic matter on the surface and a somewhat acidic pH (McArthur 1991, Stoneman 1992).

The original reason for the reservation of SRNR was as a water reserve (designated at 9 May 1899). Its purpose was changed to water and conservation of flora and fauna in July 1958 because of its perceived high conservation values (Muir 1979). SRNR is in very good condition and has been reported as one of the best reserves in the area. It has been fenced off from cattle and sheep grazing. Some areas of the reserve show some signs of disturbance, mainly in the form of felled trees and vehicle tracks. The shape of the reserve is square with a perimeter of approximately 11.2 km, and is big enough to support populations of large animals such as kangaroo and emu. Fire has not affected the reserve for over 72 years (Gow 1997), except for a very small part that was burnt in 1999. Therefore, this form of disturbance can be discounted as having influenced the vegetation in recent times. The reserve also contains stands which lie at a distance far enough from farmed land to allow some confidence to be placed in the integrity of ecosystems as they are now (Hobbs & Atkins 1988).

A preliminary inspection (December 1998) of vegetation at SRNR revealed some general patterns. The vegetation appears to consist of a mosaic of patches of various species and there are fairly distinct zones in which some species are dominant. Factors causing patchiness of communities are presumed to be related to the different life strategies of constituent plant species and to the exogenic habitat heterogeneity within the reserve. Plant species associations are mainly related to the large granite mass, which dominates the central part of the reserve. This granite outcrop has been extensively eroded. Geological forces have exposed and shaped the granite outcrop, contributing to the formation of the surrounding soils and some assemblages of distinct vegetation types are related to this.

Nine major vegetation associations at SRNR were identified by Muir (1979): 1) Jam woodland (*Acacia acuminata*); 2) Gimlet woodland (*Eucalyptus salubris*); 3) Wandoo woodland (*Eucalyptus capillosa/salmonophloia*); 4) York gum woodland (*Eucalyptus loxophleba*); 5) Black marlock mallee (*Eucalyptus subangusta*); 6) Tamma shrubland (*Allocasuarina campestris*); 7) *Acacia stereophylla* shrubland; 8) *Allocasuarina acutivalvis* shrubland; and, 9) Lithic complex. *A. acuminata* (Jam) woodland occurs on moderately well drained, pinkish-grey, gritty loam soil. Gimlet woodland is a moderately dense association with a mixed shrub understorey dominated by *Acacia* species that occurs on poorly drained, red, sandy clay. Wandoo woodland occurs with sparse, scattered shrubs on poorly drained, pinkish grey, sandy clay loam.

York gum woodland, with a sparse mixed shrub understorey (including species of *Acacia* and *Dodonaea* with the lily *Dianella revoluta* R. Br.), occurs on poorly drained, pinkish grey, sandy clay. Black Marlock mallee occurs with *A. acuminata* and *Melaleuca acuminata* on light reddish brown loam and with mixed shrubs on poorly drained, pinkish grey, sandy clay. Tamma shrubland and tamma vegetation, co-dominant with *A. stereophylla,* occurs on well-drained reddish yellow, fine sandy loam with 40-60% laterite. *A. stereophylla* shrubland (with *Baeckea* and *Calothamnus* species) occurs on moderately drained, brownish yellow, fine sandy clay loam with around 60% laterite. *A. acutivalvis* shrubland occurs with a sparse shrub layer of *Baeckea* and *Calothamnus* species. Lithic complex comprises large pavements and outcrops of granite with soil pockets of variable depth supporting areas of healthy shrubland.

To meet the long-term challenge of the decline in native vegetation, land clearing needs to be reduced; restoration and revegetation of native vegetation communities needs to be enhanced; and, improvement is needed in the protection and management of the native vegetation that remains. There is now a strong movement for conserving the remaining vegetation and increasing interest in reconstructing native ecosystems (Saunders *et al.* 1987; Lefroy, Hobbs & Atkins 1991; Fry & Main 1993). Some areas of remaining native vegetation have been designated as nature conservation reserves. However, there is still very little information available regarding the functioning of floral communities because of the paucity of detailed descriptions of vegetation in the wheatbelt. In this chapter, I propose to describe the main floral communities present, comprising the bulk of vegetation at SRNR. Structure and composition of vegetation are presented and I discuss possible determinants of the patterns found. As the area is relatively undisturbed natural vegetation, information obtained is important for management of this natural area.

2.2. Methods

Five general areas were selected for study, representing the environmental variation across the reserve. The selection was based on vegetation appearance and habitat properties. The five general areas chosen were named as: the northeast corner; entrance; west corner; CK-3 and rocks respectively. The names of these study sites had been given in various prior studies conducted by the School of Environmental Biology at Curtin University (Fox 1997). The location of these areas selected at SRNR are presented in Figure 1, Chapter 1. 1. The northeast corner area generally comprises low or medium open shrublands with few tall trees. Sites are mainly characterised by shallow, yellow lateritic sands and rocky soil. It appears very dry in summer. Most vegetation consists of low shrubs of *Baeckea* and *Grevillea* and small or shrub forms of *Allocasuarina* that are presumed adapted to dry shallow soil. 2). At the entrance area, sample sites are mainly seasonally (winter) wet areas. Several plant associations occur such as woodland, thicket and open grassland. Soil includes clay loams and sandy clay loams. Low shrubs of *Acacia jennerae*, *Hakea invaginata* and *Alyxia buxifolia* R. Br. occur with many grass species. 3). The west corner area is characterised by Myrtaceous thickets with few low trees of *Eucalyptus* present. The sites are confined to relatively deep sandy soils that become very dry in summer. *Phebalium tuberculosum* and some *Acacia* species appear to dominate some sites. 4). The CK-3 area is located between two large granite masses (Figure 1, Chapter 1), and consists of woodlands dominated by eucalypt species. These appear to be the most developed vegetation at SRNR. The soil is mainly sandy clay loam. 5). The rocks is a seasonally wet area with pockets of various soils and run-off areas related to the granite rocks. The soil is sandy loam, clay loam or fine sandy loam. Species in the genera: *Dodonaea*, *Acacia* and *Leptospermum* appear in sites of different characteristics in the rocks area.

At each of the 5 locations (except for the rocks site), 100 m transects were set up and the point-centred quarter method was employed (Mueller-Dombois & Ellenberg 1974). Eight transects were located in each of the northeast corner, entrance and the west corner, and six transects were set up at CK-3. For the rocks, a modification of the point quarter method was applied, as the vegetation was scattered in small patches among the rocks. Sampling points in the point-centred quarter method were replaced by points where selected *Acacia* species (*A. lasiocalyx*, *A. prainii* and *A. fauntleroyi*) were present. Seventy-nine (79) sampling points were used at the rocks (24, 32 and 23 sampling points for associations of *A. lasiocalyx*, *A. prainii* and *A. fauntleroyi* respectively). Therefore, a total of 379 sampling points were applied with 1516 woody perennials measured.

Transects were located arbitrarily across particular stands or communities, representative of each area. Along each 100 m transect, four distances (to the closest woody perennial) were measured at 10 m sampling points. That is, there were 10 sampling points separated by a distance of 10 m along each 100 m transect. The four quarters were established by crossing two lines. The first line ran in a cardinal compass direction and the second line ran perpendicular to the first compass direction. The point where the two lines crossed was called the sampling point (10 per line). In each quarter, the distance to the mid-point of the nearest tree from the sampling point was measured. Herbs and grasses were excluded. Density, dominance and importance values of each species were calculated. Density is the total number of individuals of a species captured in the 100 m transects, and dominance is expressed as crown cover. By adding the relative values for density and dominance, an importance value was derived (Mueller-Dombois & Ellenberg 1974). Plant species were identified with nomenclature following Green (1985).

Soil depth was measured at each sampling point by pushing a steel rod into the soil as deeply as possible. The depths of penetration for soil depths were marked and measured with a 1 m rule. Most soils were underlain by granite. Soil texture was also determined at each sampling point in the field according to the procedure outlined in Appendix 2. Plant heights were measured directly with a measuring tape for individuals < 6 m tall, while plants greater than 6 m tall were measured using a Sunto clinometer. Plant height was defined as vertical distance from trunk base to the highest leaves. Stem diameters were measured with a diameter tape at a height of 50 cm. The percentage of plants with multiple stems was calculated. Plants were classified according to their height as tall tree/canopy, sub-canopy (intermediate) and understorey species. Crown cover (Cc) was calculated from the equation: $Cc = \{(D1 + D2) / 4\}^2\prod$, where, D1 = The widest crown-diameter of the tree or bush across the centre to the other side of the crown perimeter, D2 = Crown-diameter perpendicular to D1 (Mueller-Dombois & Ellenberg 1974).

The Shannon-Wiener index was used to calculate species diversity, $H' = \Sigma\ (pi)\ (Ln\ pi)$. Equitability (evenness) $J = H' / H'\ max = \Sigma\ (pi)\ (Ln\ pi) / Ln\ s)$. Where, s = Number of species, pi = Proportion of importance value of the species, Ln = log base n. Similarity (Ss) between vegetation at the 5 areas was calculated with the Sorensen coefficient (Kent & Coker 1992), based on presence/absence of species in the areas, $Ss = (2a)/(2a + b + c)$, where, a = Species common to both sites, b = Species in site 1 only, c = Species in site 2 only.

Distributions of species across the area were assessed according to their presence in each "stand", where stand refers to one transect. Each 100 m transect and associated species at the rock site were used in stand analysis. There were 30 100-m transects (30 stands) and 3 species associations (*A. lasiocalyx*, *A. prainii* and *A. fauntleroyi*) at the rock site (3 stands), therefore giving a sum of 33 stands. Distributions of species were subjectively divided into 4 categories according to their presence in 33 stands as rare (in <3 stands), infrequent (in $3<6$ stands), abundant (in $6<9$ stands) and common (in ≥ 9 stands).

2.3. Results

From all areas sampled (379 sampling points), a total of 1516 plants was measured. These were from 20 families (Apocynaceae, Asteraceae, Boraginaceae, Casuarinaceae, Caesalpiniaceae, Chenopodiaceae, Dilleniaceae, Epacridaceae, Haloragaceae, Lamiaceae, Mimosaceae, Myoporaceae, Myrtaceae, Proteaceae, Rutaceae, Santalaceae, Sapindaceae, Solanaceae, Sterculiaceae, and Thymelaeaceae) and included 85 species of woody perennials (Appendix 1). The three most species-rich families were Myrtaceae, Mimosaceae and Proteaceae.

2.3.1. Structure and composition of vegetation at the northeast corner area

Table 2. Mean height, density, dominance and importance values (IV) of woody perennial species at the northeast corner (From 8 x 100 m transects with a sum of 80 sampling points, $\Sigma n = 320$ plants). Plant nomenclature after Green (1985)

No.	Species	Family	Mean height (m)	No. plants	Density (%)	Dominance (%)	IV
1	*Allocasuarina huegeliana*	Casuarinaceae	2.94	67	20.87	24.62	45.49
2	*Baeckea elderiana*	Myrtaceae	1.47	84	26.2	6.63	32.83
3	*Grevillea paradoxa*	Proteaceae	1.44	32	9.98	4.59	14.57
4	*Eucalyptus capillosa*	Myrtaceae	7.73	4	1.42	20.22	21.64
5	*Acacia stereophylla*	Mimosaceae	2.54	26	8.48	5.95	14.43
6	*Acacia neurophylla*	Mimosaceae	2.47	10	3.19	8.86	12.05
7	*Melaleuca pauperiflora*	Myrtaceae	1.54	21	6.96	3.96	10.92
8	*Acacia nyssophylla*	Mimosaceae	2.9	14	4.71	5.99	10.7
9	*Eucalyptus buracoppinensis*	Myrtaceae	5.81	5	1.65	12.63	14.28
10	*Allocasuarina campestris*	Casuarinaceae	3.88	21	6.73	1.94	8.67
11	*Eriostemon tomentellus*	Rutaceae	1.5	5	1.51	0.44	1.95
12	*Hibbertia exasperata*	Dilleniaceae	1.34	5	1.79	0.71	2.5
13	*Calothamnus gilesii*	Myrtaceae	1.69	4	1.23	0.78	2.01
14	*Melaleuca acuminata*	Myrtaceae	1.68	4	1.14	0.23	1.37
15	*Astroloma serratifolium*	Epacridaceae	1.04	3	0.89	0.34	1.23
16	*Hakea invaginata*	Proteaceae	2.26	2	0.63	0.52	1.15
17	*Melaleuca uncinata*	Myrtaceae	0.87	2	0.54	0.04	0.58
18	*Acacia steedmanii*	Mimosaceae	2.08	1	0.4	0.74	1.14
19	*Grevillea didymobotrya*	Proteaceae	1.33	1	0.4	0.13	0.53
20	*Acacia acuminata*	Mimosaceae	2.43	1	0.17	0.3	0.47
21	*Phebalium tuberculosum*	Rutaceae	0.8	2	0.45	<0.01	0.46
22	*Acacia hemiteles*	Mimosaceae	1.64	1	0.13	0.31	0.44
23	*Boronia ternata*	Rutaceae	0.97	1	0.18	0.02	0.2
24	*Pimelea angustifolia*	Thymelaeaceae	0.83	1	0.18	0.02	0.2
25	*Eucalyptus leptopoda*	Myrtaceae	3.0	1	0.05	0.02	0.07
26	*Glischrocaryon aureum*	Haloragaceae	1.4	1	0.05	<0.01	0.06
27	*Hakea recurva*	Proteaceae	2.4	1	0.04	<0.01	0.06
	SUM			320	100	100	200

From 8 transects, a total of 320 woody perennials was collated, consisting of 27 species and 9 families (Table 2). The most species-rich families are Myrtaceae (8 species), Mimosaceae (6 species) and Proteaceae (4 species). These three families comprise about 70% of the component species. Mean density is 2000 plants/ha. The three most frequent species were: low shrubs of *B. elderiana*; small trees of *A. huegeliana;* and low shrubs of *G. paradoxa.* Those 3 species gave 57% density in this site. The tall tree species *E. capillosa* was represented by only four records (low density), however this species has a substantial crown cover and mean height of < 8 m. Some other species present in the area but absent in the sample include *Callitris glauca* (common on rocky soil with *G. paradoxa*). *Acacia steedmanii* and *A. neurophylla* are only found in this section of the reserve.

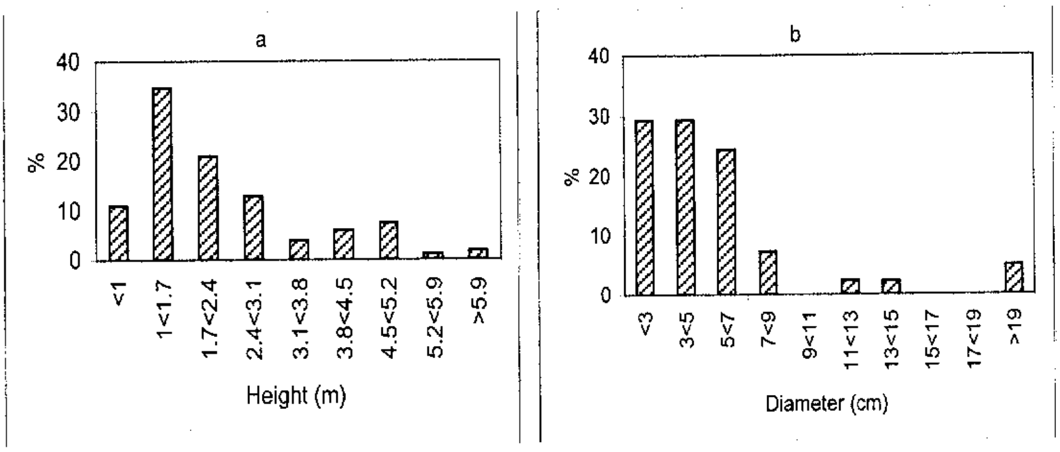

Figure 3. Percentage frequency distribution of: (a) Plant height; and, (b) Stem diameter of woody perennial species at the northeast corner site.

Tallest tree species in the northeast corner site were *E. capillosa* and *E. buracoppinensis*. Species of intermediate height include *A. campestris, A. huegeliana, A. stereophylla* and *A. neurophylla*, while abundant plants of the lower canopy are *G. paradoxa, B. elderiana, M. pauperiflora, E. tomentellus* and *M. acuminata.* Generally, the northeast corner area consists of open shrubland with only a few tall trees present. More than 80% of all plants recorded were less than 3 m tall (Figure 3a), and fall in the category of dwarf (< 1m), low (1<2 m) or medium (2<3 m) shrubs. Of all plants, 66% are multi-stemmed shrubs and 34% are of single stems. Generally, single stems occur in *A. huegeliana* and *E. capillosa.* More than 75% of the plants sampled have stem diameters less than 7 cm (Figure 3b). Only *Eucalyptus* species have substantially larger stems.

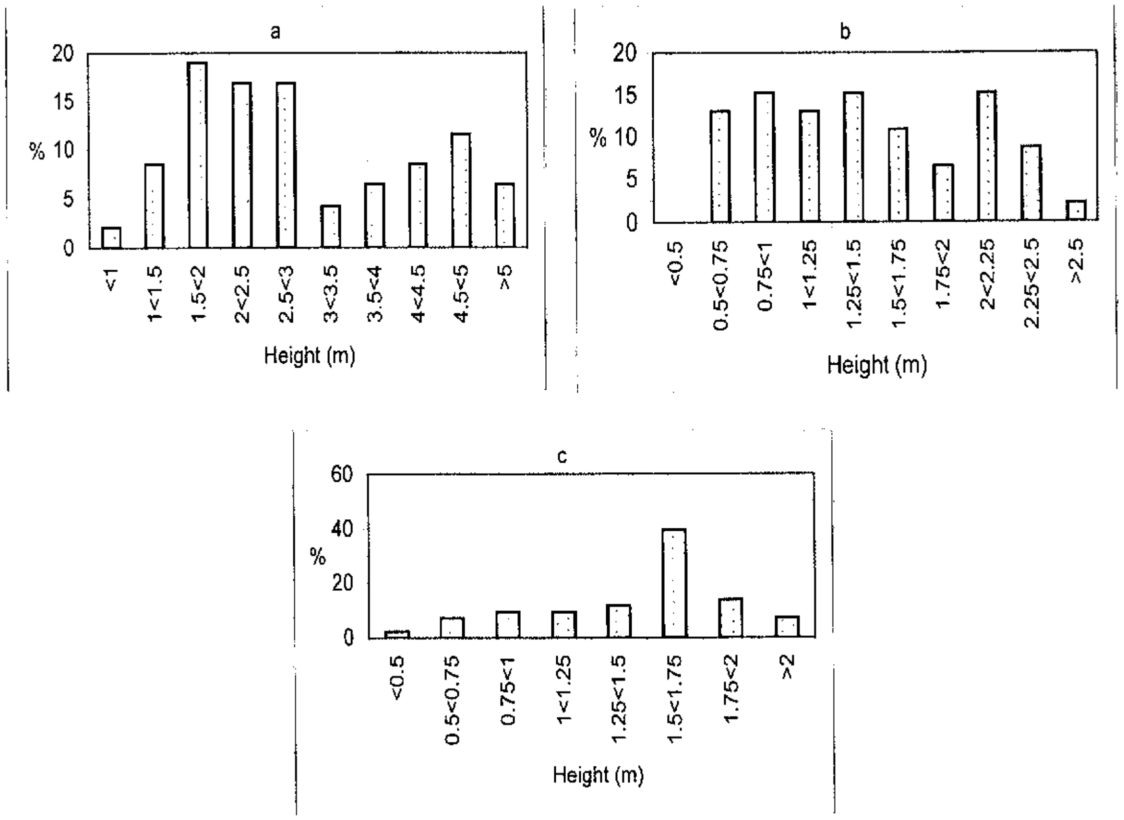

Figure 4. Frequency distribution of plant height (%): (a). *Allocasuarina huegeliana* (n = 67); (b). *Baeckea elderiana* (n = 84); and (c). *Grevillea paradoxa* (n = 32).

In the northeast corner data set, the three most abundant species are *A. huegeliana, B. elderiana* and *G. paradoxa.* They are relatively well distributed across the areas. In *A. huegeliana*, the frequency distribution of plant height suggests two sections of normal distribution (Figure 4a), implying that two cohorts are present. In *B. elderiana*, plant height is well distributed across height classes (Figure 4b), except for an absence of small plants (<0.5 m), suggesting that recruitment has not occurred recently. In *G. paradoxa*, distribution of plant heights is close to a normal distribution, with individuals present at small sizes indicating this species has good recruitment. More than 40% of plants are 1.5<1.75 m tall (Figure 4c), reflecting the small stature of *G.*

paradoxa. Distributions of plant height in *A. huegeliana* and *B. elderiana* appear to have some degree of similarity. In *A. huegeliana,* only a few plants were present in the 3<3.5 m height class and in *B. elderiana*, only a few plants were present in the 1.75<2 m class.

At the northeast corner site, soils are relatively shallow, with mean depth of 24.8 cm (± 6.3, n = 80). Most soils are yellow, lateritic sandy or rocky, which appear very dry in summer. However, in some places black or brown sandy soils occur, especially at sites where *Allocasuarina* woodland is present. Presumably, most species present at the northeast corner site have some degree of adaptation to relatively hard, shallow dry soil.

Table 3. Summary of main species in three vegetation types in the northeast corner area of SRNR.

(1). *Allocasuarina huegeliana* woodland

Species	Life form	Height (m)	Canopy % cover	Layer
Allocasuarina huegeliana	Low tree	1-6	>70	Upper
Allocasuarina campestris	Low tree	1-5.5	2-10	Co-dominant
Melaleuca pauperiflora	Shrub	1-3		Lower
Acacia nyssophylla	Shrub	1-3		Lower
Grevillea paradoxa	Shrub	0.5-2	2-10	Lower
Baeckea elderiana	Shrub	0.5-3		Lower
Astroloma serratifolium	Shrub	1-1.5		Lower

(2). *Grevillea paradoxa* low shrubland

Species	Life form	Height (m)	Canopy % cover	Layer
Grevillea paradoxa	Shrub	0.5-2.5	10-30	Lower
Allocasuarina huegeliana	Low tree	0.5-5.5	2-10	Upper
Acacia neurophylla	Shrub	1-3	2-10	Co-dominant
Eriostemon tomentellus	Shrub	1-2		Lower
Acacia stereophylla	Shrub	1-5		Co-dominant
Baeckea elderiana	Shrub	1-3		Co-dominant
Acacia nyssophylla	Shrub	1-3		Co-dominant
Melaleuca pauperiflora	Shrub	1-3		Co-dominant

(3). *Acacia neurophylla* medium shrubland

Species	Life form	Height (m)	Canopy % cover	Layer
Acacia neurophylla	Shrub	1-3	10-30	Dominant
Acacia stereophylla	Tall shrub	1-5	2-10	Co- dominant
Grevillea paradoxa	Shrub	0.5-2	2-10	Lower
Allocasuarina huegeliana	Low tree	1-5	2-10	Upper
Melaleuca pauperiflora	Shrub	1-2		Lower
Melaleuca acuminata	Shrub	1-3		Lower
Baeckea elderiana	Shrub	1-3		Lower
Eriostemon tomentellus	Shrub	1-2		Lower

Based upon the physiognomy (structure and life form) and cover of the ecologically dominant stratum, three vegetation types are recognized in the northeast corner areas (Table 3): 1) *Allocasuarina huegeliana* woodland. It commonly forms a more or less pure stand (clumping) in relation to woody species, especially on black or brown dry sandy soil. Common associates are species of *Melaleuca, Acacia* and *Grevillea.* 2) *Grevillea paradoxa* low shrubland. This occurs on dry, rocky soil with reddish-yellow, shallow soil. Soil texture is mainly fine sandy loam. 3) *Acacia neurophylla* medium shrubland, on reddish-yellow soil, fine sandy loam, moderate to well-drained, lateritic shallow soil. This also appears very dry in summer.

2.3.2. Structure and composition of vegetation at the entrance area

Much of the entrance area consists of seasonally moist habitats. Some of the species present are presumed to some extent to be relatively well adapted to only periodically moist habitats. Soil is relatively deep with a mean of 44.1 cm (± 8.7, n = 80), textures include clay loams and sandy clay loams. Of the 800 m sampled, a total of 320 woody plants were collated. These comprise 24 species from 10 families (Table 4). The most species-rich families are Myrtaceae (6 species), Mimosaceae (6 species) and Proteaceae (4 species). Mean density is 1700 plants/ha. The entrance area is locally dominated by *Acacia jennerae, Hakea invaginata* and *Alyxia buxifolia.* Those 3 species comprise some 50% of plant density.

Table 4. Mean height, density, dominance and importance values (IV) of woody perennial species at the entrance (From 8 x 100 m transects with a sum of 80 sampling points, Σn = 320 plants).

No.	Species	Family	Mean height (m)	No. plants	Density (%)	Dominance (%)	IV
1	*Eucalyptus capillosa*	Myrtaceae	17.11	5	1.52	52.57	54.09
2	*Acacia jennerae*	Mimosaceae	1.3	109	34.12	0.34	34.46
3	*Hakea invaginata*	Proteaceae	0.4	37	11.58	0.12	11.7
4	*Alyxia buxifolia*	Apocynaceae	1.57	34	10.66	0.28	10.94
5	*Acacia prainii*	Mimosaceae	2.12	27	8.53	1.05	9.58
6	*Grevillea paniculata*	Proteaceae	1.31	29	9.14	1.47	10.61
7	*Allocasuarina huegeliana*	Casuarinaceae	4.72	2	0.61	14.75	15.36
8	*Eucalyptus sheathiana*	Myrtaceae	2.15	19	5.79	0.46	6.25
9	*Acacia saligna*	Mimosaceae	2.96	8	2.44	3.93	6.37
10	*Eucalyptus subangusta*	Myrtaceae	11.9	1	0.31	7.75	8.06
11	*Hakea recurva*	Proteaceae	1	10	3.35	0.52	3.87
12	*Acacia acuminata*	Mimosaceae	2.7	2	0.61	4.14	4.75
13	*Cassia nemophila*	Caesalpiniaceae	0.98	4	1.14	2.99	4.13
14	*Acacia colletioides*	Mimosaceae	2.1	7	2.29	1.67	3.96
15	*Exocarpos aphyllus*	Santalaceae	0.7	5	1.52	0.06	1.58
16	*Hakea coriaceae*	Proteaceae	2.25	2	0.61	2.32	2.93
17	*Dodonaea viscosa*	Sapindaceae	2.28	2	0.61	2.16	2.77
18	*Acacia hemiteles*	Mimosaceae	1.54	3	0.94	1.75	2.69
19	*Keraudrenia integrifolia*	Sterculiaceae	0.64	8	2.44	0.06	2.5
20	*Melaleuca macronychia*	Myrtaceae	0.99	2	0.61	0.79	1.4
21	*Melaleuca acuminata*	Myrtaceae	1.08	1	0.31	0.38	0.69
22	*Olearia revoluta*	Asteraceae	1.55	1	0.31	0.34	0.65
23	*Dodonaea stenozyga*	Sapindaceae	1.1	1	0.31	0.02	0.33
24	*Eucalyptus myriadena*	Myrtaceae	1.2	1	0.31	0.08	0.39
	SUM			320	100	100	200.

Frequency distribution of plant height in *A. jennerae* presents a normal distribution (Figure 5a). Recruitment appears to occur regularly. However, this species regenerates well from root suckers and it is believed that many plants are members of clones (Orchard & Wilson 2001a). In *A. buxifolia,* the frequency distribution of plant height reflects two cohorts. These may represent one period of poor recruitment or separated populations in different areas (Figure 5b). As for *A. huegeliana* and *B. elderiana* (2.3.1), the pattern may be partially influenced by the severe drought of 1994. The *H. invaginata* height class frequency distribution confirms continuous recruitment, with more than 45% plants less than 0.2 m tall (Figure 5c). This species can be observed producing new recruitment in the seasonally flooded areas of low open grassland. It is an "increaser" species here (Mitchell & Wilcox 1994).

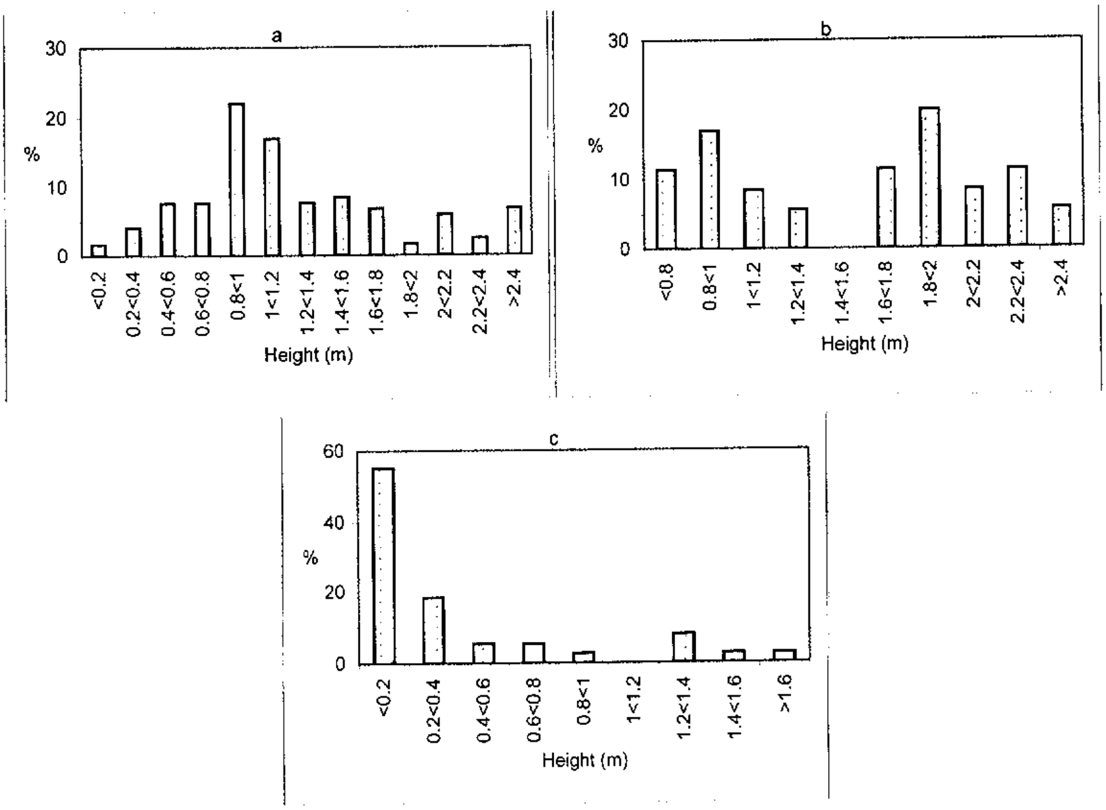

Figure 5. Frequency distribution of plant height (%): (a). *Acacia jennerae* (n = 109); (b). *Alyxia buxifolia* (n = 34); and (c). *Hakea invaginata* (n = 37).

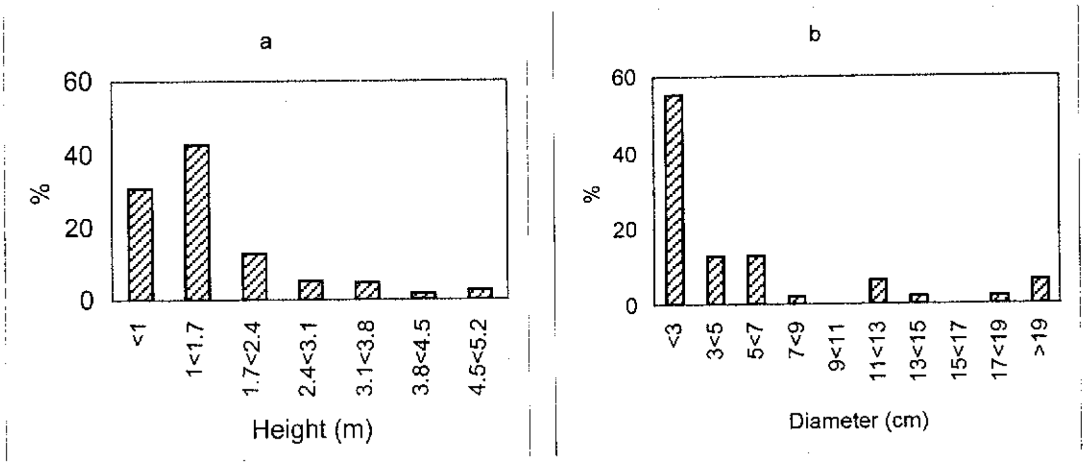

Figure 6. Percentage frequency distributions: (a). Plant height (m); and, (b). Stem diameter (cm) of woody perennial species at the entrance.

Taller trees at the entrance are *E. subangusta* and *E. capillosa.* Species of intermediate height are mainly of *A. saligna, E. sheathiana* and *A. prainii,* while the shorter plants are mainly of *A. jennerae, G. paniculata* and *A. buxifolia.* About 90% of plants recorded were less than 3 m tall (Figure 6a). Of all plants, 39% are single stemmed and 61% are multi-stemmed. More than 50% of plants had stem diameters of less than 3 cm (Figure 6b). In this area, only eucalypts had larger stems.

Table 5. Summary of main species in four vegetation types in the entrance area of SRNR.

(1). *Acacia jennerae* low open shrubland

Species	Life form	Height (m)	Canopy % cover	Layer
Acacia jennerae	Shrub	0.5-3.5	>70	Lower
Hakea recurva	Shrub	1-4	2-10	Lower
Grevillea paniculata	Shrub	0.5-2	2-10	Lower
Amphipogon strictus	Annual grass			Ground
Borya costricta	Perennial herbaceous			Ground

(2). Low open grassland

Species	Life form	Height (m)	Canopy % cover	Layer
Hakea invaginata	Shrub	0.5-1.5	2-10	Ground
Neurachne alopecuroidea	Annual grass			Ground
Eriachne ovata	Annual grass			Ground
Aristida contorta	Annual grass			Ground

(3). Wandoo woodland

Species	Life form	Height (m)	Canopy % cover	Layer
Eucalyptus capillosa	Tree	1-20	30-70	Upper
Dodonaea viscosa	Shrub	2-3		Lower
Alyxia buxifolia	Shrub	0.5-3		Lower
Acacia prainii	Shrub	0.5-1		Lower
Grevillea paniculata	Shrub	1-2		Lower
Neurachne alopecuroidea	Annual grass			Ground

(4). *Acacia saligna* thicket

Species	Life form	Height (m)	Canopy % cover	Layer
Acacia saligna	Shrub	0.5-4.5	10-30	Lower
Acacia prainii	Shrub	0.5-1.5	2-10	Lower
Hakea invaginata	Shrub	0.5-1.5		Lower
Grevillea paniculata	Shrub	0.5-2		Lower
Eriachne ovata	Perennial grass			Ground

Four vegetation types can be distinguished in this area, based on physiognomy and cover of the ecologically dominant stratum (Table 5): 1) *Acacia jennerae* low open shrubland. In this vegetation type, few other woody species are present, except for some *Hakea* and *Grevillea*. The *Acacia* forms almost pure stands in relation to the perennial woody species. Understorey species are mainly the perennial, small ring-tussock grass *Amphipogon strictus* and the perennial pin-cushion *Borya constricta*. The soil is a brown, fine sandy loam and sandy clay loam from 40-80 cm in depth; 2) Low open grassland where vegetation mainly comprises varied amount of several grass species (*Neurachne alopecuroidea*, *Eriachne ovata* and *Aristida contorta*), with some seedlings of *Hakea invaginata*. A relatively deep soil with a high soil moisture content results in good recruitment of *H. invaginata*. The soil is a brown, sandy, clay loam of between 60-90 cm in depth; 3) Wandoo woodland consists of tall trees of *E. capillosa*, over the shrubs *D. viscosa*, *A. buxifolia* and some *A. prainii*. The understorey species is mainly the grass *N. alopecuroidea*. The wandoo woodland is seasonally flooded, and has a dark, finely textured loamy soil; 4) *Acacia saligna* thicket. The understorey species in *A. saligna* thickets mainly comprise the grass *E. ovata* and seedlings of *H. invaginata*. These thickets are found in seasonally flooded areas, where the soil is a dark, finely textured, well-drained sandy clay loam or sandy loam of 40-90 cm in depth.

2.3.3. Structure and composition of vegetation at the west corner area

The west corner area is characterised by relatively deep sandy soil that becomes very dry in summer; the mean soil depth was 60.3 cm (± 11.4, n = 80). A total of 320 plants was recorded from eight transects, comprising 39 species from 7 families (Table 6). The most species-rich families were the Myrtaceae (22 species) and Mimosaceae (8 species). These families comprised some 80% of the component species at this area. Thus, myrtaceous thickets may be said to dominate the vegetation. The vegetation is relatively dense (2400 plants/ha) compared to the other areas. The western area also appears to have higher species richness among the woody perennials. In the density criterion, dominant species are *P. tuberculosum*, *A. coolgardiensis*, *B. crispiflora*, *A.*

colletioides and *A. acuminata.* These species appear adapted to growing in deep, sandy soil.

Distribution of plant heights of *P. tuberculosum* is approximately normal, reflecting a singe cohort. More than 60% of the plants are in the 1-1.5 m height classes, representing the mean and median (Figure 7a). Continuing recruitment is suggested as having occurred in *A. acuminata*, however slightly poorer recruitment in recent years may explain only few plants being present in the lower height classes (Figure 7b). The distribution of plant height for *A. coolgardiensis* is also roughly normal (Figure 7c), suggesting a single cohort for this population.

The tallest trees in the west corner site are *E. loxophleba*, *E. yilgarnensis* and *E. capillosa*. Trees of intermediate height include *A. acuminata*, *A. coolgardiensis*, *E. celastroides* and *A. colletioides*, while the lower plants are mainly *P. tuberculosum, B. behrii, B. crispiflora* and *A. hemiteles*. More than 50% of the plants are less than 1.7 m tall (Figure 8a), with only a few more than 6 m tall, thus this site is dominated by low (1<2 m) to medium (2<3 m) shrubs. Of the plants, 37.4% are single-stemmed and 62.5% multi-stemmed. Most species at this site have stems less than 9 cm in diameter (Figure 8b) and only *Eucalyptus* species have reasonably large stems.

Table 6. Mean height, density, dominance and importance value (IV) of woody perennial species at the west corner (Recorded from 8 x 100 m transects with a sum of 80 sampling points, $\Sigma n = 320$ plants).

No.	Species	Family	Mean height (m)	No. plants	Density (%)	Dominance (%)	IV
1	*Phebalium tuberculosum*	Rutaceae	1.26	96	30.08	49.34	79.42
2	*Acacia acuminata*	Mimosaceae	3.22	22	6.87	8.21	15.08
3	*Acacia coolgardiensis*	Mimosaceae	3.32	26	8.19	5.73	13.92
4	*Acacia colletioides*	Mimosaceae	3.52	20	6.21	8.38	14.59
5	*Eucalyptus celastroides*	Myrtaceae	3.72	10	3.2	3.85	7.05
6	*Baeckea crispiflora*	Myrtaceae	1.51	23	7.34	1.19	8.53
7	*Allocasuarina huegeliana*	Casuarinaceae	2.48	14	4.52	3.28	7.8
8	*Acacia hemiteles*	Mimosaceae	1.52	11	3.74	1.73	5.47
9	*Baeckea behrii*	Myrtaceae	1.47	10	3.11	1.12	4.23
10	*Acacia stereophylla*	Mimosaceae	3.04	7	2.27	2.02	4.29
11	*Malleostemon roseus*	Myrtaceae	0.83	7	2.14	0.51	2.65
12	*Hakea coriaceae*	Proteaceae	2.82	6	1.77	1.29	3.06
13	*Eucalyptus capillosa*	Myrtaceae	4.94	7	2.26	1.51	3.77
14	*Melaleuca acuminata*	Myrtaceae	3.32	4	1.25	2.69	3.94
15	*Melaleuca laxiflora*	Myrtaceae	1.21	5	1.66	0.29	1.95
16	*Allocasuarina acutivalvis*	Casuarinaceae	2.17	3	0.83	0.63	1.46
17	*Santalum acuminatum*	Santalaceae	3.29	5	1.28	1.12	2.4
18	*Verticordia chrysantha*	Myrtaceae	0.83	3	1	0.12	1.12
19	*Eucalyptus myriadena*	Myrtaceae	4.34	4	1.13	1.42	2.55
20	*Acacia erinaceae*	Mimosaceae	0.97	3	0.81	0.06	0.87
21	*Melaleuca macronychia*	Myrtaceae	1.47	4	1.14	0.21	1.35
22	*Eriostemon tomentellus*	Rutaceae	1.07	4	1.15	0.16	1.31
23	*Melaleuca uncinata*	Myrtaceae	1.67	3	0.96	0.24	1.2
24	*Acacia eremophila*	Mimosaceae	1.29	2	0.73	0.25	0.98
25	*Eucalyptus yilgarnensis*	Myrtaceae	5.3	1	0.22	1.16	1.38
26	*Melaleuca pauperiflora*	Myrtaceae	4.51	1	0.22	1.13	1.35
27	*Hakea invaginata*	Proteaceae	2.55	2	0.42	0.4	0.82
28	*Micromyrtus racemosa*	Myrtaceae	1.73	1	0.31	0.18	0.49
29	*Eucalyptus loxophleba*	Myrtaceae	7.1	1	0.32	0.49	0.81
30	*Melaleuca lateriflora*	Myrtaceae	2	2	0.57	0.17	0.74
31	*Hakea falcata*	Proteaceae	0.94	3	1.13	0.11	1.24
32	*Calothamnus gilesii*	Myrtaceae	2.7	2	0.57	0.13	0.7
33	*Baeckea maidenii*	Myrtaceae	0.92	2	0.42	0.17	0.59
34	*Melaleuca eleuterostachya*	Myrtaceae	2.38	1	0.42	0.13	0.55
35	*Olearia muelleri*	Asteraceae	0.82	1	0.42	0.12	0.54
36	*Eucalyptus leptopoda*	Myrtaceae	4.18	1	0.32	0.16	0.48
37	*Acacia jibberdingensis*	Mimosaceae	1.84	1	0.42	0.04	0.46
38	*Melaleuca hamulosa*	Myrtaceae	3.75	1	0.32	0.13	0.45
39	*Eucalyptus sheathiana*	Myrtaceae	3.26	1	0.32	0.12	0.44
	SUM			320	100	100	200

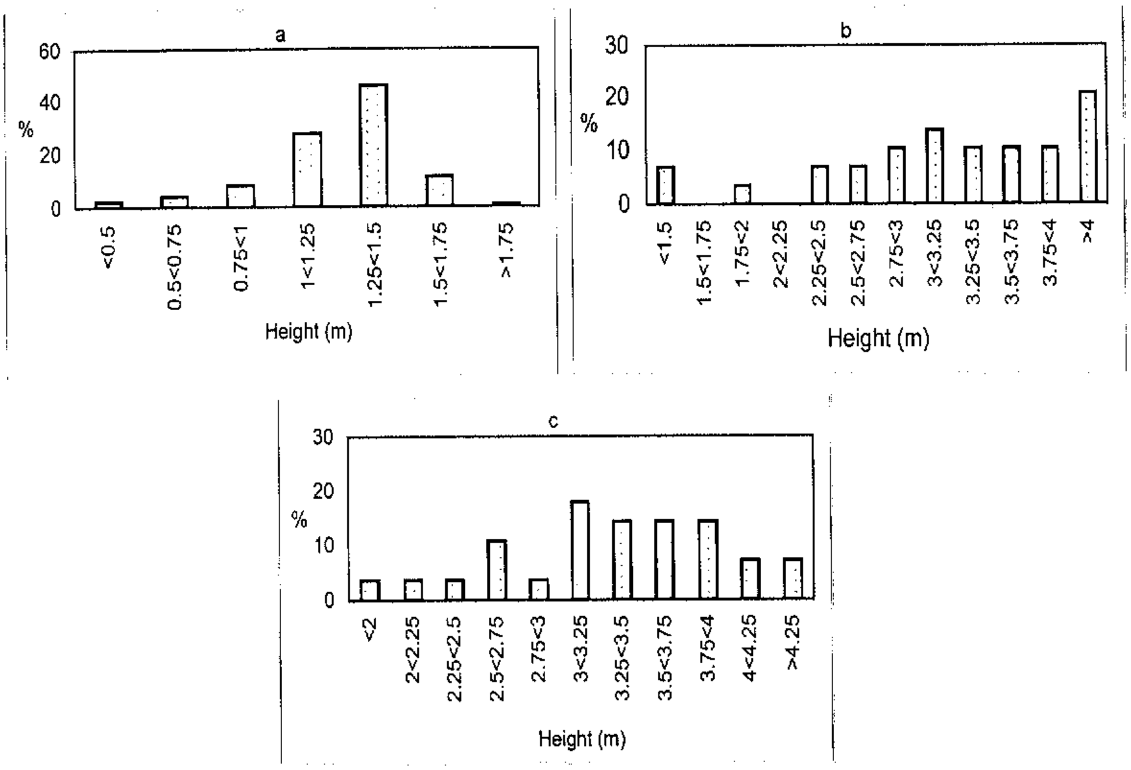

Figure 7. Frequency distribution of plant height (%): (a). *Phebalium tuberculosum* (n = 96); (b). *Acacia acuminata* (n = 22); and (c). *Acacia coolgardiensis* (n = 26).

Generally, the west corner site comprises Myrtaceous thickets with only a few tall trees (*Eucalyptus* species) present. Three vegetation types are recognised at the area (Table 7): 1) Low *Phebalium tuberculosum* shrubland, where the main association is with *Acacia* species. The soil tends to be a pinkish grey or brown sandy loam and it is poorly drained; 2) *Acacia acuminata* (jam) thicket where the common associate of jam is *A. coolgardiensis*. This thicket has a broom-bush habit. The soil is a deep, brown sandy loam and is moderately well drained; 3) *Acacia coolgardiensis* thicket, where the common associates are another *Acacia*, a *Melaleuca* and *Allocasuarina*. This also has a broom-bush habit. The soil is a brown, pinkish grey, deep sandy loam, which is moderately or poorly drained and appears to be very dry in summer.

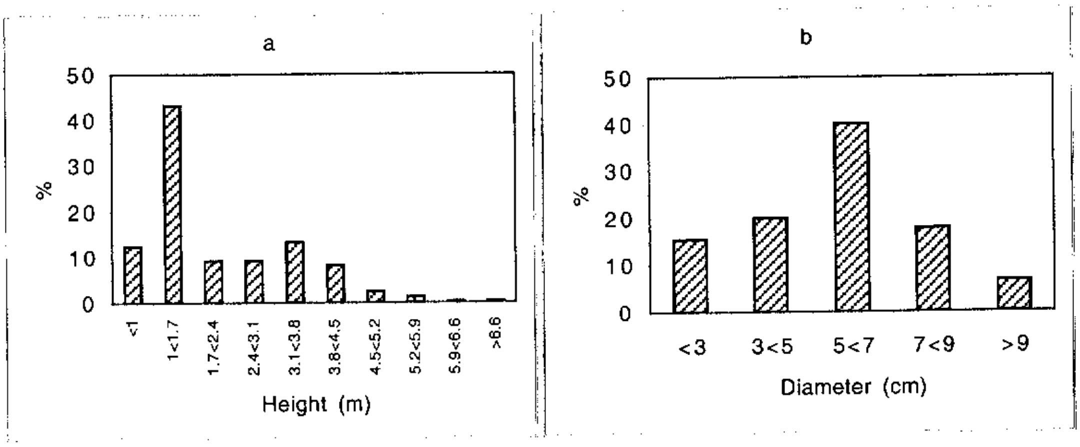

Figure 8. Percentage frequency distribution of: (a). Plant height, and (b). Stem diameter of woody perennial species at the west corner

Table 7. Summary of main species in three vegetation types in the west corner area of SRNR.

(1). *Phebalium tuberculosum* low shrubland

Species	Life form	Height (m)	Canopy % cover	Layer
Phebalium tuberculosum	Low shrub	0.5-3	10-30	Dominant
Acacia coolgardiensis	Medium shrub	2-5	2-10	Co-dominant
Acacia acuminata	Medium shrub	1-4.5	2-10	Co-dominant
Eriostemon tomentellus	Low shrub	0.5-1		Co-dominant
Acacia jibberdingensis	Low shrub	2-5		Co-dominant

(2). *Acacia acuminata* thicket

Species	Life form	Height (m)	Canopy % cover	Layer
Acacia acuminata	Medium shrub	1-4.5	10-30	Dominant
Acacia coolgardiensis	Medium shrub	2-4	2-10	Co-dominant
Phebalium tuberculosum	Low shrub	1-1.5	2-10	Co-dominant
Baeckea behrii	Low shrub	1-3.5		Co-dominant
Allocasuarina acutivalvis	Medium shrub/tree	1-3		Co-dominant
Hakea invaginata	Low shrub	1-4		Co-dominant

(3). *Acacia coolgardiensis* thicket

Species	Life form	Height (m)	Canopy % cover	Layer
Acacia coolgardiensis	Shrub	2-4.5	10-30	Dominant
Melaleuca eleuterostachya	Shrub	1-2	2-10	Lower
Acacia hemiteles	Shrub	1-3.5		Lower
Eriostemon tomentellus	Shrub	0.5-1		Lower
Baeckea behrii	Shrub	1-3.5		Lower
Allocasuarina acutivalvis	Shrub	1-3		Lower
Micromyrtus racemosa	Shrub	1.5-2		Lower

2.3.4. Structure and composition of vegetation at CK-3 area

Table 8. Mean height, density, dominance and importance value (IV) of woody perennial species at the CK-3 (From 6 x 100 m transects with a sum of 60 sampling points, $\Sigma n = 240$ plants).

No.	Species	Family	Mean height (m)	No. plants	Density (%)	Dominance (%)	IV
1	*Acacia acuminata*	Mimosaceae	4.56	49	20.49	69	89.49
2	*Eucalyptus salmonophloia*	Myrtaceae	10.7	61	25.67	11.68	37.35
3	*Allocasuarina huegeliana*	Casuarinaceae	4.13	18	7.45	1.57	9.02
4	*Eucalyptus loxophleba*	Myrtaceae	18	20	8.19	6.38	14.57
5	*Melaleuca pauperiflora*	Myrtaceae	3.12	20	8.19	2.87	11.06
6	*Dodonaea inaequifolia*	Sapindaceae	3.05	16	6.53	0.96	7.49
7	*Kunzea pulchella*	Myrtaceae	5.56	20	8.28	0.27	8.55
8	*Eucalyptus capillosa*	Myrtaceae	27.6	5	2.34	2.82	5.16
9	*Eucalyptus subangusta*	Myrtaceae	28	2	0.96	2.2	3.16
10	*Acacia hemiteles*	Mimosaceae	1.49	3	1.32	0.21	1.53
11	*Leptospermum erubescens*	Myrtaceae	1.77	4	1.65	0.24	1.89
12	*Santalum spicatum*	Santalaceae	2.49	4	1.91	0.79	2.7
13	*Grevillea yorkrakinensis*	Proteaceae	1.43	4	1.51	0.16	1.67
14	*Hakea invaginata*	Proteaceae	2.12	1	0.66	0.04	0.7
15	*Prostanthera baxteri*	Lamiaceae	1.5	1	0.6	<0.01	0.6
16	*Calothamnus asper*	Myrtaceae	2.9	1	0.6	<0.01	0.6
17	*Dodonaea caespitosa*	Sapindaceae	2.9	1	0.44	0.09	0.53
18	*Eucalyptus salubris*	Myrtaceae	16.4	1	0.22	0.6	0.82
19	*Acacia erinaceae*	Mimosaceae	1.55	2	0.66	0.07	0.73
20	*Acacia sessilispica*	Mimosaceae	1.9	1	0.5	<0.01	0.5
21	*Melaleuca uncinata*	Myrtaceae	2.22	1	0.44	0.01	0.45
22	*Grevillea paniculata*	Proteaceae	1.33	1	0.3	<0.01	0.3
23	*Alyxia buxifolia*	Apocynaceae	1.2	1	0.3	<0.01	0.3
24	*Micromyrtus racemosa*	Myrtaceae	3.1	1	0.3	<0.01	0.3
25	*Diplolaena* sp	Rutaceae	1.7	1	0.3	<0.01	0.3
26	*Eremophila scoparia*	Myoporaceae	1.73	1	0.22	0.05	0.27
	SUM			240	100	100	200.

At the area designated as CK-3, a 600 m sample was taken from 6 transects and a total of 240 woody plants were measured in the sample (Table 8). The vegetation consists of tall, open woodland of salmon gum (*E. salmonophloia*), wandoo (*E. capillosa*), York gum (*E. loxophleba*) and myrtaceous thickets. Some 40% of the component plants are of *Eucalyptus* species. Of the 10 families encountered, the most species-rich families are the Myrtaceae (11 species), Mimosaceae (4 species) and Proteaceae (3 species) and the mean density is 710 plants/ha. Taller trees at the CK-3 area are all *Eucalyptus* species; intermediate level species include *A. acuminata, A.*

huegeliana, K. pulchella, M. pauperiflora and *D. inaequifolia*, while the lower canopies are mostly of *S. spicatum, G. paniculata, A. hemiteles, L. erubescens, H. invaginata* and *A. erinaceae*, with very few dwarf shrubs (< 1 m).

The CK-3 site is located between two large outcrops (Chapter 1, Figure 1). Soil depth is presumably adequate to enable large trees to dominate at the site. The mean soil depth measured was 60.5 cm (± 4.6, n = 60), and the soil here is sandy clay loam. Much of this area is described as open salmon gum woodland. It is characterised by 25% of all measured plants, with height of more than 8 m and only 1.2% of measured plants (woody perennials) being less than 1 m tall (Figure 9a). Thus, this set includes a number of tall trees and relatively few understorey plants. Single-stemmed plants (tree forms) comprised 66.7% of the plants and 33.3% were multi-stemmed shrubs or mallees. Most plants have large stem diameters, with only a few having stems less than 3 cm (Figure 9b): *E. capillosa* and *E. subangusta* have the largest stems at this site.

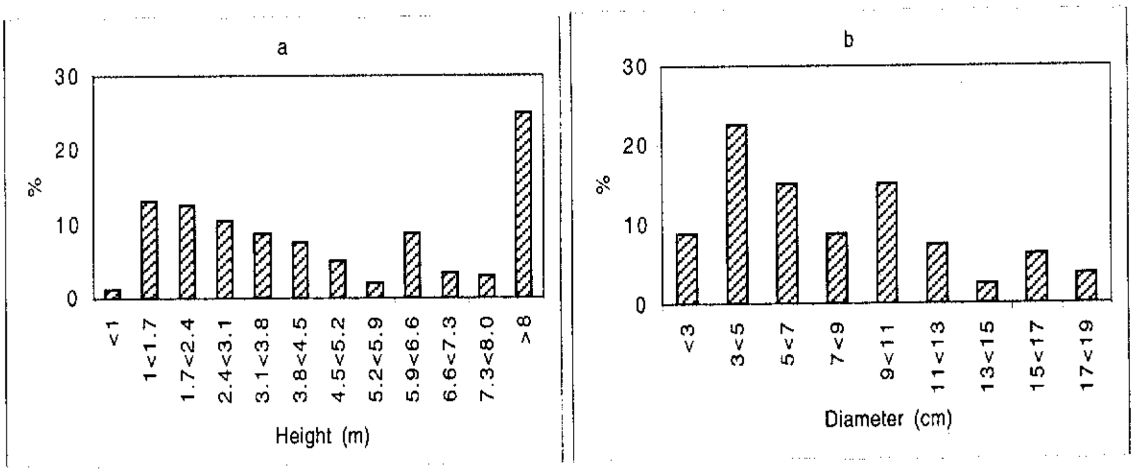

Figure 9. Percentage frequency distribution of: (a) Plant height; and, (b) Stem diameter of woody perennial species at CK-3.

Plant height distribution of *A. acuminata* is relatively equal between the height classes (Figure 10a); it is probable that this species has had a relatively continuous recruitment. However, there may have been a period of relatively poor recruitment in the recent past, as few plants were encountered in the 1.75<2.25 m and 4.75<5.25 m height classes. A comparison of these heights with *A. acuminata* growing in the west corner area (Figure 7b, section 2.3.3) suggests that the plants at this area are generally taller. More than 60% of the plants are taller than 4 m compared to more than 80% of the plants at the west corner being less than 4 m tall. Presumably, as *A. acuminata* in the CK-3 area is an understorey species in *Eucalyptus* woodland, it tends to have a taller stature that may be a response to more light.

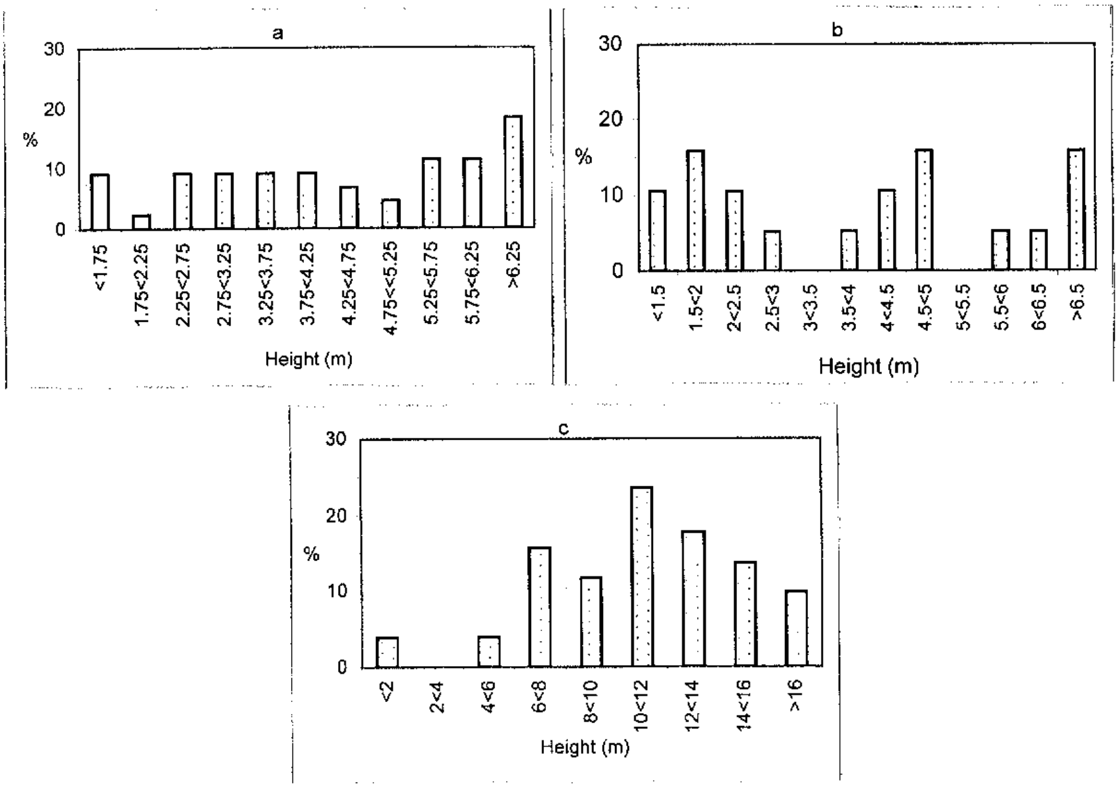

Figure 10. Frequency distribution of plant height (%): (a). *Acacia acuminata* (n = 49); (b). *Allocasuarina huegeliana* (n = 18); and (c). *Eucalyptus salmonophloia* (n = 61).

Distribution of plant height in *A. huegeliana* reveals 3 quite distinctive cohorts (Figure 10b). It is possible that two periods in the past may have had poor recruitment, reflected in no plants present in the 3<3.5 m and 5<5.5 m height classes. Comparing these to the plants of *A. huegeliana* growing in the northeast corner site (Figure 4a, section 2.3.1), those *A. huegeliana* at the CK-3 area are taller with more than 25% of the plants > 5 m, compared to less than 10% > 5 m tall in the northeast corner. Distribution of plant height of *A. huegeliana* in both sites has some similarity, with more than one cohort occurring at both sites. They may be confined to similar periods of poor recruitment in the past. In *E. salmonophloia*, plant height distribution is normal (Figure 10c). This suggests that regular recruitment has occurred for this species. More than 60% of the plants are taller than 10 m.

Table 9. Summary of main species in two vegetation types in the CK-3 area of SRNR.

(1). *Eucalyptus salmonophloia* woodland

Species	Life form	Height (m)	Canopy % cover	Layer
Eucalyptus salmonophloia	Tree	1-17	>70	Upper
Eucalyptus loxophleba	Tree	4-12	30-70	Upper
Eucalyptus capillosa	Tree	2.5-20.5	30-70	Upper
Acacia acuminata	Shrub/low tree	1-9	2-10	Co-dominant
Dodonaea inaequifolia	Shrub	1-6		Lower
Allocasuarina huegeliana	Shrub/low tree	1-8	2-10	Co-dominant
Santalum spicatum	Shrub	1-4		Lower
Melaleuca pauperiflora	Shrub	1.5-5	2-10	Lower

(2). *Kunzea pulchella* shrubland

Species	Life form	Height (m)	Canopy % cover	Layer
Kunzea pulchella	Shrub	2-4	30-70	Lower
Acacia acuminata	Shrub	1-5	2-10	Upper
Allocasuarina huegeliana	Shrub/tree	1-8	2-10	Upper
Eucalyptus subangusta	Tree	16	2-10	Upper
Leptospermum erubescens	Shrub	1-2		Lower
Santalum spicatum	Shrub	1-4		Lower
Annual grass	grass			Ground

Based upon the structure, life-form, and cover of the ecologically dominant stratum, two vegetation forms are recognized in this site (Table 9): medium trees (10-30 m) of the *Eucalyptus salmonophloia* woodland, in the middle of the CK-3 area; and *Kunzea pulchella* shrubland on the periphery of the *Eucalyptus* woodland and relatively close to the rock. In the *Eucalyptus salmonophloia* woodland, the species are mainly comprised of *Eucalyptus* species (*E. salmonophloia*, *E. loxophleba* and *E. capillosa*) as the upper canopy and *A. acuminata*, *D. inaequifolia* and *A. huegeliana* as the intermediate canopy, with very few understorey species and grass species sparse. The site is characterised by black, sandy clay loam soil with a depth of between 30-40 cm.

Relatively close to the rock, the distinct plant form of dense medium shrubs can be seen with *K. pulchella,* which has the highest density in this association, forming *Kunzea pulchella* shrubland. In this type of vegetation, some *A. acuminata* and *A. huegeliana* are present as co-dominants with a few *Eucalyptus* species present. Some annual grasses are present. The soil is a sandy loam to clay loam, containing rich humus and it is relatively deep at between 50-70 cm.

2.3.5. Structure and composition of vegetation at the rocks area

From 79 sampling points, a total of 316 woody perennials was measured, comprising 28 species from 12 families (Table 10). The most species-rich families are the Myrtaceae (8 species) and Mimosaceae (6 species) and the mean density is 1157 plants/ha. The rocks sites comprise open, low to medium shrubs mainly of *D. viscosa, A. prainii* and *L. erubescens*. These three species contribute more than 50% of the component plants; they benefit from locally high soil moisture or seasonally wet areas near the rocks, where rainfall is concentrated by run-off. Different species found to be associated with selected *Acacia* at the rocks area will be presented in Chapter 3.

The three species that are most commonly present (highest density) at the rocks area generally have good recruitment. More than 10% of *A. prainii* plants were less than 0.5 m tall, in the seedling or sapling stage. A detailed description of the population characteristics of *A. prainii* and its associated species is presented in Chapter 3 (Section 3.3.2). Distribution of plant height in *L. erubescens* reflected the occurrence of 2 cohorts or one period of poor recruitment, as shown by absence of plants in the 2.9-3.2 m tall classes (Figure 11a). Distribution of plant height for *D. viscosa* reflected good recruitment, with a tendency to large numbers of small plants (Figure 11b).

The rocks area contains sites with a high soil moisture habitat that are related to the granite rocks. The soils are relatively shallow, with mean depth of 24.2 cm (±7.2, n=47) and they are sandy loam, clay loam or fine sandy loams. The soil is relatively shallow due to the presence of rocks in the area. Various microhabitats are present, e.g. tumbled boulders, pockets of relatively shallow soil, deep soil, run-off areas, and marginally flat areas at the base of the granite rocks. Generally, the habitat is relatively rich in humus, which promotes the formation of healthy, open low to medium high shrubland. Muir (1979) designated the rock site vegetation types of SRNR as comprising a "lithic complex".

Table 10. Mean height, density, dominance and importance value (IV) of woody perennial species at the rocks area (From a point quarter survey of 79 sampling points, $\Sigma n = 316$ plants).

No.	Species	Family	Mean height (m)	No. plants	Density (%)	Dominance (%)	IV
1	*Acacia lasiocalyx*	Mimosaceae	3.66	12	3.9	3.85	7.75
2	*Acacia prainii*	Mimosaceae	1.57	50	15.91	15.73	31.64
3	*Acacia fauntleroyi*	Mimosaceae	2.29	9	2.92	2.89	5.81
4	*Alyxia buxifolia*	Apocynaceae	1.42	5	1.29	1.28	2.58
5	*Dodonaea inaequifolia*	Sapindaceae	1.45	14	4.55	4.49	9.04
6	*Leptospermum erubescens*	Myrtaceae	2.21	48	15.26	15.09	30.35
7	*Santalum spicatum*	Santalaceae	1.59	6	1.95	1.93	3.87
8	*Melaleuca macronychia*	Myrtaceae	1.71	19	6.17	6.1	12.27
9	*Hibbertia glomerosa*	Dilleniaceae	0.53	11	3.57	3.53	7.1
10	*Dodonaea viscosa*	Sapindaceae	1.18	70	22.4	22.15	44.55
11	*Allocasuarina huegeliana*	Casuarinaceae	3.07	10	3.25	3.21	6.46
12	*Calothamnus asper*	Myrtaceae	1.84	7	2.27	2.25	4.52
13	*Grevillea paniculata*	Proteaceae	1.02	6	1.95	1.93	3.87
14	*Kunzea pulchella*	Myrtaceae	2.53	3	0.65	0.64	1.29
15	*Persoonia striata*	Proteaceae	0.9	3	0.65	0.64	1.29
16	*Melaleuca eleutherostachya*	Myrtaceae	3.05	3	0.65	0.64	1.29
17	*Atriplex nummularia*	Chenopodiaceae	0.66	2	0.65	0.64	1.29
18	*Acacia sessilispica*	Mimosaceae	2.43	1	0.32	0.32	0.65
19	*Eucalyptus loxophleba*	Myrtaceae	1.15	1	0.32	0.32	0.65
20	*Melaleuca hamulosa*	Myrtaceae	1.59	7	1.95	1.93	3.87
21	*Hibbertia verrucosa*	Dilleniaceae	0.58	11	3.57	3.53	7.1
22	*Baeckea elderana*	Myrtaceae	0.82	10	3.25	3.21	6.46
23	*Halgania viscosa*	Boraginaceae	0.68	1	0.32	0.32	0.65
24	*Boronia ternata*	Rutaceae	1.5	1	0.32	0.32	0.65
25	*Acacia hemiteles*	Mimosaceae	1.15	1	0.32	0.32	0.65
26	*Allocasuarina acutivalvis*	Casuarinaceae	4.07	2	0.65	0.64	1.29
27	*Acacia acuminata*	Mimosaceae	2.2	1	0.32	0.32	0.65
28	*Astroloma serratifolium*	Epacridaceae	0.94	2	0.65	0.64	1.29
	SUM			316	100	100	200

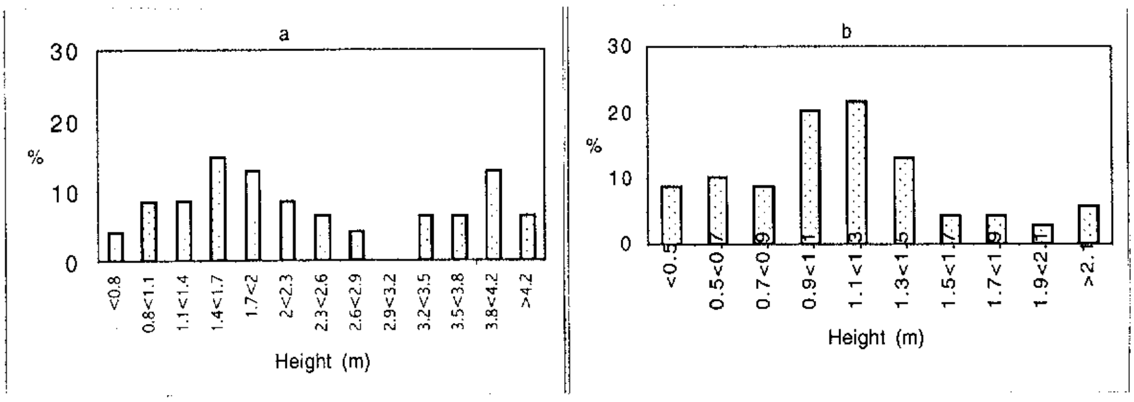

Figure 11. Distribution of plant height (%) in different classes: (a). *Leptospermum erubescens* (n = 48); (b). *Dodonaea viscosa* (n = 70).

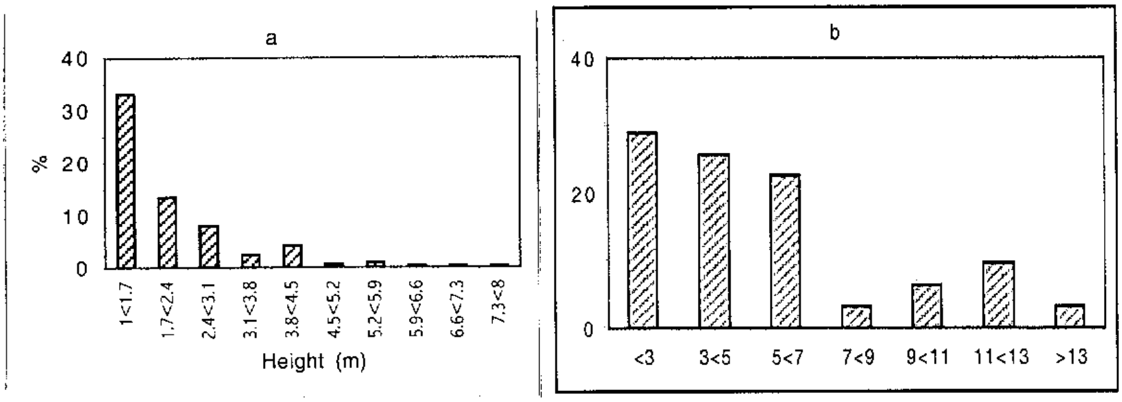

Figure 12. Percentage frequency distribution of: (a) Plant height; and (b) Stem diameter of woody perennial species at the rocks area

The taller trees in the rocks site are *A. lasiocalyx, Allocasuarina* spp. and *L. erubescens*. Those of intermediate height are mainly *D. viscosa*, *A. prainii, A. fauntleroyi* and *M. macronychia*. Understory shrubs are represented by *H. glomerosa* and *G. paniculate,* with an abundance of grasses and herbs. About 80% of the plants are less than 3 m tall (Figure 12a) and very few tall trees are present; 72% of plants are multi-stemmed shrubs and most species have small boles, only a few being more than 7 cm in diameter (Figure 12b). The species with the largest stems are *A. lasiocalyx*, *A. huegeliana* and *L. erubescens*.

Table 11. Summary of main species in three vegetation types in the rocks area of SRNR.

(1). Dense *Leptospermum erubescens* thicket

Species	Life form	Height (m)	Canopy % cover	Layer
Leptospermum erubescens	Shrub	0.5-5	30-70	Lower
Acacia lasiocalyx	Tree	1-5.5	2-10	Upper
Dodonaea viscosa	Shrub	1-1.5	2-10	Lower
Melaleuca macronychia	Shrub	1-1.5		Lower
Santalum spicatum	Shrub	1-3		Lower
Allocasuarina huegeliana	Low tree	1.5-8		Upper
Hibbertia glomerosa	Shrub	0.5-1		Lower
Dodonaea inaequifolia	Shrub	1-1.5		Lower
Calothamnus asper	Shrub	0.5-2		Lower

(2). Low open *Acacia prainii* shrubland

Species	Life form	Height (m)	Canopy % cover	Layer
Acacia prainii	Shrub	0.5-3	>70	Dominant
Dodonaea viscosa	Shrub	0.5-3	30-70	Co-dominant
Melaleuca macronychia	Shrub	1-3	2-10	Co-dominant
Dodonaea inaequifolia	Shrub	0.5-3	2-10	Co-dominant
Hibbertia glomerosa	Shrub	0.5-1		Lower
Grevillea paniculata	Shrub	1-2		Lower
Calothamnus asper	Shrub	1-2		Lower

(3). Low open *Dodonaea viscosa* shrubland

Species	Life form	Height (m)	Canopy % cover	Layer
Dodonaea viscosa	Shrub	0.5-3.5	30-70	Dominant
Hibbertia verrucosa	Shrub	0.5-1	2-10	Co-dominant
Acacia fauntleroyi	Shrub	0.5-5.5	2-10	Co-dominant
Baeckea elderana	Shrub	0.5-1		Co-dominant
Melaleuca macronichia	Shrub	1-1.5		Co-dominant
Allocasuarina huegeliana	Low tree	2-5		Co-dominant

Three different vegetation types occur in the rocks site (Table 11). In all types, *D. viscosa* is well represented: this species is relatively well distributed at the rocks area. The first vegetation type is "Dense *Leptospermum erubescens* thicket". This type has a distinct appearance and is characterised by *A. lasiocalyx* as the upperstorey with a silvery bark and *L. erubescens* as the understorey species with pronounced cover. This type of vegetation occurs in large soil pockets at the rocks site, that are rich in humus and of a sandy or clay loam soil type.

The second vegetation type is "Low open *Acacia prainii* shrubland". This is characterised by high density and cover of *A. prainii*; with *D. viscosa, M. macronichia* and *D. inaequifolia* as the co-dominant vegetation with no upperstorey. This vegetation type is commonly concentrated along creek lines or in run-off areas at the rocks. The soil associated with this vegetation type is a sandy loam, fine sandy loam or loam. Another vegetation type is "Low open *Dodonaea viscosa* shrubland"; this vegetation type occurs on the marginal flats, at the base or the edge of granite rock. It is characterised by high density of *D. viscosa* and the co-dominant *H. recurva, B. elderiana* and some *A. fauntleroyi.* It is associated with sandy loam or fine sandy loam soils.

2.3.6. Distribution of species and similarity between areas

Here I considered the overall presence of species in 33 vegetation stands. Of 85 woody species recorded, 56.5% were present in fewer than 3 stands. Some 30.5% were present in 3 to fewer than 6 stands and only a few species were in the common (10.6%) and very common (2.4%) categories. *A. huegeliana* (in 20 stands) and *A. acuminata* (in 15) were the most common species. *M. pauperiflora, M. acuminata, H. invaginata, H. coriacea, A. buxifolia, P. tuberculosum, G. paradoxa, A. hemiteles* and *G. paniculata* were in the common categories (in 6 to fewer than 9 stands). Generally, species were not evenly distributed across the areas. Distribution of the species is presumed to be related to the heterogeneity of the habitats within the reserve. Soil and moisture availability associated with each area controls the local pattern of plant distribution and tends to promote different plant associations.

The west corner area had a slightly higher diversity and species richness of woody species than the remaining areas (Table 12). It is thought that the deep, sandy soils in this area promoted high diversity. The CK-3 area has low diversity and evenness, with only few plants occurring in the understorey of this *Eucalyptus* woodland. Similarities between the study areas were in the range 0.18-0.29 (Table 13). This reflects that only a few species are present in more than a few sites. *A. acuminata, A. huegeliana* and *A. hemiteles* commonly occurred in the 5 areas (except that *A.*

hemiteles absent at the rocks). The highest similarity was between the vegetation at CK-3 and the rocks (0.29). Some of the shrubs that commonly occur in the rocks area (*A. buxifolia*, *D. inaequifolia*, *L. erubescens*, *C. asper* and *K. pulchella*) also occur at the edge of the CK-3 area, close to the rock.

Table 12. Comparison of diversity and species evenness of woody perennials between the areas.

Areas	No. species	Diversity (H')	Evenness (J)	No. plants/ha	Multi stem (%)
Northeast corner	27	2.55	0.77	2000	65.8
Entrance	24	2.61	0.82	1700	60.8
West corner	39	2.72	0.74	2400	62.5
CK-3	26	2.24	0.69	710	33.3
Rocks	28	2.59	0.78	1157	72.2

Table 13. A similarity half-matrix of woody perennials between the areas.

Areas	Northeast corner	Entrance	West corner	CK-3	Rocks
Northeast corner	*				
Entrance	0.28	*			
West corner	0.27	0.24	*		
CK-3	0.21	0.26	0.22	*	
Rocks	0.18	0.23	0.19	0.29	*

There were also relatively high similarities (0.28) between the entrance and rocks areas. In both areas, species characteristic of seasonally wet areas or high moisture were present (i.e. *A. prainii*, *A. buxifolia*, *M. macronychia* and *D. viscosa*). Between the west corner and CK-3, there was a similarity of 0.27. Some *Melaleuca* and *Acacia* species growing in the west corner were also present at CK-3. The most dissimilar sites were the rocks and the northeast corner; and the rocks and the west corner. The rocks site was dominated by species with preferences for high moisture, while both of the latter areas were characterised by species adapted to relatively dry areas.

2.4. Discussion

Vegetation at SRNR comprises a range of vegetation associations from open woodland through thickets with scattered trees, to shrublands and some open grasslands. The dominant plant in woodland areas is *Eucalyptus*, while in all other vegetation types, *Acacia, Melaleuca, Hakea, Grevillea, Baeckea, Allocasuarina, Leptospermum* or *Dodonaea* are prominent. Summing the 5 study areas, a total of 85 species from 20 families of woody perennials was recorded. All areas are dominated by the Myrtaceae, Mimosaceae and Proteaceae families. The vegetation consists of a mosaic of various species and there are fairly distinct zones in which some species are dominant. These characteristics combine, resulting in various arrangements of vegetation types or associations. Factors causing patchiness of vegetation are related to habitat heterogeneity within the reserve.

Beard (1981) classifies the vegetation of Western Australia based upon the physiognomy of the ecologically dominant stratum. Initially, classification is based on life-form/height class and then separated by appearance of the dominant stratum as either trees, shrubs, grasses, forbs, lichens/mosses or succulents. The physiognomic classification is completed by adding projected foliage-cover for each ecologically dominant stratum. Finally, floristic dominants or characteristic species are determined. Specht (1972) also presented a classification system for the vegetation of Australia. The Specht system was based on the tallest stratum of the vegetation, not on the dominant ones of Beard. Based upon the physiognomy and extent of cover of the ecologically dominant stratum, various vegetation types are observed at SRNR.

The northeast corner region is characterised by dry, shallow or rocky soil. Here I found sites dominated by plants with small leaves (nanophytes) of small stature (mesophanerophytes) or low shrubs (e.g. *G. paradoxa* and *B. elderiana*). Presumably, they are adapted to the dry, shallow, yellow lateritic sand or rocky soil. Vegetation types recognized in this area include: *A. huegeliana* woodland - this commonly forms an almost pure stand in relation to woody species, especially in black or brown dry sandy soil. In this formation, *Allocasuarina* is an upper canopy tree with *Acacia, Melaleuca* and *Grevillea* species as understorey plants; and *G. paradoxa* low shrubland, which is confined to dry, rocky soil and reddish yellow shallow soil (presumably, with small leaves and small stature, *G. paradoxa* is well adapted to such dry, shallow soil); *A. neurophylla* medium shrubland, this is confined to yellow, shallow lateritic soil which is moderately to well-drained. The main association in this vegetation type is *A. stereophylla*, *G. paradoxa* and *Allocasuarina,* with no upperstorey. The northeast corner area mainly comprises shrub associations. Beard (1981) noted that shrublands of several types are largely associated with poor siliceous soils under low rainfall conditions, and occur on shallow skeletal soils of rocky ranges or on massive laterite or ironstone ridges.

The entrance region is mainly a seasonally wet area, with relatively high soil moisture. Soil is relatively deep; the more favourable moisture regime might explain the high density of grasses in this area. Various vegetation types are present, including : "*A. jennerae* low open shrubland". In this vegetation type, only a few other woody species are present; *A. jennerae* forms almost a pure stand. Reproduction from suckers presumably results in only a little space being available for other woody species. Lower canopy species consist mainly of perennial grasses e.g. *A. strictus*, perennial herbs e.g. *B. constricta* with some pteridophytes and lichens on the soil surface; "Low open grassland" is another vegetation type found in the entrance area. This type is more likely to be an ecotone between the shrubland. The vegetation mainly comprises the grasses *N. alopecuroidea*, *E. ovata* and *A. contorta,* with many seedlings of *H. invaginata;* "Wandoo woodland" is also present, and consists of tall trees of *E. capillosa* as the upperstorey with *D. viscosa*, *A. buxifolia* and some *A. prainii* as an understorey, while the ground is mainly covered by the grass *N. alopecuroidea;* "*A. saligna* thicket" is well represented at the entrance where there is a lot of grass in the understorey, mainly *E. ovata.* This area is seasonally flooded, and the soils are dark and fine-textured, well-drained sandy clay loam and relatively deep. The wheatbelt wandoo (*E. capillosa*) is closely related to *E. wandoo* further west.

The west corner section of the reserve has deep, dry, sandy soil that appears to promote the formation of Myrtaceous thickets. Most plants here are medium-sized shrubs of the *Acacia* and *Melaleuca* genera (Fox, Keenan & Shepherd 1993). The deep, sandy soil in this area that is apparently very dry in summer is presumably an adequate environment for myrtaceous thickets. While some *Eucalyptus* species are present, they are generally of small stature. The vegetation is relatively dense. Comparing this region to the remaining areas, and considering woody perennial species, the west corner area had high species diversity and evenness. Few tall trees are present, which presumably results in less intense competition between the plants, therefore more species can exist. Beard (1981) noted that shrublands are richer in species than woodlands as there is less intense competition in shrubland than in woodland. *Acacia* species are well represented in the west corner area. As a nitrogen fixer, *Acacia* species may be beneficial as associates to other species.

Three vegetation types are recognized in the west corner. Firstly, *"Phebalium tuberculosum* shrubland", where the main association is between *Acacia* species and a few *Eriostemon tomentellus*. Secondly, *"Acacia acuminata* open thicket", where jam is co-dominant with *Acacia coolgardiensis*, *Phebalium*, *Baeckea*, *Allocasuarina* and *Hakea*. The last vegetation formation is *"A. coolgardiensis* open thicket", with main associations with *Melaleuca eleuterstachia*, *Acacia hemiteles*, *Eriostemon* and *Baeckea*. Thickets are widespread on sand plains and the dominant species are usually various *Acacia*, *Casuarina* and *Melaleuca* (Beard 1981). So the thicket forms of vegetation could be grouped as an *Acacia-Casuarina-Melaleuca* alliance with the same growth habit (broom-bush). *A. acuminata* and *A. coolgardiensis* thickets in this area also form a broom-bush habit.

At the area designated as CK-3, the vegetation consists of tall, open woodland of *Eucalyptus* species and Myrtaceous thickets. Most component plants are eucalypts. This area has many tall trees and few understorey plants. Of the 5 areas examined, the tallest trees were found in CK-3; stem diameters were also large in this area and the percentage of multi-stemmed plants was low. The CK-3 area is located between two large outcrops, and run-off from the adjacent outcrops provides the area with increased amounts of water and nutrients. The outcrops also provide shelter from strong winds and as a result of this tall trees are abundant. Presence of only a few understorey species at CK-3 area is presumed to result from root competition for water. Root competition for water is regarded as a likely cause of shrub suppression beneath *Eucalyptus wandoo* (Lamont 1985).

Two distinctive vegetation types are recognized at the CK-3 area: firstly, "*Eucalyptus salmonophloia* (salmon gum) woodland" where the vegetation consists of an emergent of *Eucalyptus* species (*E. salmonophloia*, *E. loxophleba* and *E. capillosa*), uppercanopy of *E. salmonophloia* and *A. acuminata*, *D. inaequifolia* and *A. huegeliana* as an intermediate canopy, with relatively few understorey species. This vegetation type is confined to the most well-developed vegetation at SRNR, and is generally similar to *E. salmonophloia* and *E. loxophleba* woodland in the Avon District (Beard 1981) and salmon gum woodland (Keenan 1993), which also has *A. acuminata*, *A. huegeliana* and *M. pauperiflora* as understorey species. Beard (1981) also noted the presence of *Atriplex* as an understorey plant, which I also observed in *E. salmonophloia* woodland at SRNR in local patches. Another type of vegetation observed at the CK-3 area is "*Kunzea pulchella* shrubland" on the periphery of the *Eucalyptus* woodland or relatively close to the rocks. Species present are assumed to be tolerant of occasional high soil moisture. This vegetation type is characterised by the prominent cover and high density of *K. pulchella*, with *A. acuminata* and *A. huegeliana* as co-dominants. The soil is a sandy loam or clay loam, with plentiful humus and some annual grasses also present in the area.

The rocks area is centred on location with locally high soil moisture habitats related to granite rocks. The soils in the area are relatively shallow and of sandy loam or clay loam texture. Various habitats are present in the area, such as tumbled boulders, soil pockets of shallow or deep soil, run off areas and marginal flats at the base of granite rocks. Generally, the low-lying habitats are locally rich in humus, which promotes the formation of a healthy, open, low to medium shrubland or thicket. The rocks site was dominated by those species that presumably gain advantage from material eroded from the granite rocks. *Eucalyptus* species were quite rare and may have been affected by the relatively shallow soil. Muir (1979) designated the vegetation type of the rocks site of SRNR as a "lithic complex". A lithic complex is characterised by large pavements and outcrops of granite gneiss with *Parmelia* and other lichens and *Grimmea* moss. Soil pockets of variable depth are associated with healthy shrubland formations and run-off areas and surrounding flats with shrubland or woodland. Muir divided species at the rocks site as either being present in tumbled boulders, shallow soil, deep soil, run-off areas or marginal flats.

The vegetation formations recognized in the rocks site include: "Dense *Leptospermum erubescens* thicket", with *A. lasiocalyx* as an upperstorey and *L. erubescens* as the main canopy or understorey. This type of vegetation occurs in large pockets of soil at rocky sites, rich in humus and with sandy and clay loam soils. *L. erubescens* thickets tend not to develop a broom-bush habit. Another vegetation type at the rocks site is "Low open *Acacia prainii* shrubland", where *D. viscosa, M. macronichia* and *D. inaequifolia* are co-dominant and there is no upperstorey. Vegetation in this plant formation is often concentrated along creek lines or at run-off sites around the rocks. Another vegetation type is "Low open *Dodonaea viscosa* shrubland", which occurs on marginal flats at the base or edge of granite rocks. Co-dominant species include *L. erubescens*, *H. recurva, B. elderiana* and *A. fauntleroyi.*

In Southern Australia, Burgman (1987) observed that a major feature of rocks of dissected sheet granite is the support of pockets of skeletal soil; there is often a scree slope surrounding such pockets made up of shallow sand, gravel and boulders. These areas support differently structured vegetation types. Typically, on sheet granite there are limited areas of open dwarf shrublands less than 0.5 m high and open herbfields. This vegetation is often restricted to drainage channels where pockets of skeletal soil have accumulated. Scree slope communities are more variable but are often characterised by tall shrubland to 3 m, open shrubland to 1 m with a variety of sedges and herbs.

The distribution of species across the areas confirms that most species at SRNR were present only at particular sites. Of the 85 woody species encountered, *A. huegeliana* and *A. acuminata* were the most common species (highest distribution) across the areas. These two species were present in all areas studied. Lange (1960) categorised *A. huegeliana* and *A. acuminata* as continuous distribution; they have broad distributions around Narrogin, WA. *A. huegeliana* occurs on various soils, particularly granitic skeletal soil and their associated sands. *A. acuminata* occurs on various soils, particularly sandy alluvium, loam and granitic skeletal soils. Low species distribution at SRNR is also reflected in the low similarity coefficient of vegetation between the 5 study areas (0.18-0.29). Of all of the species, *A. acuminata*, *A. huegeliana* and *A. hemiteles* most commonly occurred. However, *A. hemiteles* is not present at the rocks site. This may reflect lack of moisture retentive soil at the rocks. Plant distributions are controlled by various physical factors such as soil, water availability and micro-topographic variations. Such patterns are generally affected by differential seed accumulation, variation in species germination requirements and differences in growth and mortality (Aiba & Kitayama 1999). In arid and semi-arid lands (arid ecosystems), water is the single most important limiting factor, hindering growth and allowing both establishment and survival of plants.

Of the five study areas, the most similar are CK-3 and the rocks areas. Some of the shrubs that are associated with the rocks also occur at CK-3, mainly in the *K. pulchella* vegetation association. At the entrance and rocks areas, species characteristic of seasonally wet areas or high moisture were present (e.g. *A. prainii, G. paniculata*). The greatest dissimilarities were between the rocks and northeast corner areas; and the rocks and west corner areas. The rocks area was dominated by species that require high soil moisture, while both latter areas were characterised by species able to tolerate relatively dry areas.

On examination of the height distributions of various selected species, it is presumed that the severe drought of 1994 (only 214.8 mm rainfall) resulted in poor recruitment in many species as well as some losses. Species apparently affected include: *A. huegeliana* and *B. elderiana* (in the northeast corner site); *A. jennerae*, *A. buxifolia,* and *H. invaginata* (in the entrance site); *A. coolgardiensis* (in the west corner site); *A. huegeliana* and *A. acuminata* (in the CK-3 site) and *L. erubescens* (in the rock site). This is representation of one period of poor recruitment in the past. However, further investigation is required to confirm this.

CHAPTER 3

POPULATION STUDY OF *ACACIA LASIOCALYX, ACACIA PRAINII, ACACIA FAUNTLEROYI* AND *ACACIA HEMITELES* AT SANDFORD ROCKS NATURE RESERVE (SRNR)

3.1. Introduction

The genus *Acacia* is represented in most biomes in Australia, with over 900 species present (Atkins *et al.* 1998). *Acacia* dominates the woody vegetation of the arid and semi-arid regions and is also well represented in more mesic environments. At SRNR, about 18 species occur. These species are mainly locally abundant and occupy particular habitats. They are present as subordinate species in various associations of eucalypt woodland, melaleuca thicket and scrub, and clearly play an important role in the associations present.

In previously discussed studies (Chapter 2), *A. acuminata* was found to be a well-distributed species at SRNR; it is present in dry to moist habitats and in open to relatively closed shrubland or woodland. *A. hemiteles* is also well distributed across these areas, except in relatively moist open habitats, particularly near the rocks. Presumably, *A. hemiteles* is not adapted to moist habitats and does not grow well in material eroded from rocks. In contrast, *A. prainii* grows well in these areas and is relatively well distributed in seasonally wet areas, mainly along the creek lines and around granite rocks edges.

Several members of the genus: *A. colletioides, A. densiflora, A. coolgardiensis, A. eremophila, A. stereophylla* and *A. jibberdingensis* all grow well in relatively deep, dry-sandy soil. *A. neurophylla* and *A. steedmanii* are only found in the northeast corner where both species occur on lateritic yellow, shallow, dry-sandy soil. *A. erinaceae* and *A. nyssophylla* are also found on dry soils. *A. erinacea* is commonly observed growing with *A. hemiteles* as an understorey component species in eucalypt woodland. *A.*

tetragonophylla is sometimes found in eucalypt woodland, however this species is extremely scarce at SRNR.

A. jennerae is only found at the entrance site, in relatively deep, moist sandy soil. This species reproduces by root suckers and tends to form inter-connected, almost pure stands. *A. lasiocalyx* and *A. fauntleroyi* are only present in the vicinity of the granite rocks. Both species appear dependent on material eroded from rock. *A. fauntleroyi* is mainly found at the base of granite rocks, in lenses of shallow, very well-drained, coarse, granitic sandy soil with much organic matter. None of these plants are found far away from rock and all sites are water gaining. The distribution of *A. lasiocalyx* is relatively sparse; it occurs in small clusters in shallow lenses of soil or soil pockets at the edge of rocks. This species is not found away from rocks either. *A. sessilispica* is also present at the base of granite rock, however this species is uncommon. *A. saligna* is present in relatively moist habitats; it is present in seasonally wet run-on areas and in some extremely favourable water gaining sites adjacent to the slopes of granite rocks.

At SRNR, population numbers of several of these *Acacia* are generally low. The pattern of seedling recruitment of the species is not well known. Some species appear to be able to support seedlings, with many seedlings being found, however, these may not persist. In other species, seedlings are rarely found. To understand the ecology of any particular plant species, an understanding of the populations present and their dynamics *in vivo* is required. In this study, population characteristics of four selected *Acacia* species (*A. fauntleroyi, A. lasiocalyx, A. prainii* and *A. hemiteles*) and their associated species are investigated.

In three species, *A. fauntleroyi, A. lasiocalyx* and *A. prainii* have some association with granitic rock. In contrast, *A. hemiteles* is common as an understorey species of *Eucalyptus* woodland in relatively dry soil of finer texture. Populations of *A. hemiteles* tend to be relatively large and well distributed. The main populations are found at some distance (about 1 km) from granitic rock. This species is particularly common in gimlet (*E. salubris*) and salmon gum (*E. salmonophloia*) woodland. As each of the four species tends to have a distinct distribution and to occupy "unique" microhabitats, they are assumed to form different species associations. The aim of this study is to investigate the apparent pattern of natural regeneration of these plants from their population characteristics, and also to investigate relevant characteristics of their associated species.

3.2. Methods

A modification of the point centred quarter method of Mueller-Dombois & Ellenberg (1974) was employed to investigate these four *Acacia* populations and their associated woody species. This method was employed because some populations were small and sparsely distributed, and were therefore not suited to investigations using standard transect or quadrat analysis. In the method used, the sampling point of the point centred quarter method was replaced with a point where a specimen of the selected *Acacia* species was present. As each target *Acacia* species was found, four quarters were established by crossing two lines. The first line was run in a cardinal compass direction and the second line ran perpendicular to the first. The point where the two lines crossed was called the sampling point (i.e. the point where the target species plant was rooted). The distance from the sampling point to the nearest plant was then measured in each quarter. The distance between target species was also measured. Herbs and grasses were excluded, as previously (Chapter 2).

Plant height, bole height, stem diameter and crown architecture (crown cover and crown depth/height) were measured, and plants were classified according to their height and diameter. Plant height was defined as the vertical distance from the base of the trunk to the highest leaves. Bole height was defined as the vertical distance from the base of the trunk to the first main branch, and crown depth/height was defined as the distance from the highest leaves to the lowest leaves. Stem diameters were measured at a height of 0.5 m, and where plants were multi-stemmed, the largest stem was measured; the percentage of plants with multiple stems was calculated. Soil depth was also measured at each sampling point by inserting a soil probe into the profile as deeply as possible. The depth of penetration for soil depths were marked and then measured with a 1 m rule. The texture of each sample soil was determined in the field according to the procedure outlined in Appendix 2.

Data from the quarters were analysed using the point centre quarter methods of Mueller-Dombois & Ellenberg (1974). Density and dominance values for each species were calculated. Dominance was expressed as crown cover and an importance value was derived by addition of the relative values of density and dominance (Mueller-Dombois & Ellenberg 1974). Numbers of plants per ha of the target acacias were calculated from mean distance. The mean distance was equal to distance/number of plants, and the number of plants per ha was equal to 10,000 m^2/mean distance^2 (Mueller-Dombois & Ellenberg 1974). The Shannon-Wiener index was used to calculate species diversity ($H'=\sum$ pi ln pi), and equitability or evenness ($J = H' / H'$ max $= \sum$ pi ln pi / ln s, where: s= the number of species; pi = proportion of importance value of the species; and Ln = log base n). Similarity (Ss) between the associated species was measured using the Sorensen coefficient (Kent & Coker 1992), which is based on the presence/absence of species in association.

For comparison of the stature of *A. lasiocalyx* growing in natural habitats (SRNR) to those of cultivated plants, the dimensions of five sample plants grown at the Field Trial Area (FTA) of Curtin University of Technology were measured. The sample plants were 10 years old and the parent seed came from SRNR; the seedlings were grown during 1990.

3.3. Results

3.3.1. *Acacia lasiocalyx*

At SRNR, the distribution of *A. lasiocalyx* was relatively restricted and sparse, and it was found in small clusters. The mean distance between plants was 88.8 m, giving only

1.3 plants/ha. *A. lasiocalyx* is mainly found in areas where local flooding of gnammas occurs. It is found in small patches of lenses (ledges) in the granite rock. The rock is characterised by a series of eroded "holes" (gnamma holes or lagoons) scattered over some distance in the rock; small holes are bare but filled with water, while larger ones have a lot of soil (granite sand and humus) and some *A. lasiocalyx* is present in these. The habitat characteristics result in relatively large distances between plants and low plant densities.

The plants had a mean height of 3.6 m and stem diameter of 4.4 cm (Table 14). Tree height (Th) is strongly related to stem diameter (Dm), (Th = 2.17 + 0.336 Dm, F = 30.41, P <0.001). Larger stem diameters are associated with taller plants. However, bole height (Bh) is not dependent on stem diameter (P = 0.672). Crown depth (Cd) is only marginally dependant on tree height (Cd = 0.934 + 0.265 Th, F = 3.61 P = 0.075), however crown cover (Cc) is highly dependant on tree height (Cc = - 3.81 + 2.45 Th, F = 10.05, P = 0.004), where taller trees have larger crown covers. Bole height (Bh) tends to be taller in taller trees (Bh = 0.524 + 0.222 Th, F = 3.06, P = 0.097), however this relationship is weak. Crown depth and crown cover are not related (P = 0.310).

Table 14. Dimensions of *A. lasiocalyx* at SRNR (*n = 34). Standard deviation in brackets.

	Stem diameter (cm)	Plant height (m)	Bole height (m)	Crown depth (m)	Crown cover (m^2)
Mean (SD)	4.4 (3.4)	3.6 (1.6)	1.5 (0.7)	1.9 (0.8)	4.5 (3)
Maximum	11.1	5.8	2.8	3.6	28.1
Minimum	0.6	0.9	0.3	0.6	0.2

*n = 34 (from 24 sampling points + 10 in quarter)

Table 15. Dimensions of *A. lasiocalyx* at the FTA (n = 5). Standard deviation in brackets.

	Stem diameter (cm)	Plant height (m)	Bole height (m)	Crown cover (m^2)
MEAN (SD)	6.0 (2.4)	6.7 (3.7)	2.4 (1.0)	33.2 (18.9)
Maximum	8.3	12.5	4.1	77.7
Minimum	2.1	2.7	1.4	17.3

A. lasiocalyx grows in either sandy loam (88.2%) or clay loam (11.8%) soil; plants being more commonly found in sandy loam. The deepest soil depth recorded for an *A. lasiocalyx* association was 55 cm, with a mean of 22 cm (n = 24). *A. lasiocalyx* appears adapted to growth in relatively shallow soil and it was found growing in less than 10 cm of soil. Tree height ($P = 0.578$) and stem diameter ($P = 0.929$) are not dependant on soil depth.

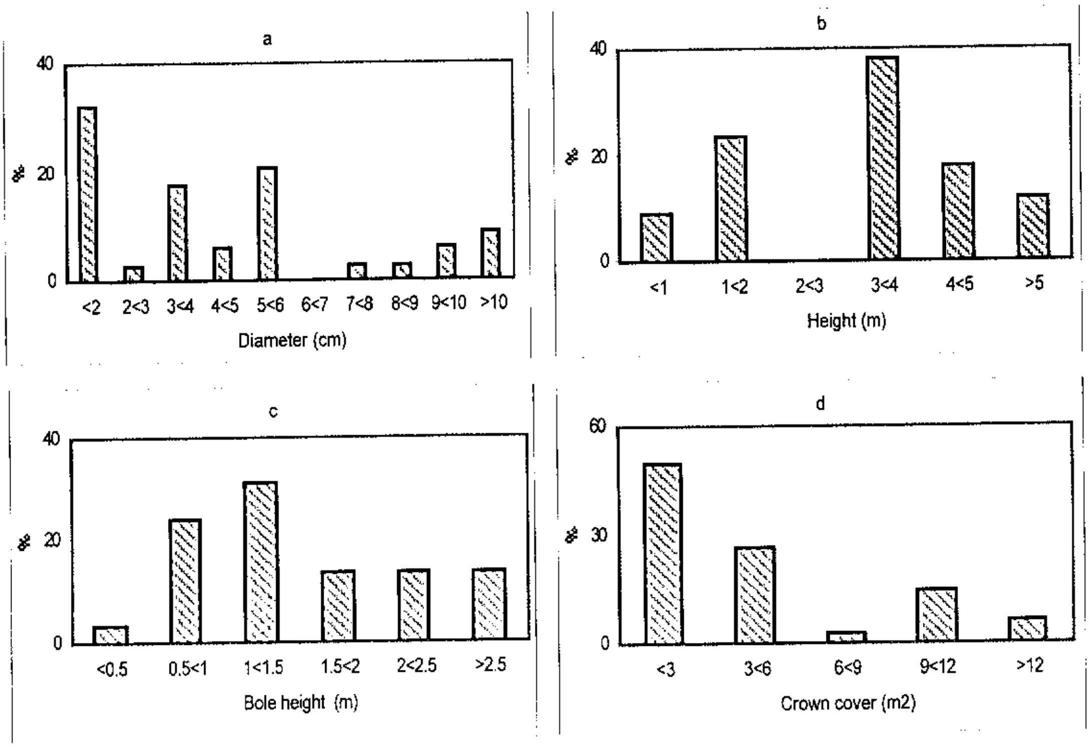

Figure 13. Population characteristics of *A. lasiocalyx* at SRNR (n = 34). Frequency distribution (%) of: (a) Stem diameter; (b) Plant height; (c) Bole height and (d) Crown cover.

A. lasiocalyx growing naturally (at SRNR) had a different stature from that of the same species growing in an artificial habitat at the Field Trial Area (FTA) at Curtin University of Technology. In the natural habitat, trees tended to have a straight stem or bole and less crown cover, while those in the FTA tended to have a short stem or bole compared to the height, with more branches and crown cover. Generally, the plants growing at the FTA are also taller than those at SRNR. This variability in plant stature is presumed to be due to more water availability, and less intensive competition in the cultivated area compared to the natural habitat.

For *A. lasiocalyx* growing at the FTA (n = 5 plants), each of tree height (Th), bole height (Bh), crown depth (Cd) and crown cover (Cc) are significantly related to stem diameter (Dm): Th = 1.85 + 0.110 Dm, $F = 21.48$, $P = 0.019$; Bh = 1.11 + 0.0283 Dm, $F = 9.88$, $P = 0.052$; Cd = 0.74 + 0.0821 Dm, $F = 17.56$, $P = 0.025$; Cc = 11.9 + 0.623 Dm, $F = 9.10$, $P = 0.057$. Crown cover (Cc = 3.7 + 5.29 Th, $F = 9.23$, $P = 0.056$) and bole height (Bh = 0.656 + 0.254 Th, F 17.68, $P = 0.025$) are related to tree height. Taller trees have larger crown covers and taller boles. Crown cover is marginally related to crown depth (Cc = 10.0 + 6.71 Cd, $F = 6.66$, $P = 0.082$). Crown cover and bole height are also significantly related (Cc = - 7.2 + 19.7 Bh, $F = 10.97$, $P = 0.045$).

The distributions of plant dimensions of *A. lasiocalyx* at SRNR (Figure 13) are generally indicative of several cohorts collectively far from a normal distribution; this reflects the fact that a number of "populations" were included for *A. lasiocalyx*. It is hypothesised that actual "transects" (based on different soil pockets) which are scattered over some distance on the rock, separate the plants into populations (forming several genotypes). This is thought to affect successful recruitment at the different sites. Alternatively, non-normality in plant size distribution may reflect a period when recruitment did not occur in the past.

At SRNR, more than 30% of *A. lasiocalyx* plants had stem diameters less than 2 cm (Figure 13a). The smallest plant measured (March 2001) was 0.9 m tall and no seedlings of shorter stature were observed at that time. However, 9% of the population was less than 1 m tall (Figure 13b), suggesting existence of a cohort and that some recruitment had occurred recently. The maximum height recorded was 5.8 m, less than half (12.5 m) that for cultivated plants at the FTA at Curtin University (Table 15). All plants of *A. lasiocalyx* at SRNR were single-stemmed and the plants had quite tall boles, ± 1.5 m (Figure 13c) compared with other *Acacia* spp. growing at SRNR. Generally, the plants formed branches after more than 1m of bole height was attained. Most plants had a crown depth of 1.3-1.8 m. Some 50% of the plants had crown covers less than 6 m^2 (Figure 13d). Crown cover of *A. lasiocalyx* growing at SRNR (Max. 11.1 m^2) was also much smaller than that at the FTA, which was up to 77.7 m^2.

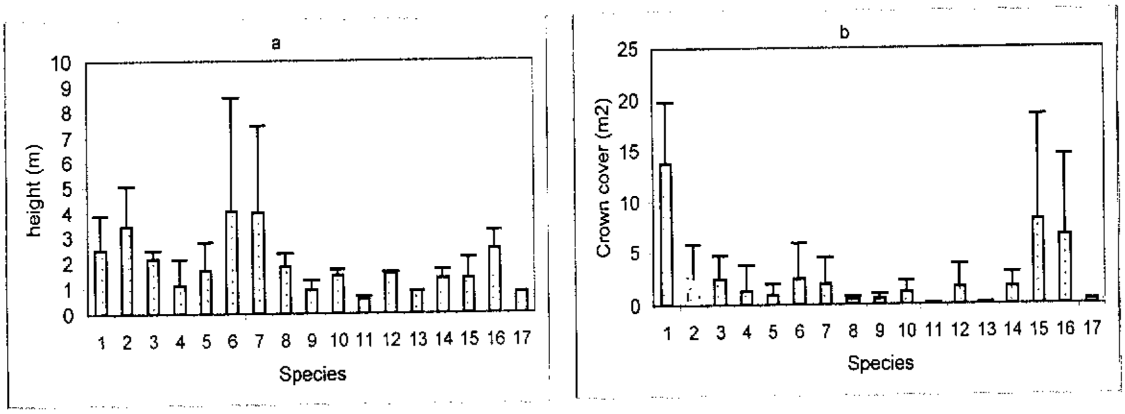

Figure 14. Mean height and crown cover of woody species associated with *A. lasiocalyx*. a) Mean height and b) Mean crown cover. Species numbers as in Table 16. Bars represent standard errors.

Table 16. Structure and composition of woody perennial species associated with *A. lasiocalyx* (From a point quarter survey of 24 sampling points).

No.	Species	Mean height (m)	No. plants	Mean crown cover (m^2)	Density (%)	Dominance (%)	IV
1	*Leptospermum erubescens*	2.53	32	13.76	33.33	29.74	63.07
2	*Acacia lasiocalyx*	3.44	10	2.62	10.75	5.66	16.41
3	*Acacia fauntleroyi*	2.18	3	2.44	3.23	5.27	8.49
4	*Acacia prainii*	1.13	4	1.28	4.30	2.76	7.06
5	*Santalum spicatum*	1.70	6	0.88	5.38	1.90	7.27
6	*Allocasuarina acutivalvis*	4.07	2	2.47	2.15	5.35	7.50
7	*Allocasuarina huegeliana*	3.98	3	1.95	3.22	4.21	7.43
8	*Alyxia buxifolia*	1.83	2	0.50	2.15	1.07	3.22
9	*Astroloma serratifolium*	0.94	2	0.53	2.15	1.13	3.29
10	*Melaleuca macronychia*	1.49	4	1.19	4.30	2.58	6.88
11	*Hibbertia glomerosa*	0.58	3	0.05	3.23	0.11	3.34
12	*Dodonaea inaequifolia*	1.57	3	1.62	3.23	3.51	6.73
13	*Persoonia striata*	0.90	2	0.18	2.15	0.39	2.54
14	*Dodonaea viscosa*	1.38	14	1.63	13.99	3.53	17.51
15	*Calothamnus asper*	1.37	3	8.11	3.23	17.52	20.75
16	*Kunzea pulchella*	2.53	2	6.67	2.15	14.43	16.58
17	*Grevillea paniculata*	0.83	1	0.39	1.08	0.84	1.919
	SUM		96	42.26	100	100	200

Sixteen other woody species occur in association with the *A. lasiocalyx* population (Table 16). This association mainly comprises large shrubs of *Leptospermum erubescens;* small trees of *Acacia lasiocalyx;* and small shrubs of *Dodonaea viscosa.* It is of interest that no *Eucalyptus* species occur in the *A. lasiocalyx* association. The taller trees of the association are *Allocasuarina* and *A. lasiocalyx* (Figure 14a). *Allocasuarina* is represented by two species (*A. huegeliana* and *A. acutivalvis*). The intermediate level is comprised mainly of *L. erubescens* and *Kunzea pulchella* and the lower canopy is mainly *Hibbertia*, *A. prainii* and the perennial hummock grass species *Spartochloa scirpoidea*. Most vegetation cover is provided by *L. erubescens*, *C. asper* and *K. pulchella* (Figure 14b). *L. erubescens* and *D. viscosa* have an apparent tendency to grow close to *A. lasiocalyx*, such that in general, where one *A. lasiocalyx* is present, one *D. viscosa* and three *L. erubescens* are also found. It is possible that *A. lasiocalyx* and *L erubescens* share some mutually beneficial relationship. *L. erubescens* may provide shelter for seedlings of *A. lasiocalyx*, and nodules on roots of *A. lasiocalyx* may provide nitrogen by leaching/decay to the roots of *L. erubescens*.

3.3.2. *Acacia prainii*

A. prainii tends to form a rather dense, concentrated population on an alluvial flood-out soil adjacent to the main creek channel at SRNR. The mean distance between plants was 9.7 m, representing a density of 105.4 plants/ha. From the 32 sample soils determined for each sampling point, 70% of *A. prainii* occur in sandy loam, 17.5% in fine sandy loam and 12.5% in loam. These soils were moist and rich in organic matter.

The mean height of *A. prainii* was 1.2 m (SD 0.7, n = 81). The tallest plant was 2.7 m and the shortest was 0.2 m (Table 17). *A. prainii* has regular (probably annual) recruitment and many seedlings were found. Some 15% of measured plants were less than 0.5 m tall and thus can be classified as seedlings or saplings (Figure 15a). More than 40% were less than 1 m tall, with only about 10% >2 m tall. The few tall plants present are presumably more resistant to the rust fungus infection (*Uromycladium tepperianum*) that is commonly observed to infect this species and to be more prevalent on the larger individuals.

Plant size distribution (height) suggests that the periodic drought that sometimes occurs at SRNR has not affected recruitment much. Presumably, as the main habitat is a seasonally wet area with a long period (June-September) when moisture is generally available, plant recruitment may not be affected much by summer drought. Although many mature plants may be infected by the rust fungus, this may not seriously infect plant regeneration for the first 1-2 yr of growth. Presence of a favourable seedbed may enable seedlings to appear each year.

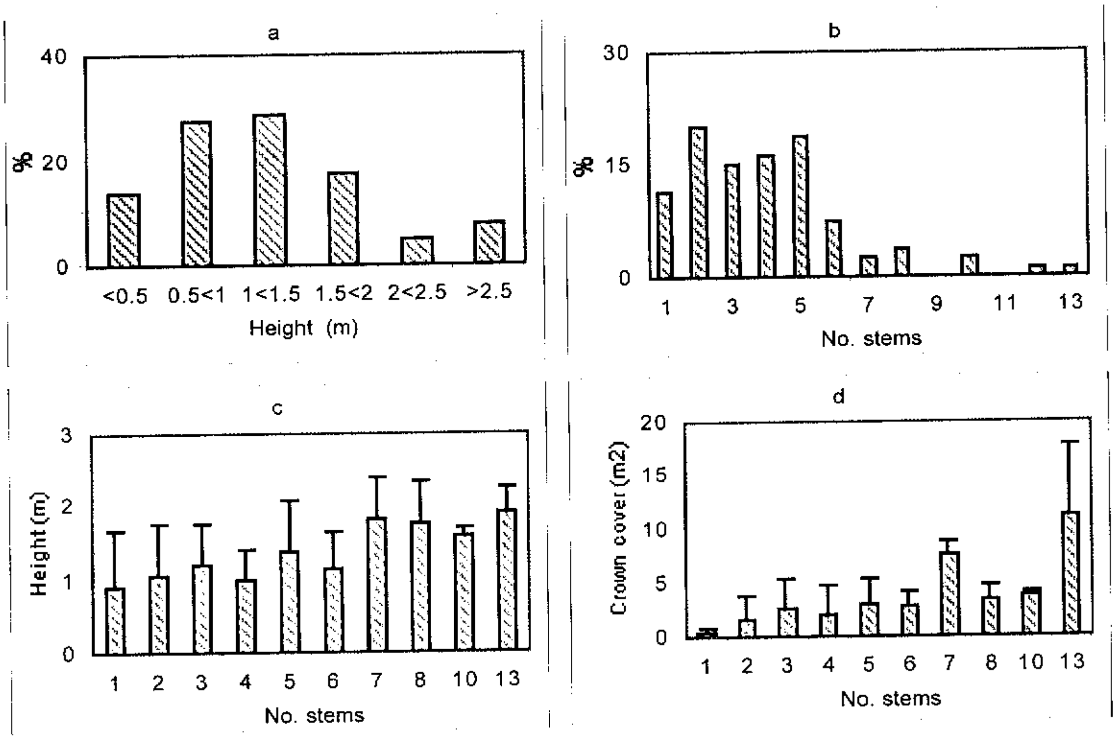

Figure 15. Population and dimension characteristics of *Acacia prainii* (n = 81). (a) Height frequency distribution (%), (b) No. of stem frequency distribution (%), (c) Mean height by number of stems, (d) Mean crown cover by number of stems. Bars represent standard errors.

Table 17. Dimensions of *A. prainii* (*n = 81). Standard deviations in brackets.

	No. stems	Height (m)	Crown cover (m^2)
Mean (SD)	4.2 (2.7)	1.2 (0.7)	2.5 (1.9)
Maximum	13	2.7	17.3
Minimum	1	0.2	0.3

*n = 81 (from 32 sampling points + 49 in quarter)

A. prainii had up to 13 stems per plant (Figure 15b), with the mean number of stems per plant being 4.2. Of 81 plants measured, only 11% had a single stem. Of those with multiple stems, more than 80% had 2-6 stems per plant, that is, number of stems rarely exceeded 6 per plant. Generally, plants with more stems are taller and have more crown cover (Figures 15c and d). It is possible that plants initiate a new stem after attaining a particular height or age. Plants of *A. prainii* have distinctive shapes, such as linear regression. Linear regressions between: number of stems (Ns) and plant height (Ph), Ph = 0.813 + 0.0950 Ns, F 13.94, $P < 0.001$; number of stems and crown cover (Cc), Cc = - 0.168 + 0.671 Ns, $F = 39.74$, $P < 0.001$; and plant height and crown cover: Cc = -1.60 + 3.49 Ph, $F = 92.87$, $P < 0.001$ all gave strong relationships.

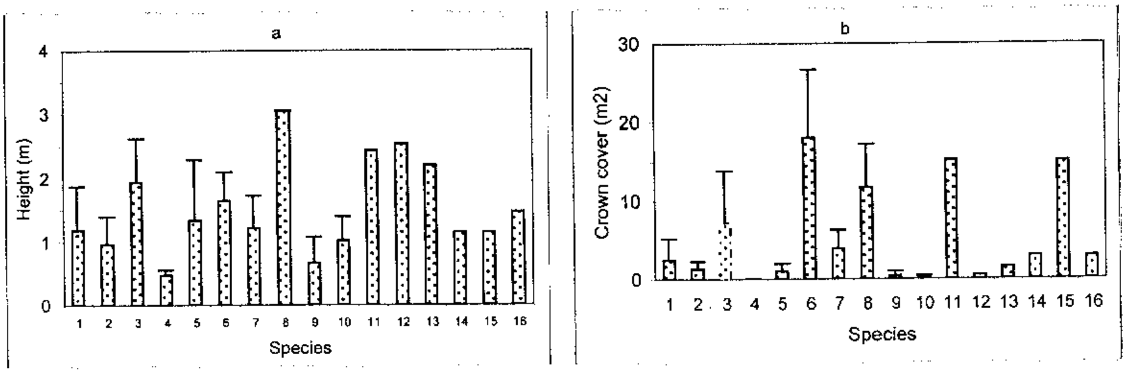

Figure 16. Mean height and crown cover of woody species associated with *A. prainii*. a. Mean heights, b. Mean crown covers. Species numbers as given in the first column of Table 18. Bars represent standard errors.

Fifteen other woody species are associated with the *A. prainii* population (Table 18). The association is characteristic of an open, low shrubland. Eight of the species present are in the genera *Dodonaea, Acacia* and *Melaleuca,* and are mainly low shrubs of *A. prainii*, *D. viscosa*, *M. macronychia*, *D. inaequifolia* and *H. glomerosa*. Those 5 species comprise about 80% of the association. In this association there are no tall trees. *M. eleutherostachya*, *A. huegeliana*, *A. sessilispica* and *A. acuminata* are the taller plants of the area (Figure 16a), and while *A. prainii* is subordinate, it is not confined to a lower canopy as it is normally in the open. Five species have significant cover (>5%) in this association (Figure 16b), however, of these five species only *M. macronychia* is present at a high density (11.7%). Other densities are <3%, where plants are rarely found or are scattered over the landscape. *A. prainii* appears to grow well in the vicinity of *D. viscosa*, *M. macronychia*, *D. inaequifolia* and *H. glomerosa*. These species are characteristic of seasonally moist areas and may benefit from nutrient materials leached from the rocks higher in the landscape.

Table 18. Structure and composition of the woody perennial species associated with *A. prainii* (From a point quarter survey of 32 sampling points).

No.	Species	Mean height (m)	No. plants	Mean crown cover (m^2)	Density (%)	Dominance (%)	IV
1	*Acacia prainii*	1.18	49	2.43	38.28	2.88	41.16
2	*Dodonaea viscosa*	0.96	25	1.31	19.53	1.55	21.08
3	*Melaleuca macronychia*	1.94	15	7.25	11.72	8.57	20.29
4	*Hibbertia glomerosa*	0.47	8	0.04	6.25	0.05	6.30
5	*Dodonaea inaequifolia*	1.33	11	0.93	8.59	1.10	9.70
6	*Calothamnus asper*	1.64	3	18.02	2.34	21.31	23.66
7	*Grevillea paniculata*	1.22	5	3.93	3.91	4.65	8.56
8	*Melaleuca eleutherostachya*	3.05	2	11.68	1.56	13.82	15.38
9	*Atriplex nummularia*	0.66	2	0.43	1.56	0.51	2.07
10	*Alyxia buxifolia*	1.02	2	0.21	1.56	0.25	1.81
11	*Acacia sessilispica*	2.43	1	15.19	0.78	17.97	18.75
12	*Allocasuarina huegeliana*	2.53	1	0.45	0.78	0.54	1.32
13	*Acacia acuminata*	2.2	1	1.59	0.78	1.89	2.67
14	*Acacia hemiteles*	1.15	1	3.00	0.78	3.55	4.33
15	*Eucalyptus loxophleba*	1.15	1	15.13	0.78	17.89	18.67
16	*Santalum spicatum*	1.47	1	2.94	0.78	3.48	4.26
	SUM		128	84.56	100	100	200

3.3.3. *Acacia fauntleroyi*

At SRNR, *A. fauntleroyi* occurs in small populations of limited distribution. These are found in narrow strips of land at the base of granite rocks. The mean distance between plants of 15.5 m gives a notional density of 41.6 plants/ha. Plants grow in sandy loam or fine sandy loam soils, where the mean soil depth is 26.3 cm (SD±2.8). Of 29 plants measured, *A. fauntleroyi* had a mean height of 2.4 m (SD±1.1), a crown depth of 1.7 m and a crown cover of 3.4 m^2 (Table 19). The maximum height was 5.2 m and the minimum was 0.3 m.

The normal distribution of plant height suggests that new seedlings are added regularly (Figure 17a). Senescing adults are presumed to be continually replaced by movement through the height classes. Plants tend to have a short bole height free of branches, with branching occurring beyond a bole height of about 0.8 m from the ground. Some 70% of all *A. fauntleroyi* plants were single stemmed or had a single main stem (Figure 17b). The remaining 30% were multiple-stemmed with between 2-6 stems.

Table 19. Dimensions of *A. fauntleroyi* (*n = 29). Standard deviation in brackets.

	No. stems	Height (m)	Bole height (m)	Crown depth (m)	Crown cover (m^2)
Mean (SD)	1.7 (1.3)	2.4 (1.1)	0.8 (0.7)	1.7 (0.6)	3.4 (3.9)
Maximum	6	5.2	3.3	2.8	15.2
Minimum	1	0.3	0.2	0.7	0.4

*n = 29 (from 23 sampling points + 6 in quarter)

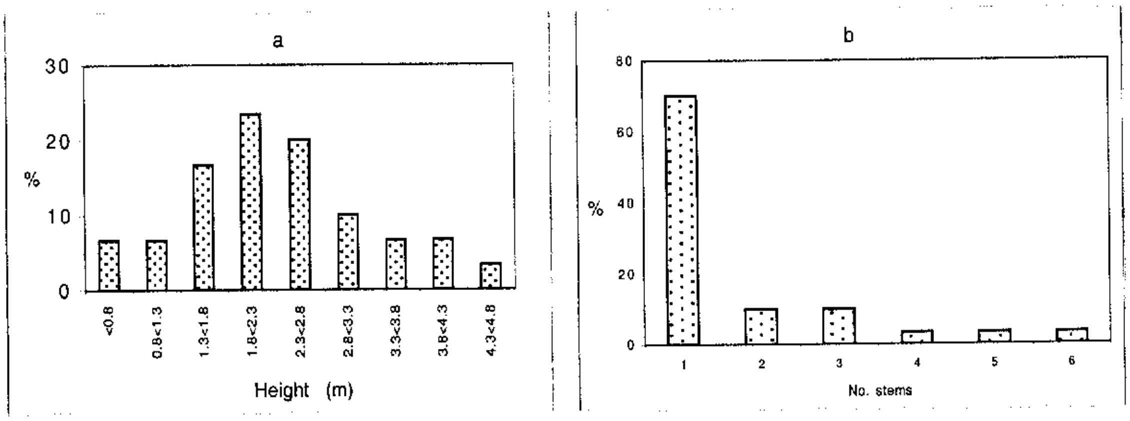

Figure 17. Population characteristics of *A. fauntleroyi* (n = 29). a. Height frequency distribution (%), b. No. of stems frequency distribution (%).

Linear regression reveals that plant height is not related to the number of stems ($P = 0.552$). Plants with more than 1 stem (Ns) have larger crown cover (Cc), $Cc = -0.575 + 2.32\ Ns$, $F = 46.08$, $P = <0.001$. Taller plants (Ph) also have larger crown cover, $Cc = -0.09 + 0.0148\ Ph$, $F = 5.28$, $P = 0.029$). The relationships between plant height and soil depth ($P = 0.150$) and soil depth and crown cover ($P = 0.630$) are not significant.

Eleven other woody species are associated with the *A. fauntleroyi* population (Table 20). The association produces an open low shrubland, mainly comprised of low shrubs of *D. viscosa*. Frequent associates are *D. viscosa*, *L. erubescens*, *H. verrucosa*, *B. elderana* and the perennial grass *Spartochloa scirpoidea*. Generally, *A. fauntleroyi* does not grow as an understorey plant. In this association, *A. fauntleroyi* forms the middle height (Figure 18a), and the tallest plant is *A. lasiocalyx*. The highest crown covers are attained by *A. lasiocalyx* and *Calothamnus asper* (Figure 18b). However, both these species are present at low densities.

Table 20. Structure and composition of the woody perennial species associated with *A. fauntleroyi* (From a point quarter survey of 23 sampling points).

No.	Species	Mean height (m)	No. plant	Mean crown cover (m^2)	Density (%)	Dominance (%)	IV
1	*Dodonea viscosa*	1.20	31	0.97	33.70	3.48	37.18
2	*Acacia lasiocalyx*	3.88	2	7.80	2.17	28.06	30.24
3	*Melaleuca hamulosa*	1.59	6	1.54	6.52	5.53	12.05
4	*Hibbertia verrucosa*	0.58	11	0.11	11.96	0.41	12.36
5	*Baeckea elderana*	0.82	10	0.56	10.87	2.02	12.89
6	*Allocasuarina huegeliana*	2.71	6	1.17	6.52	4.20	10.72
7	*Acacia fauntleroyi*	2.40	6	1.20	6.52	4.31	10.83
8	*Leptospermum erubescens*	1.90	16	2.71	17.39	9.75	27.14
9	*Calothamnus asper*	2.51	1	9.07	1.09	32.66	33.75
10	*Halgania viscosa*	0.68	1	0.17	1.09	0.60	1.685
11	*Acacia prainii*	2.40	1	1.96	1.09	7.05	8.14
12	*Boronia ternata*	1.50	1	0.53	1.09	1.92	3.01
	SUM		92	27.78	100	100	200

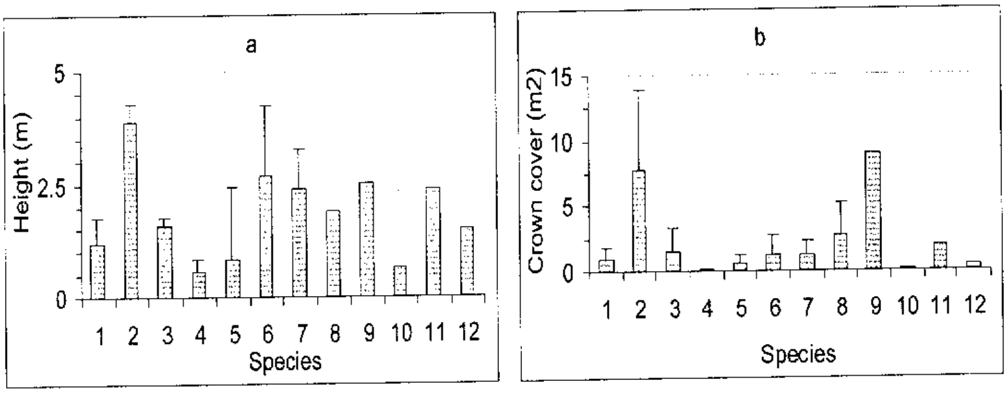

Figure 18. Mean height and crown cover of woody species associated with *A. fauntleroyi*. a. Mean heights, b. Mean crown covers. Species numbers as in column 1 of Table 20. Bars represent standard error.

3.3.4. *Acacia hemiteles*

A. hemiteles forms large populations of high density and relatively wide distribution. It commonly occurs as an understorey plant in *Eucalyptus* woodland, however it is also present in open shrubland, except at the rocks and areas that seasonally flood. The mean distance between plants of 4.6 m implies that 472.6 plants/ha of this understorey shrub are present in eucalypt woodland. *A. hemiteles* grows in various soil types; three soil types recorded were sandy clay loam, clay loam and sandy loam. These soils are grey or grey-brown in colour. About 39% of *A. hemiteles* was found in sandy loam, 32 % in clay loam and 28% in sandy clay loam. Soils were relatively shallow (mean 8.3 ± 3.23 cm, n = 45).

Table 21. Dimensions of *A. hemiteles* (*n = 59). Standard deviations in brackets.

	No. stems	Plant height (m)	Crown cover (m^2)
Mean (SD)	4.4 (2.1)	1.3 (0.5)	2.2 (1.8)
Maximum.	10.0	2.9	7.2
Minimum.	1.0	0.6	0.3

*n = 59 (from 45 sampling points + 14 in quarter)

The mean height of *A. hemiteles* was 1.3 m (SD ± 0.5, n = 59), the maximum height was 2.9 m and the minimum height 0.6 m (Table 21). Seedling stages were not found and recruitment is poor. Some 65% of the measured plants are 1-2 m tall (Figure 19a), with only few (<5%) more than 2 m tall. *A. hemiteles* has between 1 and 10 stems per plant, with a mean of 4.4 stems (Figure 19b). Most of the plants are multi-stemmed with only 8% having single stems. Of the plants with multiple-stems, 28% had 3 stems per plant. The form of this shrub is not multi-stemmed so much as a shrub, with frequent forking/branching near ground level. No one branch assumes apical dominance. This form is well adapted for a plant that has a sub-ordinate role in relation to very tall *Eucalyptus* trees.

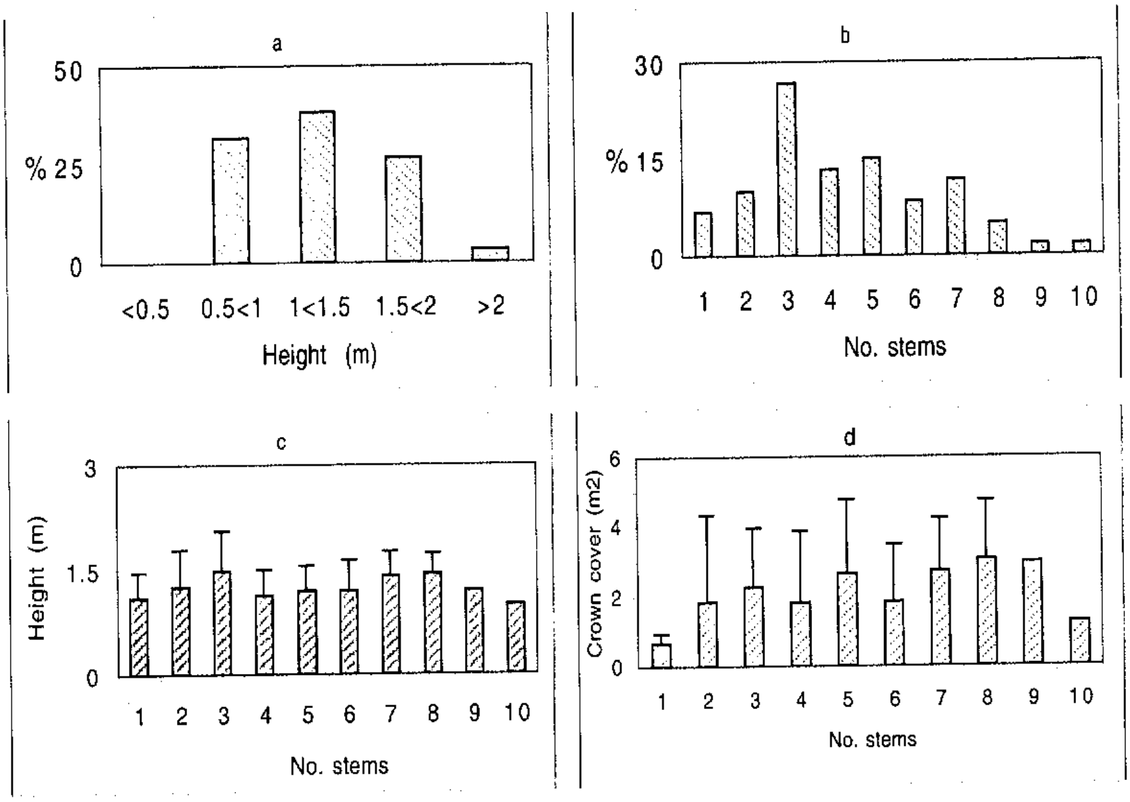

Figure 19. Population characteristics of *A. hemiteles* (n = 59). a. Plant height frequency distribution (%), b. Frequency distribution of no. stems per plant (%), c. Mean height vs. No. stems per plant, d. Mean crown cover (m^2) vs. No. stems per plant. Bars represent standard errors.

There is no apparent relationship between mean height (P = 0.991) and the number of stems per plant or crown cover (P = 0.147), (Figure 19cd). This presumably reflects that the plant is a shrub, not a tree. However, crown cover (Cc) and plant height (Ph) are strongly related (Cc = - 1.08 + 0.0251 Ph, F = 38.10, $P < 0.001$). Taller plants have greater crown cover. Plant height and soil depth (Sd) are not related (P = 0.297), however, crown cover and soil depth are related (Cc = 0.801 + 0.166 Sd, F = 5.71, P = 0.020). Presumably, in deeper soil, plants tend to develop a larger crown cover. The number of stems and soil depth are not related (P = 0.908). In comparison with the three previous *Acacia* associations (Section 3.3.1-3.3.3), the *A. hemiteles* association is confined to relatively dry, hard, poorly drained, shallow soil (± 8 cm). In the three other *Acacia* associations, the soils are relatively moist and deep (22-26 cm). *A. hemiteles* commonly grows in sandy clay loam or clay loam, while the three other associations are commonly found in sandy loam and fine sandy loam soils.

Fifteen other species are present in association with *A. hemiteles* (Table 22). Samples were taken in an area where the *Eucalyptus* overstory component was gimlet (*Eucalyptus salubris*), which is moderately dense woodland with a mixed shrub understorey, mainly of the low shrubs *Olearia muelleri* and *Acacia erinaceae.* Those two species comprise more than 50% of plant density. The upper canopy, taller trees are *Eucalyptus* species (*E. salubris* and *E. capillosa*), and these have large crowns. Elsewhere in the vicinity, salmon gum (*Eucalyptus salmonophloia*) forms the upper canopy. Intermediate level plants include *A. acuminata* and *E. aphyllus. O. muelleri, A. erinaceae* and *A. hemiteles* dominate the lower canopy or understorey (Figure 20a), with a considerable presence of the grass species *Austrostipa elegantissima.* Most of the canopies comprised of *E. salubris* and *E. capillosa* (Figure 20b); those two species accounted for more than 80% of the crown cover.

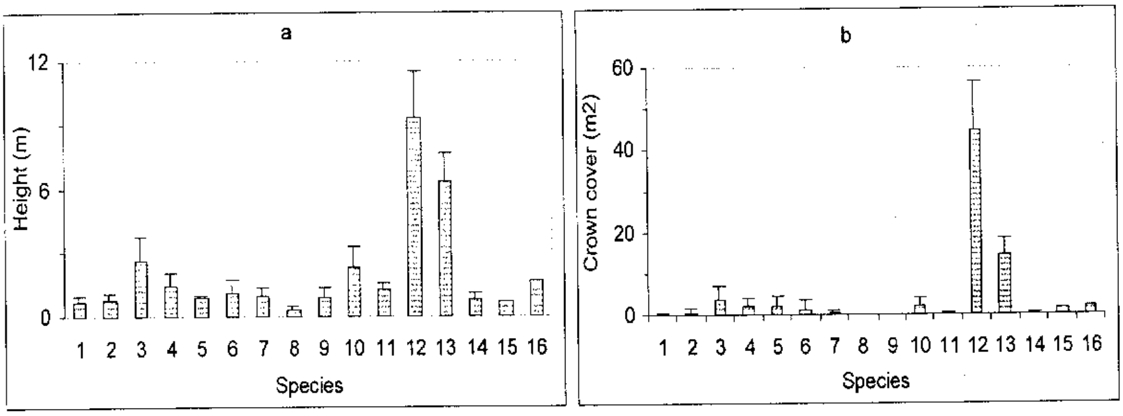

Figure 20. Mean height and crown cover of woody species associated with *A. hemiteles*. a. Mean heights. b. Mean crown cover. Species numbers as in column one of Table 22. Bars represent standard errors.

Table 22. Structure and composition of the woody perennial species associated with *A. hemiteles* (From a point quarter survey of 45 sampling points).

No.	Species	Mean height (m)	No. plant	Mean crown cover (m^2)	Density (%)	Dominance (%)	IV
1	*Olearia muelleri*	0.70	60	0.34	33.52	0.38	33.90
2	*Acacia erinacea*	0.79	42	0.60	23.63	0.67	24.29
3	*Acacia acuminata*	2.58	14	3.41	7.69	3.77	11.47
4	*Acacia hemiteles*	1.46	14	2.11	7.69	2.33	10.03
5	*Melaleuca macronychia*	0.84	3	2.07	1.65	2.28	3.93
6	*Alyxia buxifolia*	1.09	13	1.11	7.14	1.22	8.37
7	*Cassia nemophila*	0.92	7	0.43	3.85	0.48	4.32
8	*Westringia dampieri*	0.33	10	0.05	5.49	0.06	5.55
9	*Hakea invaginata*	0.85	2	0.08	1.10	0.09	1.19
10	*Exocarpus aphyllus*	2.32	3	1.88	1.65	2.08	3.73
11	*Grevillea paniculata*	1.28	2	0.46	1.10	0.51	1.61
12	*Eucalyptus salubris*	9.32	2	44.10	1.10	66.45	67.55
13	*Eucalyptus capillosa*	6.33	3	14.14	1.65	15.63	17.28
14	*Dodonaea stenozyga*	0.77	3	0.26	1.65	0.29	1.94
15	*Solanum nummularium*	0.66	1	1.33	0.55	1.47	2.02
16	*Santalum spicatum*	1.67	1	2.07	0.55	2.29	2.84
	SUM		180	90.45	100	100	200

3.3.5. Similarities and diversity of woody perennial species associated with four *Acacia* species

The similarity (Ss) value between species found in association with the four *Acacia* species examined varied between 0 and 0.38 (Table 23). The most similar associations were *A. lasiocalyx* and *A. prainii* (0.38), while the associations *A. fauntleroyi* and *A. hemiteles* were 100% dissimilar. Of the four associations examined, the *A. hemiteles* association had the least evenly distributed component species. This association was also less diverse, compared to the remaining associations (Table 24). Apparently, the eucalypt woodland in the area sampled has few species present (Table 22).

Table 23. A similarity (Ss) half-matrix of woody species associate with four *Acacia* species.

Association	*A. lasiocalyx*	*A. prainii*	*A. fauntleroyi*	*A. hemiteles*
A. lasiocalyx	*	-	-	-
A. prainii	0.38	*	-	-
A. fauntleroyi	0.33	0.22	*	-
A. hemiteles	0.15	0.27	0.00	*

Table 24. Comparison of diversity of woody species associate with four *Acacia* species.

Association	No. species	Diversity (H′)	Evenness (J)
A. lasiocalyx	17	2.37	0.84
A. prainii	16	2.42	0.87
A. fauntleroyi	12	2.24	0.90
A. hemiteles	16	2.14	0.77

3.4. Discussion

Frequency distribution of plant size in *A. lasiocalyx* suggests no recent seedling establishment has occurred. Distribution of size classes shows a lack of normality, suggesting that several cohorts may be present, representing different establishment periods. Lack of normality may reflect the spatial distribution of plants in particular eroded "holes" or soil pockets at the rock. Several genotypes may have formed and this could affect variation in success of recruitment at different sites. Lack of normality may also represent periods of recruitment failure over the year.

Recruitment may have been affected by the severe droughts of 1991 and 1994 (Figure 2, Chapter 1). Periodic drought may have prevented germination or establishment. About 10% of the plants are less than 1 m tall and 33% are less than 2 cm in stem diameter. These plants are presumably recruits after the heavy rains of 1999 and were therefore 27 months old at the time of measurement. Rainfall in 1999 (597.6 mm) was the heaviest to occur at Westonia in the last 20 years and no month in the year experienced an absence of rain (99 days rain during the year). As these plants are associated with rock and the soils are generally shallow in these areas, it is almost certainly the case that recruitment depends on run-off water from the rocks.

Continuous recruitment seems to be the pattern in *A. prainii*, with both seedling and sapling stages represented in this relatively short-lived and small-stature species. Opportunities for germination and establishment of new seedlings may occur each year in the creek-site flood-plain environments where the largest concentrations of this species exist. Even a relatively severe drought in 1994 may not have altered the population of this species unduly. Individual plants may not survive much longer than 5-

10 years as the population is severely affected by the rust fungus *Uromycladium tepperianum*. This is manifest on relatively small plants resulting in physiological disruption and induction of juvenility in foliage. It is probably the main cause of death in older plants of this species. The other *Acacia* at SRNR that appears severely affected by *U. tepperianum* is *A. saligna*. This species is also present in seasonally wet areas watered by the main creek. The gall rust, *U. tepperianum,* is commonly seen on three species of *Acacia* at SRNR. This fungus seems to affect the species in this order of susceptibility (Gathe 1971): Highly susceptible, *A. prainii* (life span <5 yr); moderately susceptible, *A. saligna* (life span 5< 10 yr); and, mildly susceptible, *A. acuminata* (life span > 10 yr).

At SRNR, *A. fauntleroyi* occurs in small populations of limited distribution. They grow near the edges of the main granite rock outcrops, in sites that receive additional water from rain shed across the granite. In March 1997, at the end of summer it was observed that many specimens of *A. fauntleroyi* were dead (Fox pers. comm.); this was presumably caused by the severe drought during the 1996-1997 summer. The last important rain in 1996 was on 7 November 1996 (11.4 mm, Westonia records used). Only 0.5 mm of rainfall fell in December 1996, none in January 1997, and 8.1 mm of rain fell on 20 February 1997. Thus, there was a period of 104 days of very little rain, and a hot day in that summer preceded the mass death of *A. fauntleroyi*. A similar phenomenon was observed 4 years later in March 2001. From 6 September 2000, when 7.4 mm rain fell, the total over the period 7 September to the end of December 2000 (115 d) was only 5.9 mm. Good rain fell in January 2001, but this appears to have come too late, as many plants had already died.

From the rainfall records, between 1990-2001, three similar drought periods could be observed that were presumably sufficient to have induced mass deaths in *A. fauntleroyi*. Besides the two enunciated above, in the period 7 October 1990 to 17 January 1991 (101 d) only 13.4 mm rain fell. By analogy, this is presumed also to have killed many *A. fauntleroyi*. Thus, the small populations of *A. fauntleroyi* that exist at SRNR are affected by droughts that occur periodically. The "population" as a whole may fluctuate with the periodic droughts, killing a number of mature plants that may be about the same age (if not size) and equivalent to "cohorts". That is, they probably established at a time of very moist conditions when the particular environment received adequate run-off to enable growth for sustained periods. It is hypothesised that *A. fauntleroyi* makes its major contribution to growth in the absence of long dry periods. Persistent seed banks of this species are presumed present in the soil, which enable rapid early seedling establishment with the onset of winter rain following summer drought.

In *A. hemiteles,* no seedling stages were found (section 3.3.4) and there was poor recruitment. As seed was produced (Chapter 4, section 4.2) and germinable (Chapter 5, section 5.2), some other non-reproductive factors are presumably involved. As *A. hemiteles* is an understorey species, failure to regenerate could be a result of canopy shade. Dense *Eucalyptus* trees in the *A. hemiteles* association may also strongly influence soil moisture availability. During dry periods, the major factor determining plant growth is the ability of roots to draw water from the soil. *Eucalyptus* species have high water needs which could result in limited growth of the understorey. Grasses may also inhibit the establishment of seedlings or the persistence of new seedlings from one winter to the next year.

In March 1997, Barrett (1997) sowed seed of *A. hemiteles* into a number of spots at the entrance area of SRNR. After the first winter rains of May 1997, some 11 seedlings germinated out of 100 seed sown. However, by October 1997 no seedlings remained and there were no signs of any dead seedlings. It is hypothesised that root competition from the surrounding plants may have prevented survival. Fresh kangaroo droppings were also found in the area, indicating that grazing might also have removed the seedlings. In nature, seedlings may be able to survive in exceptionally moist years or when pre-existing specimens of *A. hemiteles* have died and no longer cause root competition. It is not known whether kangaroos do eat seedlings of *Acacia* from time to time.

Successful recruitment of arid zone shrubs is typically intermittent and seedling mortality is high (Shea, McCormick & Portlok 1979). Each of high seed predation; heavy browsing; herbivore activity; severe competition; poor seedbed and shade from established vegetation could limit seed germination and seedling establishment in the field. High seed predation may result in only a small portion of the seed produced surviving in the soil. For example, a high ratio of seed production to seed storage is found for *Acacia cyclops* in Western Australia (Gill 1984), where seed may be destroyed by insects or birds. Ants, termites and birds may all disperse *Acacia* seed. Parrots, particularly galahs (*Kakatoe roseicapilla*) eat mulga seed (Preece 1971b) and in Arava, Israel, ungulates are the main dispersers of *Acacia raddiata* and *A. tortilis* as they browse the pods and excrete seed in their faeces (Bond, Smythe & Balfour 2001).

Disturbance in the form of browsing is reported to significantly limit recruitment and survival in many African acacias. Heavy browsing has been found to prevent juvenile acacias moving into taller size classes, thus preventing early seedling recruitment (Pellew 1983; Prins & Van der Jeugd 1993; Bond *et al.* 2001). Stem, rather than leaf removal is more important in preventing the promotion of juvenile plants into taller size classes (Pellew 1983; Barnes 2001). Black rhino are important browsers of *Acacia* trees in Africa, they bite off branches up to 25 mm in diameter (Bond *et al.* 2001). At SRNR, rabbits, kangaroos, galahs and parrots are all suspected of defoliating plants. Barnes (2001) found that only *Acacia erioloba* and *A. hebeclada* had green leaves in the open grass in the dry season and this increases the risk of predation. Failure of natural regeneration may be affected by seed, microsite or herbivore limitations (Hulme 1996). In the natural regeneration of many perennials, both predation and microsites may limit plant regeneration (Hulme 1996). Regeneration may become increasingly microsite-limited as populations develop and more intense predation may occur beneath shrubs compared to open sites. Presence of grass also suppresses growth of *Acacia* (Bond *et al.* 2001) and *Acacia nilotica* is unable to establish under canopy shade (Smith & Goodman 1986). Grass layers shade woody seedlings and reduce establishment as they compete for water and nutrients.

The four *Acacia* populations examined differ in associated species, suggesting that the *Acacia* differ in their response to habitats at the small scale. *A. lasiocalyx* grows well with *L. erubescens* and *D. viscosa*. These three species characterise the granite edge vegetation. These species can grow well in the detritic material eroded from granite rocks. *A. prainii* grows well with *C. asper* and *M. macronychia*. These species are characteristic of the vegetation in seasonally wet areas. The main associates of *A. fauntleroyi* are *Dodonea, Hibbertia, Baeckea* and the grass species *S. scirpoidea*. *A. hemiteles* is an understorey species in eucalypt woodland, growing well with *O. muellerii, A. erinaceae* and some perennial grasses e.g. *A. elegantissima*.

A. prainii, A. lasiocalyx and *A. fauntleroyi* species suites occur in relatively high moisture habitats that are related to granite rocks, while the *A. hemiteles* type occurs in dry areas under *Eucalyptus* woodland. *A. hemiteles* appears to be shade tolerant. This species is relatively abundant in *Eucalyptus* woodland. In contrast, *A. lasiocalyx, A. prainii* and *A. fauntleroyi* appear to be sun-loving (heliophytes) and grow well in open shrubland or granite areas. *A. buxifolia, S. spicatum, G. paniculata* and *M. macronichia* are present in both contrasting habitat types. These species presumably possess the ability to persist in both wet and dry areas.

The similarity between species found in association with *A. lasiocalyx* and *A. prainii* is 0.38. These two are the most similar of the four sets of species, based on the occurrence of species among the four *Acacia* associations. In both associations, there are 10 common species present (*A. prainii, A. buxifolia, D. inaequifolia, S. spicatum, H. glomerosa, D. viscosa, A. huegeliana, C. asper, G. paniculata* and *M. eleutherostachya*). However, *A. lasiocalyx* is absent in the *A. prainii* association. This suggests that while *A. lasiocalyx* grows well in soils of high moisture content, it does not grow well in seasonally wet areas, the micro-habitat characteristically occupied by *A. prainii*. The similarity between species found in association with *A. lasiocalyx* and *A. fauntleroyi* is 0.33. In both associations, the 6 common species present are: *A. lasiocalyx, A. prainii, L. erubescens, D. viscosa, A. huegeliana* and *C. asper*. Both *Acacia* species occur in relatively similar microhabitats. However, *A. fauntleroyi* is mainly in strips of shallow soil that run along the edges of granite rock outcrops. In contrast, *A. lasiocalyx* mainly occurs in "rock lagoons" set into the major rocks.

The similarity between species associated with *A. lasiocalyx* and *A. hemiteles* is 0.15. There are only 3 species common to both associations: *A. buxifolia, S. spicatum* and *G. paniculata*. These two species of *Acacia* are unlikely to be found growing together. The similarity between species associated with *A. fauntleroyi* and *A. prainii* is 0.22. In both associations, there are four species commonly present: *A. prainii, D. viscosa, A. huegeliana* and *C. asper*. *A. prainii* is well represented in the *A. fauntleroyi* association, while *A. fauntleroyi* is less likely to occur in the main *A. prainii* microhabitat. There is no similarity between the vegetation associated with *A. fauntleroyi* and *A. hemiteles;* they are 100% dissimilar. The similarity between the vegetation associated with *A. hemiteles* and *A. prainii* is 0.27. In both associations there are four species commonly present (*A. buxifolia, S. spicatum, M. macronichia* and *G. paniculata*). Of the four acacias described, *A. prainii* is of widest distribution. It grows well in association with *A. lasiocalyx* and *A. fauntleroyi,* but is not present in association with *A. hemiteles*.

Generally, the distribution of *Acacia* species at SRNR mainly depends on habitat moisture availability. The distribution of *Acacia* species in the Negev and Sinai was found by Halevy & Orshan (1973) to be related to an adequate water supply during the summer. High temperature is another main factor that controls the spatial distribution of *Acacia* species in that region. *Acacia* trees are restricted to channel beds forming a concentrated vegetation type. In Arava, much *Acacia* tree mortality is caused by an insufficient water supply (BenDavid-Novak & Schick 1997). It is concluded that the trees are sustained by water present in the upper most layer of the alluvium and trees are therefore, predominantly dependent on surface flows. That conclusion is also supported by a survey of *Acacia* tree root systems, while not deep they may extend laterally up to 20 m from the trunk.

CHAPTER 4

ASPECTS OF REPRODUCTION IN *ACACIA* SPECIES

4.1. General introduction

The genus *Acacia* is represented in most biomes in Australia, with some 1165 taxa (Orchard & Wilson 2001a,b). *Acacia* species dominate the woody vegetation of the arid and semi-arid regions but are also well represented in more mesic environments. Sandford Rocks Nature Reserve (SRNR) contains a complex mosaic of exposed granite rock, with shrublands and woodlands. *Acacia* species are locally abundant, generally grow in mixed-species assemblages and clearly play important roles in the associations present. In three years of observations (1998-2001), most *Acacia* flowered in July to September and produced seed in December. An exception was *Acacia jennerae* Maiden; this flowered in March 1999 and 2000. Pods have not been observed. This plant appears to be clonal at this reserve, sprouting from root suckers.

The reproductive capacity or potential of a plant is a critical aspect of plant reproduction. Reproductive capacity of many plants is extremely great and there are large differences between species (Schaal 1980). These differences may be the result of different selective pressures and are related to the ability of a species to persist in time and space (Harper, Lovell & Moore 1970; Harper & White 1974). Reproductive potential or capacity of a plant is of practical concern as it often has an impact on management and recovery strategies. This is especially important when considering the conservation and management of small, isolated, peripheral populations of plant species that are commonly found as remnant vegetation. Such populations may vary in their reproductive capacity due to their size and isolation, resulting in restricted cross-fertilisation and gene flow and adaptation to selfing (Jones & Gliddon 1999). Variation will also arise due to environmental factors, where isolated populations often occur in sub-optimal habitat, necessitating adaptation to survive and reproduce.

In arid environments, flowering plants must overcome many problems for successful reproduction. Factors that may reduce reproduction include a short growing season, extremes of temperature (frost) or moisture availability (flood, drought), low nutrient availability, herbivore activity, humidity, wind at the time of pollination, competition, disease and scarcity of pollinators. All these factors may reduce the possibility of flowering and seed setting in one season (Fitter & Hay 1992; Jones & Gliddon 1999). Reproduction may vary within a reproductive episode due to weather conditions. Late spring frost, winter cold and drought have been proposed as causing fluctuations in reproduction.

In this chapter some aspects of reproduction in *Acacia* species were investigated. I sought answers to these questions: What is the potential reproductive capacity in a given species of *Acacia* and what factors can reduce its potential? Does environmental variation lead to variation among flowering individuals? To what extent do rainfall variables affect *Acacia* reproductive production? Does any temporal variation in pod production occur from year to year?

4.2. Study No. 1. Reproductive potential of *Acacia* species at Sandford Rocks Nature Reserve (SRNR)

4.2.1. Introduction

An upper limit to the number of fruits that can be produced by an individual during a reproductive episode is set by the number of flowers, while an upper limit to the number of seeds is set by the number of ovules within these flowers. The fraction of this reproductive potential that is realised depends upon the number of pollinated flowers, the number of fertilised ovules, fruit/seed predation, weather conditions and the ability of the maternal parent to provide the necessary resources for development (Stephenson 1981).

In the case of *Acacia* reproduction, it could be stated that an upper limit to the number of pods that can be produced during a reproductive episode is set by the number of inflorescences and the number of flowers per inflorescence. Similarly, an upper limit to the number of seeds is set by the number of ovules within the flowers. Therefore, in *Acacia* species, reproductive capacity is dependant on the number of inflorescences, the number of flowers per inflorescence, the number of pollinated flowers, the number of fertilised ovules, the extent of pod and seed predation, weather conditions and the ability of the maternal parent to provide resources for development. These factors may reduce the possibility of flowering and seed set or reduce reproductive capacity.

The resources available for reproduction may vary within reproductive episodes due to weather conditions, herbivory, inter and intra-specific competition and disease (Harper *et al.* 1970; Harper 1977; Stephenson 1980). These factors not only affect the rate of resource assimilation but may also affect stored reserves. Many arid zone plants respond to rain by flowering. Rainfall in the arid zone is erratic and patchy in its distribution and timing but rainfall at particular times of the year will induce flowering (Preece 1971a). For mulga, rainfall in spring and late summer are important for reproduction and rainfall in late summer promotes seed production.

For acorn production, the most parsimonious explanation of annual variation in production is dictated by weather conditions (Sork & Bramble 1993). Weather conditions in certain years promote greater photosynthate production and therefore enable plants to produce more seeds. Norton & Kelly (1988) call this the "resource matching hypothesis" because the tree matches reproductive output to available resources each year. Weather might also determine seed crop size because certain aspects of reproductive biology require specific weather conditions. Several weather factors have been proposed as causing fluctuation in acorn production. These include late spring frost, winter cold, temperature, humidity, and wind at the time of pollination; drought, and high temperature. Within the genus *Quercus*, each species may respond to different environmental factors and species responses may vary among sites (Sork & Bramble 1993).

A 3-yr study was conducted to investigate the potential for natural regeneration of *Acacia* species present at SRNR. Answers were sought to the following questions: 1. What proportion of inflorescences initiated result in formation of pods? 2. Does any temporal variation in pod production occur from year to year? 3. Do leafiness and tree shape affect reproduction?

4.2.2. Methods

In 1999-2000, eight *Acacia* species: *A. acuminata, A. fauntleroyi, A. hemiteles, A. lasiocalyx, A. neurophylla, A. saligna, A. steedmanii* and *A. stereophylla* were examined. Plants were selected depending on the availability of flowering individuals in the area and time in the field. One to three plants and 15 to 35 branches from each plant were labelled. Position of branches was divided subjectively as top (distal), middle (central) or lower (basal) part of the plant crown. Parameters recorded were: numbers of phyllodes and inflorescences per branch. After all pods had matured (or nearly so), plants were re-measured. Calculations were made of the number of inflorescences that set pods and number of pods per inflorescence.

On an earlier occasion (December 1998), pods were harvested to investigate the productive capacity of 13 species (6 of the 8 listed above, plus a further 7: see legend to Figure 24 for names). Number of seeds and aborted or diseased/damaged seeds per pod and dimensions of pods (weight and/or length) were recorded. Seeds were then germinated to obtain percentage germination (details of germination procedure are in Chapter 5, page 119). Number of aborted seeds was determined by counting both empty locules and locules containing aborted seeds. Aborted seeds were seeds that started to develop but died before full maturation. Aborted seed were easily discriminated from the other categories by their size and texture. In this study, an empty locule was considered as an aborted seed. Sound seed were used in germination tests.

Analysis of variance was conducted to test whether reproductive characteristics differ among branch positions. Tukey's family error rate was used to detect any significant differences among means for different positions. The relationships between the number of inflorescences initiated, pods set, pods produced and number of pods per inflorescence and the number of phyllodes were explored using linear regression with number of phyllodes as predictor variables (Y at $P \leq 0.05$ was used to confirm the relationship between the parameters). The relationships between the number of seeds and aborted seeds per pod; and the dimensions of pods were also analysed with regression in the same manner.

4.2.3. Results

4.2.3.1. Comparison of reproductive characteristics in different years

All species sampled were flowering together in the period July-December. However, species differed slightly in the optimum time of flowering. They may share common pollinators and partition time to optimise pollinator availability. The flowering rank among the eight species, based on percentage of open inflorescences and sizes of initial pods was from *A. fauntleroyi* (first), then, in turn to *A. acuminata, A. steedmanii, A. hemiteles, A. neurophylla, A. lasiocalyx, A. stereophylla* to *A. saligna* (last).

Except for *A. hemiteles*, all species produce about the same numbers of inflorescence in 1999 and 2000 (Figure 21a). Reproductive success of each species was calculated based on the relative number of pods produced, number of pods per inflorescence and number of inflorescences initiated that produced a mature pod (b, c, d respectively in Figure 21). This procedure gave these 3 characters sets of values totalling 100 and in sum the reproduction success criterion (RSC) has a maximum value of 300. Based on the percentage of inflorescences that set pods (d), the numbers of pods produced (b) and the number of pods per inflorescence (c), reproduction varied considerably among species and between years. Reproduction was better in 1999 than in 2000 (Figure 21). More inflorescences set pods (d), more pods were produced (b) and there were more pods per inflorescence in 1999 (c).

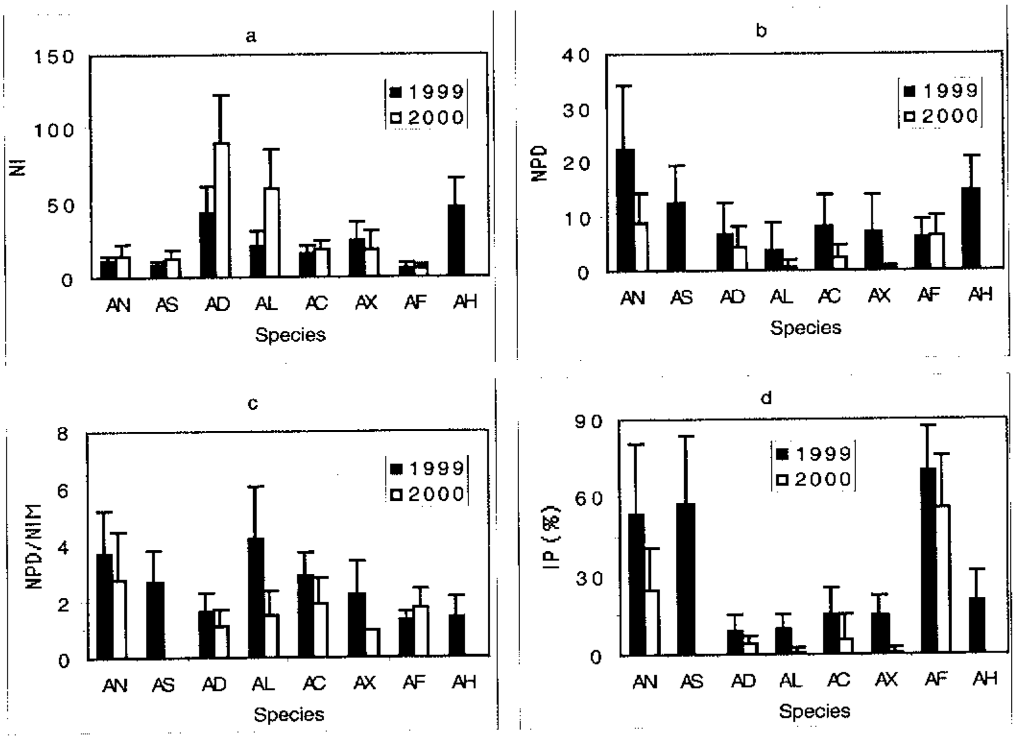

Figure 21. Comparison of *Acacia* reproductive characteristics 1999 and 2000. a: No. inflorescences initiated (NI); b. No. pods produced (NPD); c. No. mature pods per inflorescence (NPD/NIM); d. Percentage of inflorescences that set pods (IP%). Species: AN = *A. neurophylla*; AS = *A. stereophylla*; AD = *A. steedmanii*; AL = *A. saligna*; AC = *A. acuminata*; AX = *A. lasiocalyx*; AF = *A. fauntleroyi*; AH = *A. hemiteles*.

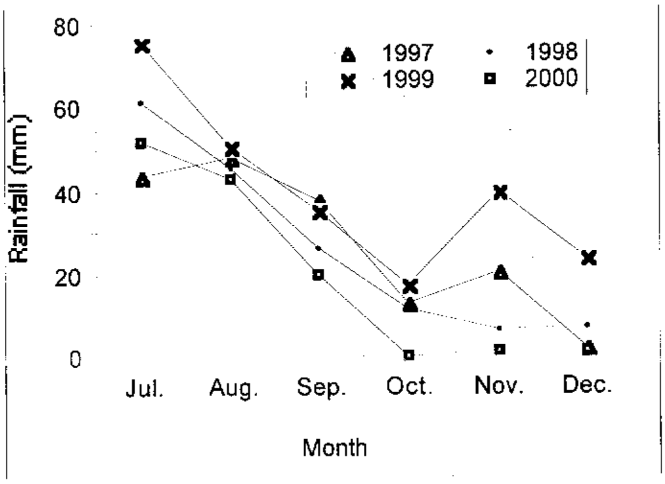

Figure 22. Monthly rainfall at Westonia during the reproduction season (July-December) 1997-2000.

Of the 8 species studied in 1999, the best reproduction (RSC) was attained by *A. neurophylla*, followed by *A. stereophylla* and *A. fauntleroyi* (Table 25). The poorest reproducers were *A. steedmanii*, followed by *A. lasiocalyx* and *A. saligna*. In the year 2000, the best reproduction was in *A. fauntleroyi*, followed by *A. neurophylla* and *A. acuminata.* The poorest reproduction was in *A. stereophylla,* followed by *A. lasiocalyx* and *A. saligna,* while *A. hemiteles* failed to flower.

Reproductive success is presumed to have been affected by lack of rain in 2000 from September onwards (Figure 22). Between July and November 1999, approximately the period of inflorescence initiation to pod development and seed set, 335.3 mm of rainfall fell over 50 days compared with only 117.1 mm over 39 days in 2000. There was no rain in October 2000 at the time of pod development. It is of interest that the rainfall in 1999 (Total: 597.3 mm) was the heaviest recorded at Westonia in the last 20 years (1980-2000).

Although all species suffered from drought in 2000, there were differences in the degree of susceptibility. Of the species studied, *A. fauntleroyi, A. neurophylla, A. acuminata* and *A. steedmanii* were less affected than other species by lack of rain in 2000. *A. stereophylla* was severely affected and failed to develop pods; *A. hemiteles* did not flower and less than 1% of inflorescences developed a pod in *A. saligna* and *A. lasiocalyx* (Table 25).

Table 25. Reproduction success criterion (RSC) and its components for each of eight *Acacia* species (1999 and 2000).

Species	1999				2000			
	NPD	NPD/NI	IP	RSC	NPD	NPD/NI	IP	RSC
A. neurophylla	27.45	18.84	21.31	67.58	38.64	27.18	27.05	92.87
A. stereophylla	15.41	13.73	22.73	51.87	0.00	0.00	0.00	0.00
A. steedmanii	8.48	5.67	3.57	17.72	19.43	11.01	4.49	34.93
A. saligna	4.39	21.49	4.02	29.91	2.27	14.98	0.71	17.96
A. acuminata	9.82	14.75	6.26	30.83	10.47	19.15	6.51	36.13
A. lasiocalyx	8.85	11.28	5.92	26.06	0.85	9.92	0.62	11.39
A. fauntleroyi	7.54	6.74	27.96	42.24	28.34	17.76	60.62	106.72
A. hemiteles	18.07	7.50	8.22	33.79	*	*	*	*
SUM	100	100	100	300	100	100	100	300

NPD = Mean number of pods produced per branch; NI = number of inflorescences; IP = total of inflorescences that set pods; RSC = reproduction success criterion; * = no flowers in 2000.

Of all species studied in 1999 and 2000, *A. neurophylla* attained the best reproduction (Table 26). This species produced most pods and most pods per inflorescence. Some 39% of inflorescences initiated developed a pod; there were 15.5 pods per branch and 3.2 pods per inflorescence. Although growing on well-drained, dry, shallow sandy soils, these plants were not severely affected by the lack of rain in 2000. Only a small population of this species was observed. As seedlings were present, it may be assumed that there were no barriers to recruitment of new seedlings.

The second greatest number of pods produced was in *A. fauntleroyi.* A mean of 63% of inflorescences initiated developed a pod, with 6.3 pods per branch and 1.6 pods per inflorescence. Reproduction in *A. fauntleroyi* was not severely affected by the lack of rain in 2000, presumably because the species is early flowering and plants had developed pods before the severe drought had set in by October-November 2000. This species grows at the apron around edges of granite rock. Although this species produced many pods and seeds, only a few seedlings were found in the field.

Table 26. Two year mean reproduction success criterion (RSC) of 6 *Acacia* species (1999 and 2000).

Species	Inflorescence initiated	NPD	NPD/NI	IP (%)	RSC
A. neurophylla	7.88	40.48	25.21	29.54	95.23
A. steedmanii	40.55	14.71	8.70	4.94	28.35
A. saligna	24.65	5.34	22.42	4.06	31.82
A. acuminata	10.32	13.51	18.89	8.18	40.58
A. lasiocalyx	13.07	9.66	12.58	5.83	28.07
A. fauntleroyi	3.53	16.31	12.19	47.45	75.95
SUM		100	100	100	300

Reproductive legend is as in Table 25; *A. stereophylla* (no pods) and *A. hemiteles* (no flowers) in 2000, excluded from the table.

At SRNR, 2 varieties of *A. acuminata* occur (narrow-terete and broader phyllode types). The taxon studied here was the narrow/terete phyllode type. Of all inflorescences initiated, 11% developed a pod with 5.2 pods per branch and 2.4 pods per inflorescence. Of the *Acacia* species at SRNR, *A. acuminata* has the greatest population and the widest distribution. It is generally found in moister sites, which may explain why this species was less severely affected by drought. The species has good recruitment; many seedlings were observed in the field (Chapter 3, section 3.3.3).

In *A. lasiocalyx,* of all inflorescences initiated, 8% developed a pod with 3.7 pods per branch and 1.6 pods per inflorescence. This species was also drought-affected in 2000 with only 0.6% of inflorescences initiated developing a pod, compared to 15% in 1999. This species grows in clefts or soil pockets among the granite rocks and no seedlings of this species were found in the field. However, some saplings were found, suggesting that seedling establishment does occur in particular periods (Chapter 3, section 3.3.1).

A. steedmanii initiated 67 inflorescences per branch (more than all other species). However, from all inflorescences initiated only 6.6% developed a pod with 5.6 pods per branch and 1.1 pods per inflorescence. This species was less severely affected by drought in 2000, perhaps because it flowers earlier. Plants developed pods during the severe drought in October-November 2000, thus it can be said that drought only slightly affected pod development. This species was found in small numbers and over 3 years of observations, seedlings or small plants (<1 m) were never encountered in the field.

In *A. saligna,* of inflorescences initiated, 5.4% developed a pod with 2.1 pods per branch. This was lower compared with *A. saligna* observed at the FTA, Curtin University of Technology (Section 4.3.3.1.2), where about 13% of inflorescences initiated developed a pod and there were about 12 pods per branch. This species also suffered from drought in 2000 as 10% of inflorescences initiated developed a pod in 1999 but only 0.7% did so in 2000. Although only a few pods were produced by *A. saligna*, the plants have quite good recruitment and many seedlings were found in the field.

For *A. hemiteles,* the reproduction in 1999 saw 48 inflorescences initiated per branch, 21% developed a pod; there were 14.7 pods per branch and 1.5 pods per inflorescence. Low rainfall in May-June 2000 may have inhibited flowering of *A. hemiteles* or more rainfall may be needed to induce flowering. Only 22.5 mm of rain over 9 days occurred in May and June 2000 compared with 152 mm and 22 days in May and June 1999. *A. hemiteles* has a large population and wide distribution. It occurs as an understory species in *Eucalyptus* woodland. Despite the large population, seedlings were very rarely found in the field (Chapter 3, section 3.3.4).

A. stereophylla initiated many inflorescences each year but very few pods and seeds were produced. Only in 1999 did plants produce many pods: 12.6 pods per branch and 57% of inflorescences initiated developed. However, most pods were empty or failed to develop seeds. This species has a localised distribution, occurring in bands at the edges of *Eucalyptus* woodland. Seedlings of this species were not observed in the field.

4.2.3.2. Effect of phyllode numbers and branch positions on reproductivity.

Generally, higher numbers of phyllodes were associated with more inflorescences initiated and more inflorescences that set a pod ($P \leq 0.05$). Numbers of pods per inflorescence were generally not related to the number of phyllodes per branch (Table 27). This result suggests that inflorescence initiation and subsequent pod development are related to the number of phyllodes as donor of resources or affected by resource availability, while number of pods per inflorescence may be determined by plant orthogonal development. High numbers of inflorescences affected by phyllode numbers may be a reflection of inflorescence initiation in axils (angle between phyllode and stem).

Table 27. Significance values of linear regression between reproductive characters in 8 *Acacia* species (combined 1999 and 2000, except* *A. stereophylla* and *A. hemiteles* 1999 only).

Characters/species	AN	AS*	AD	AL	AC	AX	AF	AH*
NI vs NP	<0.001	0.007	0.813	<0.001	0.008	<0.001	0.001	<0.001
NIM vs NP	0.183	<0.001	0.042	0.070	0.754	0.245	0.089	0.092
NPD vs NP	0.573	0.783	0.050	0.198	0.709	0.719	0.002	<0.001
NPD/NIM vs NP	0.366	0.736	0.115	<0.001	0.238	0.204	0.011	0.310

NI = No. inflorescences initiated; NIM = No. inflorescences set pods; NPD = No. pods produced; NPD/NIM = No. mature pods per inflorescence; NP = No. phyllodes. Species legend is as in Figure 21.

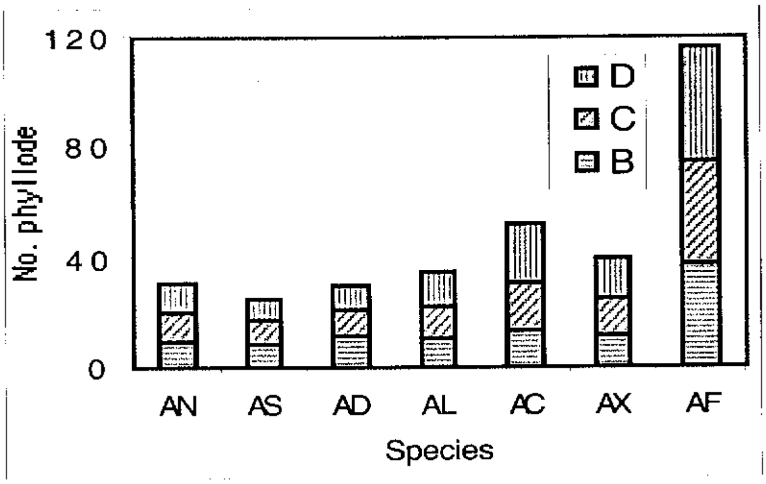

Figure 23. Mean number of phyllodes per branch of 7 *Acacia* species in basal (B), central (C) and distal (D) position of branches (combined 1999 and 2000). Species legend is as in Figure 21.

Table 28. Mean reproductive characters in basal (B), central (C) and distal (D) branch positions, for 7 *Acacia* species (combined 1999 and 2000).

SP	PS	NI	NPD	NPD/NIM	I (%)
AN	B	11.90b	20.25a	3.79	33.20a
	C	11.91b	18.67a	3.95	18.51b
	D	14.85a	15.45b	2.69	17.82b
	P	*	*	ns	*
AS	B	9.36	14.90b	2.79b	23.41b
	C	11.48	41.03a	9.32a	11.43c
	D	10.74	13.00b	2.57b	34.55a
	P	ns	*	*	*
AD	B	94.50a	4.5	0.97	2.6
	C	70.40b	4.82	1.18	2.7
	D	78.27b	5.56	1.46	2.7
	P	*	ns	ns	ns
AL	B	34.04b	0.23b	0.29b	0.4b
	C	44.13a	2.24a	1.05a	3.0a
	D	48.05a	2.97a	2.69a	2.4a
	P	*	*	*	*
AC	B	16.36	4.14b	1.12	6.7b
	C	16.67	10.50a	1.66	20.7a
	D	17.42	0.73c	0.83	4.6b
	P	ns	*	ns	*
AX	B	12.50b	2.43	1.17	4.8b
	C	18.90 a	4.19	1.06	8.2a
	D	25.33a	3.35	0.83	4.2b
	P	*	ns	ns	*
AF	B	9.94b	7.67c	2.53	18.4b
	C	8.51b	10.20b	2.62	20.8b
	D	14.75a	14.40a	3.08	38.3a
	P	*	*	ns	*

Entries with different letters in a column indicate a significant difference between the means using Tukey's family error rate; Significance (*P*), * *P* = ≤ 0.05, ns = not significant. PS = Position (B: basal; C: central; D: distal); NI = mean number of inflorescences initiated; NPD = number of pods produced; I = inflorescences that set a pod. Species (SP) legend is as in Figure 21.

Number of phyllodes per branch was much greater in *A. fauntleroyi* compared to other species (Figure 23). All others had about the same number of phyllodes per branch. Except for *A. stereophylla* and *A. steedmanii*, branches in the distal position generally had slightly more phyllodes than those in the basal position, whereas differences between the basal and central positions were not as great.

In *A. neurophylla*, the number of inflorescences initiated was greater in the distal than in the basal parts of the crowns (Table 28). However, more inflorescences set pods and more pods were produced in the basal position than in the distal position of the crown. In *A. stereophylla*, the number of inflorescences initiated and pods produced were greater in the central position of crowns. It would appear that more pods and more pods per inflorescence may result when fewer inflorescences initiated result in pods, allowing more resources to be available for pod development. In *A. steedmanii,* inflorescences initiated were greater in the basal position, however pods produced did not differ among branch positions. In *A. saligna*, inflorescences initiated and pods produced were greater in the distal position than in the basal position. In *A. acuminata*, the number of inflorescences initiated was slightly greater in the distal position than in the basal position. However, the numbers of inflorescences that set a pod and numbers of pods produced were greater in the central position. In *A. lasiocalyx*, the number of inflorescences initiated was greater in the distal position than in the basal position while the number of inflorescences that set a pod and the number of pods produced were greater in the central position of the plant. In *A. fauntleroyi*, the number of inflorescences initiated and pods produced were greater in the distal position than in the basal position. In general, the number of pods per inflorescence was not affected by position of branches.

4.2.3.3. Seed and pod characteristics

Seed and pod characteristics derived from pods collected in December 1998 suggest that late spring frost, plus lack of rain in October-November 1998 (17.6 mm and 8 days rainfall) probably affected seed development. Most species had low seed weight, with many immature and infected seed, and gave poor germination (Figure 24). Many pods contained empty locules or locules that contained seeds that had started to develop but had died before full maturation.

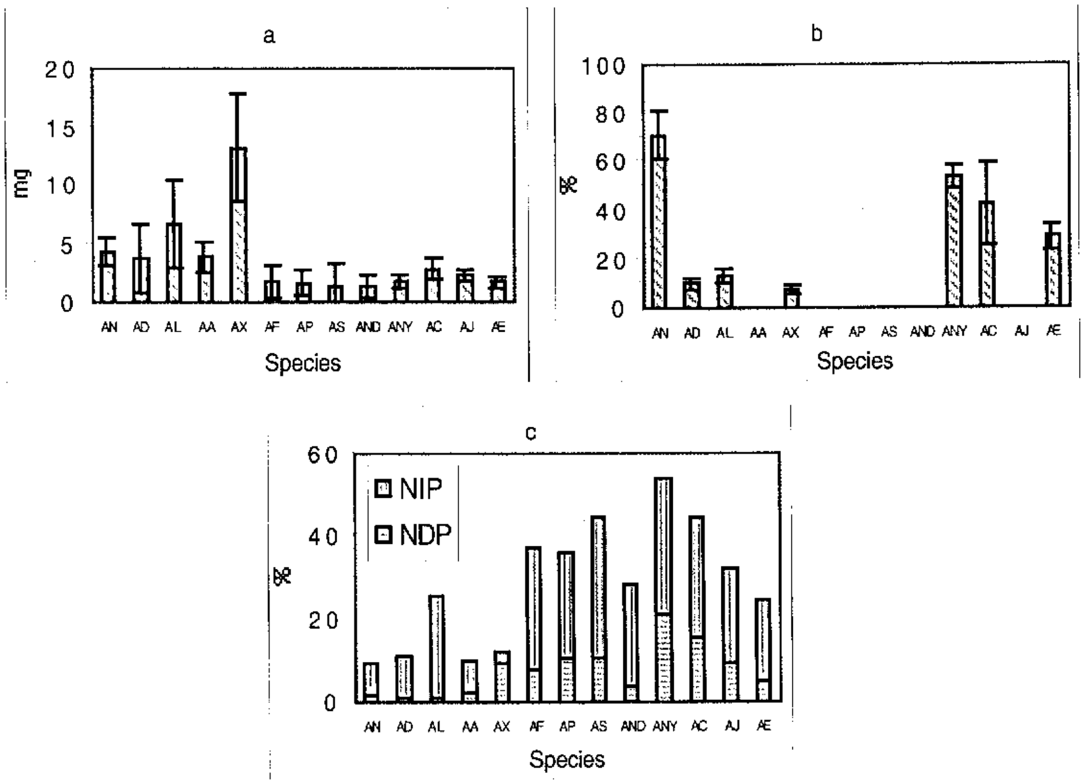

Figure 24. Seed characteristics of 13 species, from pods collected December 1998. a. Mean seed weight (n = 100); b. Germination percentage (n = 4-8, for replicates, 50 seeds per replicate); c. Percentage of immature (NIP) and diseased seed (NDP). Species: AN = *A. neurophylla*; AD = *A. steedmanii*; AL = *A. saligna*; AA = *A. acuminata*; AX = *A. lasiocalyx*; AF = *A. fauntleroyi*; AP = *A. prainii*; AS = *A. sessilispica*; AND = *A. densiflora;* ANY = *A. nyssophylla*; AC = *A. coolgardiensis*; AJ = *A. jibberdingensis*; AE = *A. eremophila.*

A. neurophylla had 9.8 (±2.02) seeds per pod. There was a mean of 1.4% diseased seeds and 8% immature seeds per pod. Mean seed weight was 4.33 ±1.14 mg and 71% of seeds germinated. The pods were 5 cm in length and weighed 54.4 mg. Larger numbers of seeds per pod were associated with longer and heavier pods and more immature seeds were found in these pods (Table 29), suggesting that competition for resources between seeds occurs. Number of seeds per pod was not related to the number of seeds found to be infected. More immature seed was associated with lower pod weight suggesting that some pods may have been unable to acquire sufficient resources.

A. steedmanii had 9.1 (± 1.94) seeds per pod. The pods were 5.8 cm in length and weighed 120.7 mg. Mean seed weight was 3.64 ± 2.93 mg, which was considerably less than the mean weight of seed collected in 1994 (12.01 ± 1.24 mg). Only 10% of the 1998 seeds germinated; this is much lower than the up to 95% germination obtained from seeds collected in 1994 (Chapter 5, section 5.2). There were 1.2% diseased seeds and 10% immature seeds per pod, giving 11.2% of seed aborted. Larger numbers of seeds per pod were associated with longer and heavier pods; more immature seeds occurred in pods with larger numbers of seeds per pod.

Table 29. Significance values of linear regression between reproductive characters in 13 *Acacia* species (from pods collected in December 1998).

Character/species	AN	AD	AL	AA	AX	AF	AP
Lengths pod vs No. seeds/pod	+ <0.001	+ <0.001	*	+ <0.001	+ <0.001	*	*
Weights pod vs No. seeds/pod	+ <0.001	+ <0.001	+ <0.001	+ <0.001	+ 0.005	+ <0.001	+ <0.001
No. seeds immature/pod vs No. seeds/pod	+ 0.047	+ 0.047	0 0.775	+ 0.022	+ 0.040	0 0.246	+ 0.002
Weights pod vs No. seeds immature/pod	- <0.001	0 0.718	0 0.413	0 0.238	- 0.051	0 0.069	- 0.023
Weight pods vs No. seeds diseased/pod	0 0.577	0 0.898	0 0.752	0 0.150	0 0.751	0 0.744	0 0.230
No. seed diseased vs No. seeds immature	0 0.523	0 0.558	0 0.806	0 0.810	0 0.545	0 0.077	0 0.620

Character/species	AS	AND	ANY	AC	AJ	AE
Lengths pod vs No. seeds/pod	*	*	*	*	*	+ 0.019
Weights pod vs No. seeds/pod	+ <0.001	+ <0.001	0 0.808	+ <0.001	+ <0.001	+ <0.001
No. seeds immature/pod vs No. seeds/pod	0 0.702	+ 0.001	+ <0.001	+ <0.001	0 0.244	0 0.452
Weights pod vs No. seeds immature/pod	- <0.001	- 0.003	0 0.711	0 0.302	0 0.458	0 0.303
Weight pods vs No. seeds diseased/pod	+ <0.001	0 0.933	0 0.575	+ 0.0525	0 0.397	+ 0.053
No. seed diseased vs No. seeds immature	+ 0.022	0 0.369	0 0.062	0 0.608	0 0.065	0 0.959

Species legend is as in Figure 24; $P = \leq 0.05$ positive (+) or negative (-) relation; $P > 0.05$ no (0) relation; * = not available.

A. saligna had 6.2 (± 1.6) seeds per pod. The pods weighed 76.8 mg. There were some 1.2% diseased and 24.1% immature seeds per pod. Mean seed weight was 6.64 ±3.79 mg. Some 13.3% of seeds germinated. Larger numbers of seeds per pod were associated with heavier pods. It is noted that many mature plants of *A. saligna* at SRNR were infected by the rust fungus, *Uromycladium tepperianum* (Sacc.) McAlpine.

A. acuminata had 9.2 (± 2.5) seeds per pod and the pods were 6.4 cm in length and weighed 69.6 mg. Mean seed weight was 3.85 ±1.34 mg. This is less than half the weight of the seeds collected in 1996 (8.95 ± 0.47 mg). No seeds germinated, while up to 48% of 1996 seed germinated. There were 2.3% diseased and 7.5% immature seeds per pod. Larger numbers of seeds per pod were associated with longer and heavier pods; there were more immature and infected seeds with larger numbers of seeds per pod. Therefore, competition for resources between seed occurred. Infection in one seed may be associated with infection of more seeds in the same pod.

A. lasiocalyx had 9.85 (± 2.8) seeds per pod. The pods were 10.7 cm in length and weighed 171 mg. Mean seed weight was 13.21 ±8.66 mg. Larger numbers of seeds per pod were associated with longer and heavier pods and more immature seeds were found in these pods. However, it was also found that more immature seed were associated with lower pod weight. There were 9.3% diseased and 2.9% immature seeds per pod. Of the 13 *Acacia* species studied, *A. lasiocalyx* had the third largest number of seeds per pod; the heaviest seeds and pods; and the least number of immature seeds. About 5% germinated (Figure 24b).

A. fauntleroyi had 10.2 (± 2.1) seeds per pod and the pods weighed 144.3 mg. Mean seed weight was 1.78 ±1.29 mg, much lighter than the weight of seeds collected in both 1996 (3.38 ±1.54mg) and 1999 (8.30 ± 2.00 mg). Seeds collected in 1998 were significantly lighter than 1996, and the 1996 seed lighter than 1999 (all $P<0.001$). This species had the third highest number of immature seeds (30%). Larger numbers of seeds per pod were associated with heavier pods; and more immature seeds were associated with lighter pod weight. It was also found that more immature seeds were associated with more infected seeds. No seeds collected in 1998 germinated, while seeds collected in 1999 produced up to 100% germination (Chapter 6, section 6.2).

A. prainii had 7.7 (± 2.3) seeds per pod and the pods weighed 53 mg. Mean seed weight was 1.66 ±1.08 mg, much lighter than the weight of seeds collected in 1996 (3.12

± 1.26 mg) and 1999 (8.00 ± 3.40 mg). There were some 10.6% diseased and 25.3% immature seeds per pod, resulting in 35.9% of the seeds being aborted. Larger numbers of seeds per pod were associated with heavier pods and more of these seeds were immature. More immature seeds were associated with lower pod weight. There was no germination from seeds collected in 1998, while of seeds collected in 1996, up to 81% germinated (Chapter 5, section 5.2) and up to 100% seed germination was recorded from seed collected in 1999 (Chapter 6, section 6.3). At SRNR, most mature plants of *A. prainii* become infected by the rust fungus (*U. tepperianum*). Symptoms include a distinct lack of green foliage and many brown, globose, corky galls on stems, phyllodes, peduncles and fruits. Some inflorescences are also deformed, witches brooms develop and juvenile foliage is produced. The latter symptom suggests hormonal dysfunction (Van den Berg 1978).

A. sessilispica had 6.4 (± 1.5) seeds per pod and the pods weighed 12 mg. Mean seed weight was 1.46 ±1.92 mg, much less than seed collected in 1996 (3.13 ± 0.83 mg). There were some 10.7% diseased and 33.8% immature seeds per pod resulting in 44.5% of seeds being aborted. Of all *Acacia* species investigated, *A. sessilispica* had the highest percentage of immature seeds and no seeds collected in 1998 germinated. Larger numbers of seeds per pod were associated with heavier pods. More immature seed were associated with lower pod weight. More infected seed was associated with heavier pods and more immature seed with more infected seeds.

A. densiflora had 5.7 (± 1.7) seeds per pod and the pods weighed 21 mg. Mean seed weight was 1.30 ±1.00 mg, much less than the weight of seeds collected in 1996 (2.84 ±0.47mg). There were some 4.0% diseased and 24.4% immature seeds per pod. Larger numbers of seeds per pod were associated with heavier pods and more immature seed. More immature seeds were associated with lower pod weight. Seeds collected in 1998 did not germinate, while up to 79% of seeds collected in 1996 germinated.

A. nyssophylla had 10.6 (± 2.0) seeds per pod and the pods weighed 50.7 mg. Mean seed weight was 1.78 ±0.59 mg and 54% of seeds germinated. There were some 21.2% diseased and 32.6% immature seeds per pod. Of all *Acacia* species studied, *A. nyssophylla* had the greatest numbers of immature and infected seeds, with a total of 53.8% seeds aborted. Greater numbers of seeds per pod were associated with more immature seeds. More immature seeds were associated with more seeds being infected.

A. coolgardiensis had 8.5 (± 2.3) seeds per pod and the pods weighed 35.3 mg. Mean seed weight was 2.76 ±0.87 mg and 42.9% of seeds germinated. There were some 15.3% diseased and 29.1% immature seeds per pod. This species had the third highest number of immature seeds (44.4% of the seeds aborted). Greater numbers of seeds per pod were associated with heavier pods and more immature seeds. More seed infected was associated with heavier pods.

A. jibberdingensis had 7.5 (± 1.7) seeds per pod and the pods weighed 19.9 mg. There were some 9.5% diseased and 22.5% immature seeds per pod. Mean seed weight was 2.29 ±0.43 mg. There was no germination from seeds collected in 1998. Greater numbers of seeds per pod were associated with heavier pods and more immature seeds were associated with more infected seeds.

A. eremophila had 8.2 (± 1.6) seeds per pod. The pods weighed 16.4 mg and they were 4.4 cm in length. Mean seed weight was 1.67 ±0.52 mg and 29% of seeds germinated. There were some 5% diseased and 19.5% immature seeds per pod. Greater numbers of seeds per pod were associated with heavier and longer pods. More infected seed were found to be associated with heavier pods.

4.2.4. Discussion

4.2.4.1. Reproductive characteristics of *Acacia* species between years

A reproductive success criterion (RSC) of each *Acacia* species was calculated based on the relative numbers of pods produced, pods per inflorescence and inflorescences initiated that produced a mature pod. This procedure suggests that reproduction varies considerably among species and between years. Reproduction was generally better in 1999 than in 2000. It appears that not only is good rainfall an important requirement for flowering, but it is critical for good fruit set in many *Acacia* species, since all species suffered from the drought of 2000 but produced good pod numbers in 1999. It seems that a wet winter is required to induce flowering (inflorescence formation) and that further rain is required after flowering to promote pod development and good seed set. In the absence of the latter, a proportion of pods will dry off without attaining good seed set. Less reproduction in 2000 than in 1999 is also reported by Yates & Broadhurst (2002) in two *Acacia* species (*A. aprica* and *A. cochlocarpa*) from southwest WA.

Other studies in a range of species suggest that a general response of flowering to rainfall occurs. Morgan (1998) suggests that rainfall stress is an important overriding determinant of plant fecundity. Preece (1971a, b) has found that irrigation stimulates heavier flowering and fruiting in *Acacia aneura* F. Muell. ex Benth. Davies (1968) reports that a certain amount of rainfall will stimulate flowering in arid zone species but more rainfall is necessary for good seed set. Porter (1978) notes that cool, wet winters favor flower and bud formation in spring for *Eucalyptus sideroxylon* A. Cunn. ex Woolls. For Myrtaceous species generally, Law *et al.* (2000) observe that high autumn rainfall is usually followed by prolific flowering in late spring. Pook, Gill & Moore (1997) report flower buds and fruits of *Eucalyptus maculata* Hook in southern NSW are destroyed by severe drought.

In a comprehensive glasshouse study on faba bean, Xia (1997) showed that water stress applied in the period between pod development and full pod set reduced seed yields by up to 45%, while water stress imposed after the flowering period reduced pod and seed number per plant up to 38%. That study showed that drought during pod-filling significantly reduces seed weight compared to the un-stressed control. According to Mwanamwenge *et al.* (1999), the early podding stage of development is the most sensitive to water deficit in faba bean. Similarly, Xia (1994) reduced pod set by imposing water deficits, particularly during the reproductive phase due to the abortion of flowers and small pods. The precise stage of generative development that is most sensitive to drought in *Acacia* species awaits further investigation.

Although all species suffered from the drought in 2000, there were differences in degree of susceptibility. *A. fauntleroyi, A. neurophylla, A. acuminata* and *A. steedmanii* were the least affected. Of these, *A. fauntleroyi, A. acuminata* and *A. steedmanii* may avoid drought damage to some extent because they flower earlier. Only *A. neurophylla* seems to have considerable tolerance to drought. *A. stereophylla* was severely affected and failed to develop pods. The explanation for poor seed set, even in 1999, at the time of relatively heavy rain is not known. It is possible that a combination of inadequate pollination and embryo abortion due to selfing may have affected seed quality, as the population size is relatively small. Species most affected by the severe drought of 2000 included: *A. hemiteles* which did not flower; only 0.6% and 0.7% of inflorescences developed a pod in *A. lasiocalyx* and *A. saligna* respectively. *A. hemiteles* may be especially drought-sensitive and it is likely that for this species, a wet winter is necessary to produce new shoot growth. Observations in the field suggest that floral buds are produced only on the new shoot growth.

Apart from *A. stereophylla*, there was no apparent effect of population size on seed set and pod development. In most species, only small fractions of inflorescences initiated developed to a pod. In *Acacia brachybotrya* Benth. (central New South Wales), Cunningham (2000) found that habitat fragmentation was associated with a decline in pollination and subsequent fruit set. Low reproduction obtained in this study could be associated with the plants present being in fragmented habitats. The reserve is relatively small and surrounded by cleared farmland. Low seed production, coupled with small population size may result in seed production falling below a threshold level necessary to maintain population size.

For some species such as *A. steedmanii, A. fauntleroyi, A. neurophylla* and *A. lasiocalyx*, seed set appears sufficient to replace senescing adults but recruitment (seedling establishment) does not occur every year. These species had nil to very few seedlings observed in the field. Natural regeneration failure may be due to high seed predation, unsuitable seedbed and competition from established vegetation. In order to maintain these populations, it may be necessary to provide conditions advantageous to seedling recruitment as an important component of any conservation strategy; if not, local extinction of some of the small populations may occur. An obvious artificial strategy is to burn small areas, in different places, from time to time.

Prof Fox and I were walking over the rocks (SRNR) on November 25th 1999. At the hottest time of the day, we observed from a distance a plume of smoke that indicated a fire. This may have been a local lightning strike or the result of the sun's rays striking a shard of glass; 28 months later the following regeneration was observed (on March 19th 2002): *Acacia lasiocalyx, A. prainii, A. fauntleroyi*; some genera of *Dodonea, Melaleuca* and *Leptospermum*; and, perennial grass *Spartochloa scirpoidea* has regenerated.

4.2.4.2. Effect of phyllode and branch positions on reproduction.

The number of phyllodes per branch affected plant reproductivity. Plants bearing more phyllodes initiated more inflorescences; more inflorescences set pods; flowering was earlier; and, fewer inflorescences dried off. These observations suggest that leaves/phyllodes donate carbohydrates (and nutrient) to fruits (Hocking & Pate 1977) and resources tend to flow into fruits from the nearest phyllodes (Mooney 1972). Preston

(1999) noted that current assimilates flow from a source leaf into the nearest most active sink that has a direct vascular connection to the source leaf (Watson & Casper 1984; Wardlaw 1990). Stephenson (1980) found that energy necessary to develop and mature fruits on *Catalpa speciosa* Warder comes from leaves on the same branch that bears an infructescence. Leaves are a source of carbohydrates that may be expended on flowering, whereas reproductive structures may be significant resource sinks (Stephenson, Devlin & Horton 1988). Therefore, in *Acacia* species any damage to phyllodes caused by disease or herbivory could reduce primary resources and this would be reflected in reduced plant reproductivity.

Branch position also affected plant reproductivity. Generally, those branches in the upper part of the crown bear heavier inflorescences. However, the pods that develop in a particular species tend to be present in greater numbers at central parts of the crown. Generally, in *Acacia* species flower production is virtually confined to new shoots produced after the previous season. Only plants with abundant new shoots can bear many flowers. It is proposed that when lower parts of the crown initiate fewer new shoots than the upper parts, fewer flowers are initiated in the lower crown. More pods develop in the central than distal parts of the crown. Fewer inflorescences initiated in some species could result from smaller phyllodes at distal parts as they come from newer shoots. Furthermore, the difference in form or architecture of branches among the species may affect resource partitioning, which in turn reduces reproductive capacity (Lechowicz 1984).

In *Rosa* x *hybrida* L., the stem is characterized by three distinct zones (Erwin *et al.* 1997). The first zone is located at the base of the stem, the second zone is at the middle and the third zone is at the top of the stem. Axilliary shoots arising from each zone differ. The distal zone has higher axilliary shoot and flower numbers. The axilliary shoot number depends on mother shoot vigour, the presence or absence of leaves and the growth status of the remaining parts of the plant. Leaf removal decreases the flower number per mother stem. The removal of leaves also decreases the axilliary shoot number. Defoliation may reduce carbon allocation to inflorescences immediately because it reduces photosynthesis.

Plant architecture may constrain flower production by limiting the number of meristems available for flowering. However, Preston (1999) notes that although meristem number limits inflorescence number, inflorescence number does not necessarily limit flower or seed number. In compensation for limited number of inflorescences, individuals can increase the number of flowers or seeds produced by each inflorescence. Cunningham (2000) found that inflorescence production in *Calyptrogyne ghiesbreghtiana* H. Wendl. was correlated with trunk diameter and leaf area. A large leaf area and thick trunk may help a plant harvest light and store carbohydrates. Preston (1999) suggests that plant architecture also influences carbohydrate translocation patterns, and the location of the source leaf also significantly affects the pattern of carbohydrate translocation

4.2.4.3. Seed and pod characteristics.

Of the pods collected in 1998, all species produced apparently mature seed of low weight. There were many immature and diseased seed, and poor germination resulted. Many of the pods contained empty locules or locules that contained seeds that had started to develop but had died before full maturation. A late spring frost in 1998 is believed responsible for limited seed development. Of 13 species examined, 9 had more than 20% of seed produced aborted. Only *A. neurophylla, A. nyssophylla* and *A. coolgardiensis* had germination of more than 40%. *A. prainii, A. fauntleroyi, A. sessilispica, A. acuminata, A. jibberdingensis* and *A. densiflora* were severely affected, with no germination. All other species examined had less than 30% germination. Throughout the central wheatbelt, late spring frost in 1998 also caused much damage to crops.

All species produced many diseased seed. In some species, the number of immature seed was associated with number of infected seed. Damage to seed by frost may have provided foci for seed infection. A greater number of seeds per pod was associated with longer and heavier pods, suggesting that more resources were devoted to larger pods. As a greater number of seeds per pod was also associated with more immature seeds, there is an indication that competition occurs for resources within seeds in the pod. In some species, a greater number of diseased/infected seed per pod was associated with heavier pods, suggesting that in the case of infected seed/pods, plants devoted more resources as a response to infection stimuli.

The ecological and economic effects of frost are best known for crop plants. For native species such as *Acacia,* information is very limited. The effect of frost at the cellular level, with sub-freezing temperatures can cause formation of ice crystals within or between cells. This can cause physical damage and trigger physiological problems through loss of solute. At the organ level, consequences of frost are primarily mediated through its effect on sensitive parts of plants. Reproductive organs of plants are usually most sensitive to frost (Sakai, Paton & Wardle 1981). Flowers and ovaries are often killed when older leaves are not affected and frost damage can become a site for infection of buds or flower stalks. Thus, Inouye (2000) found that frost kills or damages flower buds and open flowers, but causes minimal damage to leaves and stems in *Helianthella,* where late spring frosts kill some developing buds. Late frosts during spring are occasionally a principal cause of fruit mortality in *Pinus resinosa* Ait. Trees located on lower ground lost all first year conelets to late spring frost whereas in trees grown higher, abscised conelets came from only the lower part of their crowns (Hard 1963).

One possible effect of global climate change is that the frequency and distribution of frost events will change. Increased length of growing season in Europe is one indication of a change that may result in more frequent spring frost damage to plants (Menzel & Fabian 1999). A change in climate, accompanied by an increase in the frequency of late spring frost has been recorded previously in Virginia, U.S.A. (Inouye

2000). If global warming results in earlier flowering in temperate species, flowers might become more susceptible to frost damage.

4.3. Study No. 2. Effect of phyllode and inflorescence removal on reproduction in *Acacia saligna* and *Acacia lasiocalyx*

4.3.1. Introduction

Plants accumulate resources and allocate them to growth, maintenance and reproduction (Willson 1972). The resources needed for reproduction come from several sources. Inorganic nutrients and water move into fruits via the xylem while carbohydrates and recycled nutrients from vegetative organs enter fruits from the phloem (Kozlowski 1971). Leaves donate carbohydrates and nutrients to fruits (Hocking & Pate 1977). Fruits can potentially attract resources from leaves a metre or more away but the tendency is for resources to come from the nearest leaves (Mooney 1972). Consequently, in terms of the assimilates provided by leaves, each inflorescence and its adjacent leaves behave more or less as an independent unit (Harper & White 1974).

The resources available to a given flower or fruit depend on the total resources of the individual or branches and the number of reproductive structures drawing upon those resources. Initially, more flowers may be produced than can be supplied by the resources that become available. Throughout the process of flower and juvenile fruit abscission, plants match the reproductive output to the resources available over a wide range of environmental conditions. Many species produce mature fruits from only a small portion of the flowers (Stephenson 1981). *Acacia* species seem to be included in this category. Within species, the ratio of flowers to fruits can vary among populations, among individuals, and from year to year.

Variation in flowering is typically assumed to reflect underlying variation in the resources that plants have available for reproduction. Plants with more resources might increase fecundity by producing more flowers, either by flowering more often, or increasing flower number in each episode. This prediction is supported by studies which find that the quantity of flowers produced responds to variation in some important limiting resource, such as light or water (Cunningham 1997). Reduction in leaf area reduces resources available for fruit development. Consequently, herbivory, defoliation and leaf shading can all contribute to higher rates of abortion. In *Catalpa speciosa* Warder (Bignoniaceae: forest tree, 30 m, from Illinois, Indiana), fruit abortion increases with more leaves removed (Stephenson 1981). Similarly, the addition of resources can increase the proportion of fruits that mature. The application of macronutrient (N P K) fertiliser shortly after the flowering period in *Gomphocarpus fruticosus* (L.). Br. (Asclepiadaceae: milkbush, 1<2 m, South Africa) significantly decreases fruit drop (Willson & Price 1980).

Most abortion of fruits seems to be a response to limited resources. If resources are limited, competition among fruits and subsequent abortion are likely to increase with the number of fruits initiated. In many species, artificial thinning of flowers or juvenile fruits results in few or no abortions. The beneficial effect of additional carbohydrate and water on the proportion of juvenile fruit that mature has been demonstrated by "ringing" and irrigation experiments. Ringing prevents the transport of photosynthate out of the branch where it was produced and thereby increases the photosynthate available to fruits on the branch. The addition of nitrogen fertiliser to apple trees after flowering significantly increases the proportion of flowers that set fruits (Stephenson 1981). Six-fold increases in the inorganic nutrient supply to *Pisum sativum* (garden pea) decreases flower abscission by 75% compared to control. In *Rosa* x *hybrida* L., leaf removal decreases the flower number produced. The removal of leaves also decreases the axilliary shoot number (Erwin *et al.* 1997). Defoliation may reduce carbon allocation to inflorescences because it reduces photosynthesis. Experimentally defoliated palms (coconut) have a reduced rate of inflorescence production (Stephenson 1981). The palms are not able to harvest as much light until leaves are replaced. Thus, reduced resource availability is expressed in reduced reproduction.

The aim of this study was to investigate the role of phyllodes as a source of carbohydrate (and nutrient) on reproductive capacity in captive, cultivated trees. Specimens of *Acacia saligna* and *A. lasiocalyx* growing on the Bentley campus of Curtin University were selected. The first step was to investigate the relationship between the number and area of phyllodes on flower production. The next step was to investigate the effect of removal of phyllodes or inflorescences on legume production in these *Acacia.* Does removal of phyllodes restrict pod development? Does reduction of inflorescences increase the probability of remaining inflorescences producing a pod?

4.3.2. Methods

The study was conducted at the Field Trial Area (FTA) of Curtin University of Technology. The species studied are two of those present at SRNR. This study was conducted at the FTA because it was not possible to treat plants experimentally at SRNR, as it is a nature reserve.

4.3.2.1. Experiment 1: Natural relationship between the number of phyllodes and flower production

To determine the relationship between the number of phyllodes and flower production, 50 branches bearing inflorescences from 3 plants of *A. saligna* (15 branches from each of plants 1 and 2, and 20 branches from plant 3), and 30 branches from one plant of *A. lasiocalyx* were harvested (August 1999). Harvested branches were then taken to the laboratory. Parameters recorded were number and areas of phyllodes; number of inflorescences initiated, open and dead; and, number of flowers per inflorescence. Numbers of flowers per inflorescence were counted from 3 sample inflorescences per branch, chosen randomly. Flower numbers were counted under a dissecting microscope. For *A. lasiocalyx,* length and diameter of inflorescences were also measured with electronic callipers. At measurement, widths were taken at widest points in phyllode and inflorescence.

Inflorescences that appeared black were taken as dead. Those that were yellow, but on which all flowers had dried were categorised as dead. Inflorescences that appeared green (not yet open) or yellow, or had dried off but were not dead were categorised as live. Linear regression analysis was used to determine the relationship between number of flowers, inflorescences initiated, length and diameter of inflorescences, and the number and area of phyllodes.

4.3.2.2. Experiment 2: Effect of phyllode manipulation on reproduction.

To investigate the effect of removal of phyllodes or inflorescences on legume production, one week after the start of anthesis, signalling the commencement of flowering (August 2000), branches were selected for study on the test trees. *A. saligna* was represented by 4 plants and *A. lasiocalyx* by 2 plants (sample plants of *A. saligna* in experiment 1 are different plants from those of experiment 2; but the *A. lasiocalyx* in experiment 1 is the same plant as one of those used in experiment 2).

The treatments were 0, 50 and 100% of phyllodes removed and 0 or 50% of inflorescences removed. On the 4 plants of *A. saligna,* sufficient branches were selected to give 15 for each of 4 treatments on each tree. For *A. lasiocalyx,* 40 branches per treatment were labelled on each tree. Numbers of phyllodes, inflorescences initiated, open and dead were recorded. Individual branches were selected in sequence. Phyllodes were removed by cutting the pulvinus (phyllode stalk) with scissors. Inflorescences were removed in the same manner. After all pods had matured (or nearly so), plants were re-measured (December 2000). Numbers of inflorescences that set pods and number of pods per inflorescence on each labelled branch were recorded. Analysis of variance was conducted to test the effect of phyllode or inflorescence removal on the number of inflorescences that set pods, number of pods produced and number of pods per inflorescence. Tukey's test was used to detect any significant difference in comparisons among the treatments.

4.3.3. Results

4.3.3.1. *Acacia saligna*

4.3.3.1.1. Relationship between the number of phyllodes and flower production.

Of 50 branches harvested from 3 plants, the mean number of phyllodes per branch was 10.7 (SD 5.8); the maximum was 24 and the minimum was 2. Of all branches, 16.7% had less than 5 phyllodes, 35.4% had 5<10, 41.7% had 10<20 and 6.3% had more than 20 phyllodes per branch. Plant 1 had no branch bearing less than 5 phyllodes. Some 25% had 5<10, 62.5% had 10<20 and 12.5% had more than 20 phyllodes per branch. In plant 2, 25% of branches had less than 5 phyllodes, 41.7% had 5<10 and 33.3% had 10<20, with no branch bearing more than 20 phyllodes. In plant 3, 25% of branches had less than 5 phyllodes, 40% had 5<10, 30% had 10<20 and 5% had more than 20 phyllodes. Therefore, *A. saligna* generally had 10-20 phyllodes per branch.

Of all samples, the mean phyllode length was 13.7 (4.9) cm. The maximum was 27 cm and minimum was 2.5 cm. Of those, 20.7% were less than 10 cm in length, 69% were 10<20 cm and 10.3% were more than 20 cm. Of the 3 plants sampled, phyllodes were shortest in plant 3 (Figure 25a), with very few phyllodes more than 20 cm length. The mean phyllode width was 0.42 cm (0.21); the maximum was 2.5 cm and the minimum was 0.1 cm. Of all phyllodes, 47.5% were narrower than 0.4 cm width, 30.8% were 0.4<0.6 cm and 21.7% were more than 0.6 cm. Phyllode width was also narrowest in plant 3 (Figure 25b).

Plants had a mean of 39.1 (12.5) inflorescences per branch with a maximum of 100 and a minimum of 9. Some 67.8% of inflorescences were open and 13.6% were found dead. Of 50 branches, 50% had less than 30 inflorescences per branch, 8.3% had 30<40, 14.6% had 40<50 and 27.1% had more than 50 inflorescences per branch. The number of inflorescences per branch was also least in plant 3 (Figure 25c). Of 150 inflorescences examined, the mean number of flowers per inflorescence was 44.0 (7.2). The maximum was 58 and the minimum was 24. Of those, 28.5% had less than 40 flowers per inflorescence, 16.7% had 40<45, 26.4% had 45<50 and 28.5% had more than 50 flowers per inflorescence. Number of flowers per inflorescence was greatest in plant 3 (Figure 25d).

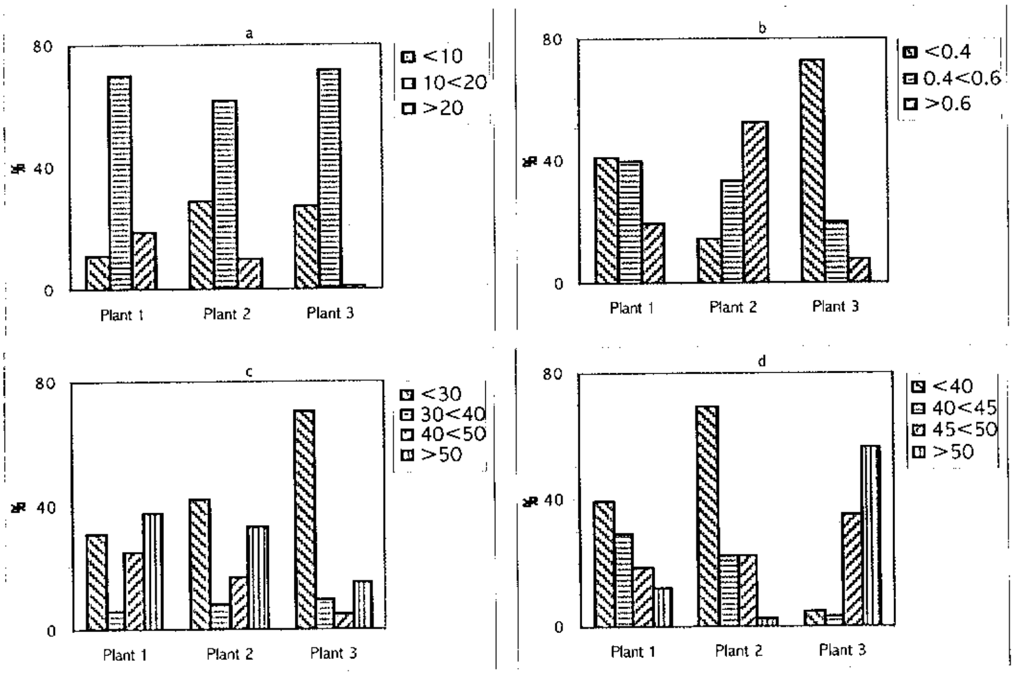

Figure 25. Distribution (%) of: a. Phyllode length (cm); b. Phyllode width (cm); c. No. inflorescences/branch; and, d. No. flowers/inflorescence; of 3 plants of *A. saligna.*

Linear regression revealed significant relationships between both the number of inflorescence initiated (Ni), (Ni = 17.1 + 2.09 Np, $P < 0.001$) and open (Nio), (Nio = 6.87 + 1.86 Np, $P < 0.001$) and the number of phyllodes (Np). Greater numbers of phyllodes were associated with more inflorescences initiated and more open inflorescences (or earlier flowering). The number of inflorescences initiated was also significantly related to phyllode area (Pa), (Ni = 24.5 + 2.46 Pa, $P = 0.007$) but not to the length or width of phyllodes. Greater phyllode area was associated with more inflorescences initiated. The number of flowers per inflorescence (Nf) was marginally related to phyllode area (Nf = 47.2 – 0.506 Pa, $P = 0.068$) but not to the numbers;

lengths or, width of phyllodes. Greater phyllode areas tended to be associated with more flowers per inflorescence. Number of inflorescences open was not related to any of length; width; or area of phyllodes. Number of inflorescences dead (Nid) was related to the number of inflorescences open (Nio), ($\mathrm{Nid} = 12.5 + 2.62\ \mathrm{Nio}$, $P < 0.001$), suggesting that most inflorescences had aborted after opening. As expected, the length of phyllodes (Lp) was strongly related to the width of phyllodes (Wp), ($\mathrm{Lp} = 1.73 + 28.9\ \mathrm{Wp}$, $P < 0.001$) in that longer phyllodes were associated with wider phyllodes.

4.3.3.1.2. Effect of removal of phyllodes or inflorescences on legume production.

The four plants of *A. saligna* sampled had mean (±SD) per branch values, prior to treatment, of: 11.23 (0.29) phyllodes; 10.41 (0.40) racemes; and, 53.87 (2.40) inflorescences, where n = 240 branches. During the reproduction period (flowering to seed maturation, August-December), *A. saligna* did not initiate any new phyllodes. *A. saligna* was observed to initiate new phyllodes only prior to the flowering season (May-July). Inflorescence and flower formation generally occur only on recently initiated shoots. However, some phyllodes were shed during the reproduction period.

Table 30. Effect of phyllode (P) removal on reproductive capacity of *A. saligna* (n = 60 for replicates, 15 branches per treatment of 4 plants).

Treatment	No. inflorescence set pods/ branch	No pods produced/ branch	Inflorescence set pod (%)	No. Pods/ inflorescence
Control	8.60 a	12.00a	12.51a	1.31
50% P removed	3.92b	5.22b	8.08b	1.34
100%P removed	3.80 b	5.17 b	7.73b	1.29
F	10.47	9.79	5.92	0.23
P	<0.001	<0.001	0.003	0.796

Entries with different letters in a column indicate a significant difference between mean using Tukey's family error rate. No letters = analysis not significant.

Table 31. Effect of inflorescence (I) removal on reproductive capacity of *A. saligna* (n = 60 for replicates, 15 branches per treatment of 4 plants).

Treatment	No. inflorescence set pods/ branch	No pods produced/ branch	Inflorescence set pod (%)	No. Pods/ inflorescence
Control	8.60	12.00	12.51	1.31
50% I removed	1.71	2.57	9.46	1.54
F	30.56	24.89	2.10	4.78
P	<0.001	<0.001	0.150	0.032

Removal of phyllodes reduces pods produced (Table 30). In the control treatment, 12.5% of inflorescences initiated developed a pod. When 50% of phyllodes were removed, 8.1% of inflorescences became pods, compared with only 7.7% when all phyllodes (100%) were removed. However, the number of pods per inflorescence was not affected by removal of phyllodes. Although removal of phyllodes limited pod development, plants could still develop a pod without any phyllodes present on the branch, suggesting that leafless branches have the capability to attract resources from phyllodes on other branches to sustain pod development.

Removal of inflorescences did not increase the possibility of the remaining inflorescences developing pods (Table 31). However, the number of pods per inflorescence was significantly greater ($P = 0.032$) when half were removed. The number of flowers that set pods may not be limited by resource availability at the time of pod initiation. Resources may be limiting factors during the period of pod development, as more pods per inflorescence were produced on remaining inflorescences.

Linear regression indicated that significant relationships occur between both the number of inflorescences that set pods (Nim), ($\text{Nim} = -4.01 + 0.848\ \text{Np}, P < 0.001$) and pods produced (Npd), ($\text{Npd} = -5.55 + 1.18\ \text{Np}, P < 0.001$) with the number of phyllodes (Np). Greater numbers of phyllodes were associated with more inflorescences initiated having set pods and more pods produced. However, the number of pods per inflorescence was not affected by the number of phyllodes.

4.3.3.2. *Acacia lasiocalyx*

4.3.3.2.1. Relationship between the number of phyllodes and flower production.

Of 30 branches harvested, the mean number of phyllodes per branch was 4.71 (1.96). The maximum was 10 and the minimum was 1. Phyllodes of *A. lasiocalyx* had a mean of 23.07 cm (5.45) length. The maximum was 34 cm and the minimum was 7 cm. Most phyllodes (73%) were 20-30 cm in length, only a few were more than 30 cm (Figure 26a). Phyllodes had a mean of 0.87 cm (0.19) width. The maximum was 1.6 cm and the minimum was 0.4 cm. Most phyllodes (80%) were of 0.5-1.0 cm width (Figure 26b).

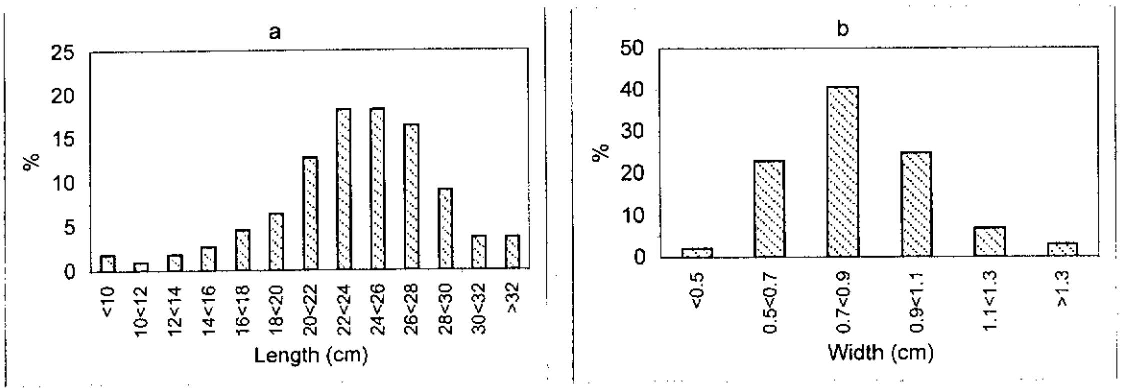

Figure 26. Percent distribution of phyllode length (a) and width (b) of *A. lasiocalyx* (n = 140 phyllodes).

Of the branches harvested, the mean number of inflorescences per branch was 30.63. The maximum was 82 and the minimum was 4. Of those, 50% had 10<30 inflorescences per branch, 25% had 30<50, only 8.3% had less than 10 and 16.7% had more than 50 inflorescences per branch. Of the 90 inflorescences examined, the mean length was 20.2 ± 4.4 mm. The maximum was 35.9 mm and the minimum was 5.4 mm. Of these, 9.3% were less than 15 mm in length, 45% were between 15<20 mm, 31.8% were between 20<25 mm and 15.2% were more than 25 mm in length (Figure 27a). Inflorescences had a mean diameter of 3.3 mm (0.5). The maximum was 4.8 mm and the minimum was 2.2 mm. Of those, 30.5% were less than 3 mm in diameter, 44.4% were between 3<3.5 mm, 19.9% were between 3.5<4.0 mm and 5.3% were more than 4.0 mm (Figure 27b). The mean number of flowers per inflorescence was 225.8 (61.3). The maximum was 380 and the minimum was 117. Most inflorescence examined had 200-275 flowers per inflorescence (Figure 27c).

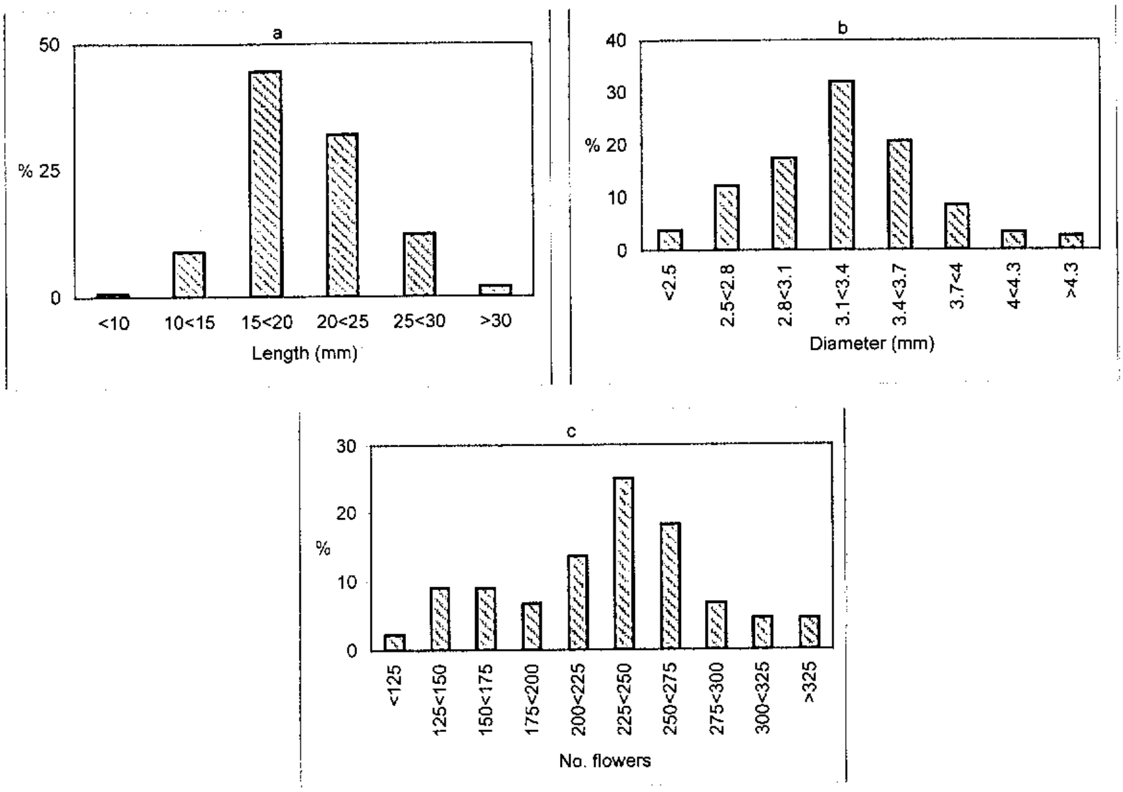

Figure 27. Percent distribution of inflorescences: (a) Length; and, (b) Diameter; and, (c) No. flowers per inflorescence of *A. lasiocalyx* (n = 90 inflorescences).

From the linear regression analysis, no relationship was apparent between the number of inflorescences initiated and the width (P = 0.270) or area (P = 0.138) of phyllodes, however number of inflorescences was marginally related to the length of phyllodes (P = 0.092). There were also no significant relationships between the diameter (P = 0.1836) and length (P = 0.1777) of the inflorescences and the number of phyllodes. Diameter of inflorescence was marginally related to inflorescence length (P = 0.0803); larger diameter inflorescences tend to be longer.

There was no relationship between the number of inflorescences open or dead and the number of phyllodes. Number of inflorescences dead (Nid) was related to the number of inflorescences open (Nio), (Nid = 0.380 + 0.130 Nio, P<0.001), suggesting that most inflorescences had died after opening. The number of inflorescences per branch did not affect the number of dead inflorescences, suggesting that dead inflorescences are not affected by competition for resources among inflorescences in given branches. As expected, the length of phyllodes (Lp) was strongly related to the width of phyllodes (Wp), ($Wp = 2.08 + 0.0585\ Lp$, $P < 0.001$). Longer phyllodes were associated with wider phyllodes.

4.3.3.2.2. Effect of removal of phyllodes on legume production.

A. lasiocalyx did not initiate any new phyllodes during the period flowering to pod maturing (August-December), and some phyllodes were shed during the reproduction period. Of the 2 sample plants, one plant failed to develop any pods at all, therefore data on pod production could only be analysed from one plant. The effect of removal of inflorescences on reproduction was also not available as very few pods developed in the treatment, therefore this was also excluded from analysis.

Table 32. Effect of phyllode (P) removal on reproductive characters of *A. lasiocalyx* (n = 40 branches per treatment)

Treatment	No. inflorescence set pods/ branch	No pods produced/ branch	Inflorescence set pod (%)	No. Pods/ inflorescence
Control	1.96a	3.88a	2.23	0.81a
50% P removed	0.89ab	1.19b	1.29	0.22b
100%P removed	0.26b	0.34b	0.69	0.10b
F	4.41	9.21	1.26	11.65
P	0.015	<0.001	0.287	<0.001

Entries with different letters in a column indicate a significant difference between means using Tukey's family error rate. No letters = analysis not significant.

Removal of phyllodes reduced the number of inflorescences that developed pods, pods produced and number of pods per inflorescence (Table 32). With all phyllodes removed, only 0.7% of inflorescences initiated developed pods compared to 2.2% in the control. Results of linear regression analysis reveal significant relationships between each of: the number of inflorescences initiated (Ni), ($Ni = 10.6 + 1.88Np$, $P<0.001$); and those that set a pod (Nim), ($Nim = -1.80 + 0.166\ Np$, $P<0.001$); pods produced (Npd), ($Npd = -1.67 + 0.246\ Np$, $P < 0.001$); and number of pods per inflorescence (Npd/Ni), ($Npd/Ni = -1.106 + 0.0343\ Np$, $P < 0.001$), and the number of phyllodes (Np). Greater numbers of phyllodes were associated with more inflorescences initiated, more pods produced and more pods per inflorescence.

4.3.4. Discussion

In both species examined, removal of phyllodes reduced the number of inflorescences initiated that developed pods and pods produced. Increased fruit abortion with number of leaves removed has been found in many studies (Leopold & Scott 1952; Janzen 1976; Stephenson 1980; Willson & Price 1980; Cunningham 1997). Cunningham (1997) manipulated the resources environment of *Calyptrogynae ghiesbrecghtiana* by removal of leaves and found that leaf removal suppresses inflorescence production, and plants with higher levels of storage have higher inflorescence production. Leopold & Scott (1952) showed that fruit set of tomato is decreased by removing leaves and by placing leaves in the dark prior to anthesis. The decreased fruit set is proportional to the number of leaves manipulated.

Presumably, removal of phyllodes reduces the photosynthate produced. Therefore, competition among inflorescences (or pods) for resources is more intense; and subsequent abortions are likely to occur. Stephenson (1981) observed that most abortions of undamaged fruits in *Catalpa speciosa* are a response to limited resources from the leaves on a branch that bears an infrutescence. These leaves are referred to as "feeder leaves". Similar evidence also comes from studies of the effects of fruit numbers, leaf area, and resource enrichment or deprivation on the number of fruits that abort. Sedgley (1985) suggest that buds produced during pod growth are generally shed from the plant, possibly due to competition between the developing pods and flower buds. Those buds which are produced immediately after seed shed develop more slowly than those which appear later in the season, with the result that flowering occurs only one a year.

In both *Acacia* examined (*A. lasiocalyx* & *A. saligna*), although removal of phyllodes limited pod development, plants could still develop a pod without any phyllodes present on particular branches, suggesting that plants have the capacity to attract resources from phyllodes on other branches to sustain pod development. Cunningham (1997) suggests that carbohydrates stored in the trunk are being used as a short-term buffer for the cost of reproduction. During the reproduction period (flowering to seed maturation), both species examined did not initiate any new phyllodes. They were observed to initiate new phyllodes only prior to the flowering season. Inflorescence and flower formation generally occurs only on recently initiated shoots. However, some phyllodes were shed during the reproduction period.

In *A. saligna*, removal of inflorescences did not increase the possibility of the remaining inflorescences developing pods. However, the number of pods per inflorescence was greater. In *A. saligna*, the number of inflorescences that set pods may not be limited by pollination or resource availability at the time of pod initiation. Resources seem to be limiting factors during the period of pod development, as more pods per inflorescence are produced on the remaining inflorescences. Stephenson (1981) found that by decreasing the number of pollinated flowers, the probability increases that the remaining flowers will set fruits. He suggests that temporal decline in fruit set can be averted if the early blooming flowers are thinned immediately before or after pollination. Flowers are limited from setting fruits if other pollinated flowers and juvenile fruits are developing, suggesting that flowers and young fruits compete for limited maternal resources.

In *A. saligna*, greater numbers of phyllodes are associated with more racemes and inflorescences initiated; earlier flowering; and fewer dead inflorescences. Greater phyllode area is associated with more inflorescences initiated and more flowers per inflorescence. Greater numbers of phyllodes are associated also with more inflorescences initiated having set pods; more pods produced; and fewer pods that die.

For *A. lasiocalyx,* greater numbers of phyllodes are associated with more inflorescences initiated, more pods produced and more pods per inflorescence. Longer phyllodes also tend to be link to more inflorescences initiated. These observations confirm that the role of phyllodes as a donor of nutrients at reproduction time is critical in *Acacia* species. Therefore, herbivore activity, defoliation, leaf shading or disease to phyllodes will all lead to higher rates of inflorescence or pod abortion.

In *Acacia* species, only some of the inflorescences (flowers) initiated result in formation of pods. In *A. lasiocalyx,* there was a mean of 226 flowers per inflorescence and a mean of 31 inflorescences per branch. If all flowers initiated were to set pods, there would be congestion among pods. The production of surplus inflorescences (flowers) and their subsequent abscission reduces numbers to reasonable levels that the plants may be able to supply. Production of many inflorescences (flowers) may attract pollinators and assist in pollen dissemination. Pods produced may vary over a range of conditions and may differ depending on resources availability.

CHAPTER 5

GERMINATION AND SEEDLING CHARACTERISTICS OF *ACACIA* AND GRASS SPECIES OF SANDFORD ROCKS NATURE RESERVE (SRNR)

5.1. General introduction

The germination of seeds is affected by a number of factors (Westoby 1981; Whalley 1987; Bewley & Black 1994). These are conveniently considered as either internal or external factors. Internal factors include: maturity at harvest, age of seeds and seed dormancy. Hard-seededness is important in dormancy of *Acacia* seed. The external factors include: water availability, temperature, light and oxygen (Whalley 1987). In arid environments, with unpredictable climate, germination is often a high-risk event. Successful species are adapted to germinate at times that provide the best chance for seedling establishment. In many parts of Australia, the relatively low rainfall and frequent drought confine germination to rainy seasons. For example, in the south-west, the winter period. Wet seasons with unreliable openings are hazardous environments for plants, particularly annuals. Some form of seed dormancy is essential as a mechanism preventing germination of seed immediately after it is shed.

The seeds of numerous species display a large physiological variability in dormancy. This phenomenon has been interpreted as germinative polymorphism that can be found among seeds from different parent plants, and/or among seeds from the same parent plants. Although the exact ecological meaning of this phenomenon has not yet been established, in theory this feature increases the possibility of at least a proportion of seeds persisting in the soil seed bank, where they remain until more favourable conditions for establishment arrive. Bewley & Black (1994) suggest dormancy can be experienced as a way of optimising the distribution of germination in time and space. A good distribution in time is achieved by spacing germination through a long period, and is related to the variability in depth of dormancy observed among populations.

For seeds, predicting the condition into which they will germinate is difficult (Westoby 1981). Fluctuation in light intensity, temperature, soil condition or presence of heat and smoke may all affect where and when a seed will germinate (Murray 1998). Temperature of the seedbed plays an important role in determining time of germination once dormancy has been broken. The duration of temperature events that affect soil in which seed are present may be important in priming seed for germination.

In this chapter, germination tests were conducted under a range of incubation temperatures (15-30°C) to identify germination responses in *Acacia* and several grass species found at SRNR. The main aims of this study were to discover for particular species: under what temperature regimes do most seeds germinate? How do seedling characteristics vary between species?

5.2. Study No. 1. Germination and seedling characteristics of *Acacia* species of Sandford Rocks Nature Reserve (SRNR)

5.2.1. Introduction

The rate of biological processes is temperature-dependent and the germination of seeds is no exception. The proportion of seeds in a sample that germinate varies with temperature. One can therefore postulate minimum, optimum and maximum temperatures for the germination of any sample of seed of any species (Whalley 1987). The optimum temperature for seeds of particular species to germinate is specific to the kind of seed. Optimal condition varies considerably between species. The experimentation required to determine these temperatures for most Australian species has not been completed (Peterson 1985). Knowledge of conditions required for a high proportion of seeds to germinate; the viability of seed; and, the length of dormancy are all important in understanding the ecology of species.

SRNR has a number of quite different plant species associations. Different *Acacia* species are locally abundant and clearly play important roles in the associations present. At SRNR, about 18 species occur. They are present as subordinate species in various associations of eucalypt woodland, melaleuca thicket and scrub (Chapter 3). *A. acuminata* is well distributed at SRNR; it is present in dry to moist habitats and in open to relatively closed shrubland or woodland. *A. hemiteles* is also well distributed across the areas, except in relatively moist habitats, especially near the rock. *A. hemiteles* is commonly found as understorey in eucalypt woodland. *A. prainii* grows well in and is relatively well distributed in sites that are seasonally wet. *A. densiflora, A. nyssophylla* and *A. coolgardiensis* grow well in relatively deep, dry-sandy soil. *A. neurophylla* and *A. steedmanii* grow well in lateritic, yellow, dry-shallow sandy soil. *A. fauntleroyi* is only present at rock sites, appearing dependant on material eroded from adjacent rock. It is mainly found at the base of granite rocks, in shallow, very well-drained, coarse granitic sandy soils that occupy shallow basin where litter and other organic matter has accumulated.

At SRNR, the pattern of recruitment of these *Acacia* appears to be little known. Some species appear to be able to support seedlings, with many seedlings being found, however, these may not persist. In other species, seedlings are rarely found. Germination tests were conducted under various conditions of incubation temperatures to identify response to temperature of a number of *Acacia* species found at SRNR. The main aims of the study were to investigate under what temperature regimes do most *Acacia* seeds germinate? How do seedling characteristics vary between species? Can these characteristics be confirmed for particular habitats?

5.2.2. Methods

All seeds used had been collected from SRNR, or near-by areas, during either 1994, 1996 or 1998. Seeds were stored at room temperature (~ 21°C) under dry conditions, until required for use. In 8 species (*Acacia acuminata, A. coolgardiensis, A.*

densiflora, A. hemiteles, A. nyssophylla, A. neurophylla, A. prainii and *A. steedmanii*), the germination response to different incubation temperatures was investigated to determine optimum temperature range for germination of these species. Incubation temperatures used were 15, 20, 25 and 30°C. Two replicate lots of 50 seeds per incubation temperature treatment (or 400 seeds per species) were used. Seeds were germinated after pre-treatment by immersion of each lot of 50 seeds in 30 ml of water in a glass beaker of 50 ml volume at a temperature of 100°C (boiling water). Seed were then left to cool to room temperature (approximately 20 minutes).

After treatment, all seeds were briefly surface-sterilised with sodium hypochlorite, then rinsed twice with deionised water. Seed lots were then placed on two Whatman No. 3 filter papers (9 and 11 cm), in plastic petri dishes (diameter 11 cm). Petri dishes were partially filled with sterilised vermiculite (approximately 0.5 cm from the bottom). The vermiculite and filter paper were then moistened with a fungicide "previcure" (Hoescht Schering Agrevo, Glen Iris, Victoria, Australia) to minimise fungal growth, and de-ionised water to maintain a humid environment within the dish. Seeds were then placed in dark, incubation cabinets.

Seeds were observed at daily intervals. Germinants were defined as seeds with 2 mm of emerged radicle. Water was replenished as necessary and previcure added to the petri dish when required. Any germinants were recorded, removed and planted into 5 x 5 x 5 cm trays, with a mixture containing 1:1:1 coarse sand: fine sand: peat moss, with no fertiliser applied. The transplant dates were recorded for each seedling to enable seedlings to be harvested at 14 d from germination. The trays were maintained in a glasshouse during October 1999 and watered daily. Counting of the germinated seeds was continued until no more germination occurred for 14 successive days.

To investigate the variation in seedling characteristics in early growth between the species, eight seedlings of each species were harvested at 14 d after transplanting. Seedlings were carefully removed from the trays and any adhering peat washed away from the root. Measurements were taken of length of shoot and root. Root and shoots were separated, placed in envelopes and dried at 60°C for 4 days, then weights were taken to the nearest 0.1 mg. Root and shoot ratios were determined.

Numbers of germinants to 50 days were subjected to analysis of variance. Tukey's test was used to detect any significant differences in comparisons between treatments. Data were transformed to Arcsine to meet normality of data. The experiment was carried out at the laboratory of Environmental Biology, Curtin University of Technology, commencing in October 1999.

5.2.3. Results

5.2.3.1. Effect of incubation temperature on germination of *Acacia* species.

Of 8 species examined, *A. steedmanii* (mean = 12.01 ± 1.24 mg, Min = 7.30, Max = 15.10), *A. hemiteles* (mean 11.20 ± 1.31 mg, Min = 7.40, Max = 15.00) and *A. acuminata* (mean = 8.95 ± 0.47 mg, Min = 1.50, Max 14.10) had a large seed (Figure 28). *A. neurophylla* (mean = 4.33 ± 1.14 mg, Min = 1.30, Max 6.40) and *A. prainii* (mean = 3.12 ± 1.26 mg, Min = 1.40 Max = 10.60) had a medium seed and *A. coolgardiensis* (mean = 2.76 ± 0.87 mg, Min = 1.40, Max = 4.80), *A. nyssophylla* (mean = 1.78 ± 0.59 mg, Min = 0.80, Max 3.10) and *A. densiflora* (mean 2.84 ± 0.47 mg, Min = 0.20, Max = 3.90) had a small seed.

Seeds of *A. hemiteles* were collected in December 1996 (34 month storage). In *A. hemiteles,* incubation temperatures of 20 and 25°C gave more germination than at 15 and 30°C (Table 33). Therefore, it appears that *A. hemiteles* is suited to germinate in the middle of the temperature range trialed. Incubation at temperatures of 15-25°C gives about the same pattern and speed of germination (Figure 29a) in that initially, germination is slow, followed by a more rapid rate. Most germination occurs between days 12-20 (a period of about 8 days), with 4-7 and 13-14 d to first and 50% final germination. Incubation at 30°C gives slow, continuous germination, with 12 and 24 d to first and 50% final germination. Surprisingly, least and slowest germination occurs at 30°C.

In *A. acuminata* also collected in December 1996 (Figure 29b), incubation at 15-25°C gave more germination than at 30°C. This suggests that in *A. acuminata*, germination at 30°C is slightly detrimental for seeds. Generally, higher temperatures give earlier germination.

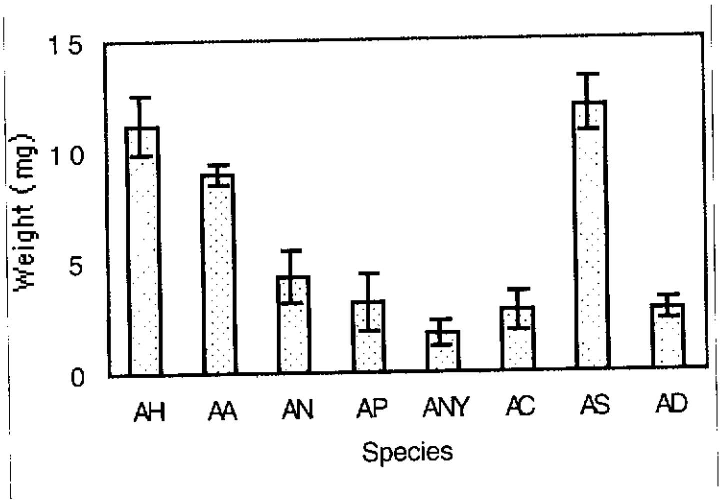

Figure 28. Mean seed weight (n= 100 seeds) of 8 *Acacia* species at SRNR. Species legend as in Table 33. Bars represent the standard error.

Table 33. Effect of incubation temperature on percentage of germination (GRM) after 50 d in 8 *Acacia* species, after immersion in boiling water, then left to cool to room temperature (n = 2 for replicates, 50 seeds per replicate).

Incubation	SP	GRM	SP	GRM	SP	GRM	SP	GRM
15°C	AH	49.1c	AN	80.0a	ANY	52.7b	AS	94.6a
20°C		76.0a		68.0b		54.0b		92.0a
25°C		69.0a		78.0a		49.0b		83.0b
30°C		58.2b		58.2c		60.0a		61.8c
F		12.805		15.405		4.377		43.174
P		<0.001		<0.001		0.005		<0.001
15°C	AA	41.8a	AP	61.8b	AC	54.5a	AD	74.0
20°C		48.0a		*		*		79.0
25°C		45.0a		81.0a		57.0a		62.0
30°C		34.6b		58.2c		40.0b		46.0
F		5.623		22.321		18.234		2.162
P		0.001		<0.001		<0.001		0.094

Entries with different letters in a half-column indicate a significant difference between means using Tukey's family error rate. No letters = analysis not significant. SP (species): AH = *A. hemiteles;* AA = *A. acuminata*; AN = *A. neurophylla;* AP = *A. prainii;* ANY = *A. nyssophylla;* AC = *A. coolgardiensis;* AS = *A. steedmanii;* AD = *A. densiflora.* * = Not available.

Seed of *A. neurophylla* were collected in December 1998 (10 month storage). Incubation at 15-25°C gave more germination than at 30°C (Figure 29c). Incubation at 15-25°C also produced earlier germination, suggesting this species appears to germinate well in cooler months of the years. At 30°C incubation temperature, very few seeds germinated before day 15, while in all other treatments most germination was under way well before day 15. Therefore, 30°C incubation results in low and slow germination and may be detrimental for seed of this species. The pattern of germination confirms that incubation temperature affects both the level and speed of germination.

Seeds of *A. prainii* were collected in December 1996 (24 month storage). In *A. prainii,* the best incubation temperature was at 25°C (Figure 29d) which gave 81% germination. Incubation at 30°C gave low germination (58%). The fastest germination was at 25°C, with only 3 and 5 d to first and 50% final germination. *A. prainii* may germinate best in the spring season. Germination at 15 and 30°C incubation had slow, continuous germination. The pattern confirms that temperature of incubation affected both rate and speed of germination.

Seed of *A. nyssophylla* and *A. coolgardiensis* were collected in December 1998 (10 mo storage). In *A. nyssophylla,* incubation temperature had little effect. At all of 15-30°C, germination was about the same level, speed and pattern (Figure 29e). Germination was initially slow, followed by a more rapid speed and then slowing again at the end of the period. Incubation at 30°C gave slightly greater germination (60.0 %) than at 15-25°C (± 50%). Incubation at 30°C also gave slightly earlier germination with only 5 and 9 d to first and 50% final germination.

In *A. coolgardiensis,* incubation at 15 and 25°C gave more germination (55 and 57%) than at 30°C (Figure 29f). Germination at 30°C incubation gave only 40% germination. Generally, the higher incubation temperatures gave slightly earlier germination. At 30°C incubation, only 3 and 7 d were required to first and 50% final germination.

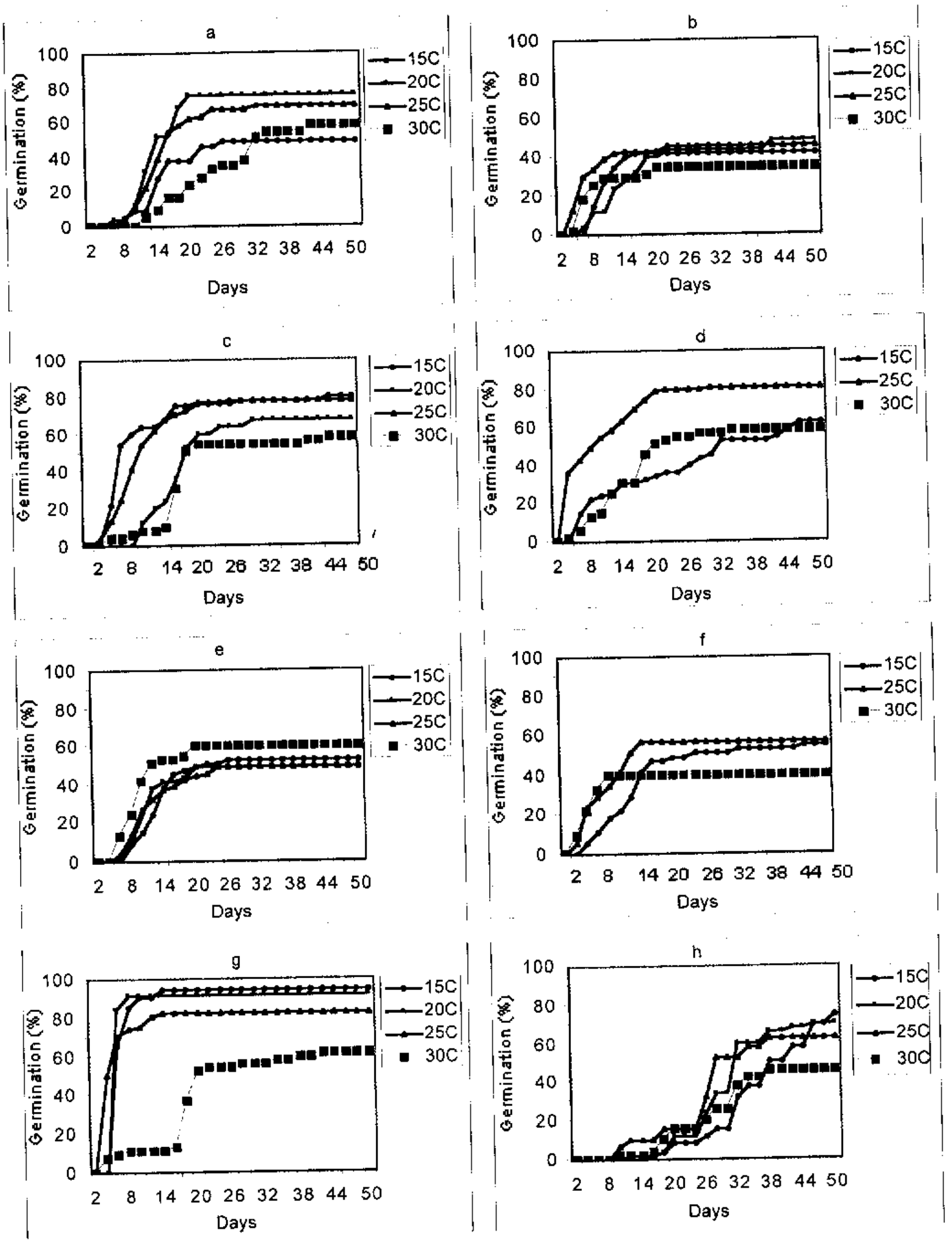

Figure 29. Effect of incubation temperature on germination of: a. *A. hemiteles*; b. *A. acuminata*. c. *A. neurophylla*. d. *A. prainii*. e. *A. nyssophylla*. f. *A. coolgardiensis*. g. *A. steedmanii*. h. *A. densiflora*. Each entry represents the means of two replicate dishes, 2 x 50 ($\sum = 100$ seeds).

Seeds of *A. steedmanii* were collected in December 1994 (58 mo storage). Incubation at 15-25°C had more germination than at 30°C (Figure 29g). The best incubation temperature was at 15°C, with 95% germination compared to only 62% at 30°C incubation. Over the range of 15-25°C incubation temperatures, lower temperatures consistently gave slightly greater germination. It is possible that *A. steedmanii* is more likely to be a species that germinates in the winter. Incubation at 30°C gave slow germination, while at 15-25°C it occurs more or less simultaneously, with all germination complete between 4–6d. Incubation at 30°C is slightly detrimental for *A. steedmanii.*

Seeds of *A. densiflora* were collected in December 1996 (34 mo storage). Incubation at 15-25°C gave more germination than 30°C (Figure 29h). At all incubation temperatures, the pattern of germination was slow and periodical. Higher incubation temperatures tended to give earlier germination.

All *Acacia* species studied showed the best germination at the lower range of temperatures (15-25°C). Only *A. nyssophylla* had best germination at 30°C. This requirement for a slightly higher temperature compared to other species suggests this species may germinate following summer rain. All other species have reduced germination when incubated at 30°C. *A. steedmanii* and *A. neurophylla* had slightly better germination at 15°C, the lowest temperature used. Both species occupy similar microhabitats, thus facing about the same microclimatic conditions in nature. Those species best adapted to germination at 20-25°C were *A. hemiteles, A. acuminata* and *A. densiflora,* with best germination at 20°C; and *A. coolgardiensis* and *A. prainii* with best germination at 25°C. These are all presumed species adapted to germination between winter and early spring.

Generally, in all species, germination at 15°C incubation temperature gave quite high germination levels but required a longer time. Therefore, 15°C incubation temperature whilst not necessarily detrimental, does tend to entail slower germination. Except for *A. nyssophylla,* incubation at 30°C was slightly detrimental for all other species. In *A. hemiteles, A. neurophylla, A. prainii* and *A. steedmanii,* incubation at 30°C gave lower and slower germination. In *A. acuminata, A. coolgardiensis* and *A. densiflora,* incubation at 30°C gave reduced but faster germination. These results suggest there is variability in the pattern of seed germination among the species in response to temperature.

Comparing the pattern of germination among the 8 species, six species (*A. acuminata, A. neurophylla, A. prainii, A. nyssophylla, A. coolgardiensis* and *A. steedmanii*) germinated well between days 2-10 (Figure 29b, c, d, e and f). In two species (*A. hemiteles* and *A. densiflora*), germination started after about 8 d (a and h Figure 29) or required longer times to initiate germination. One species (*A. steedmanii*) had intermittent germination, with only 2-4 d to finalize germination.

Germination level (50 d) varied significantly among the species ($P = 0.016$). Of the 8 species, the highest germination was attained by *A. steedmanii* with a mean of 83% (Figure 30a). The second best was attained by *A. neurophylla* with 71% germination. Another 3 species, *A. prainii, A. densiflora* and *A. hemiteles* had ± 65% germination. All other species had 42-54% germination, with the lowest level in *A. acuminata* at 42% germination. Five species (*A. steedmanii,* max 94.6%; *A. prainii,* max 81; *A. neurophylla,* max 80; *A. densiflora,* max 79; and *A. hemiteles,* max 76) attained high germination, suggesting that the boiling water treatment employed was effective in breaking seed dormancy.

Of days to germinate, the fastest germination was attained by *A. steedmanii* with only 4 and 8.5 d to first and 50% germination respectively (Figure 30b). This relatively rapid germination of *A. steedmanii* may be due to a longer period of seed storage (~5 years). Longer seed storage may result in reduced seed moisture content and drier seed may imbibe water more rapidly causing germination to occur faster. The slowest germination was in *A. densiflora,* with 12.5 and 29.3 d to first and 50% final germination. *A. densiflora* attained about the same germination level as *A. hemiteles,* however *A. densiflora* had much slower germination. Although the seeds of *A. densiflora* were collected in 1996 (~3 years storage), seeds were relatively slow to germinate.

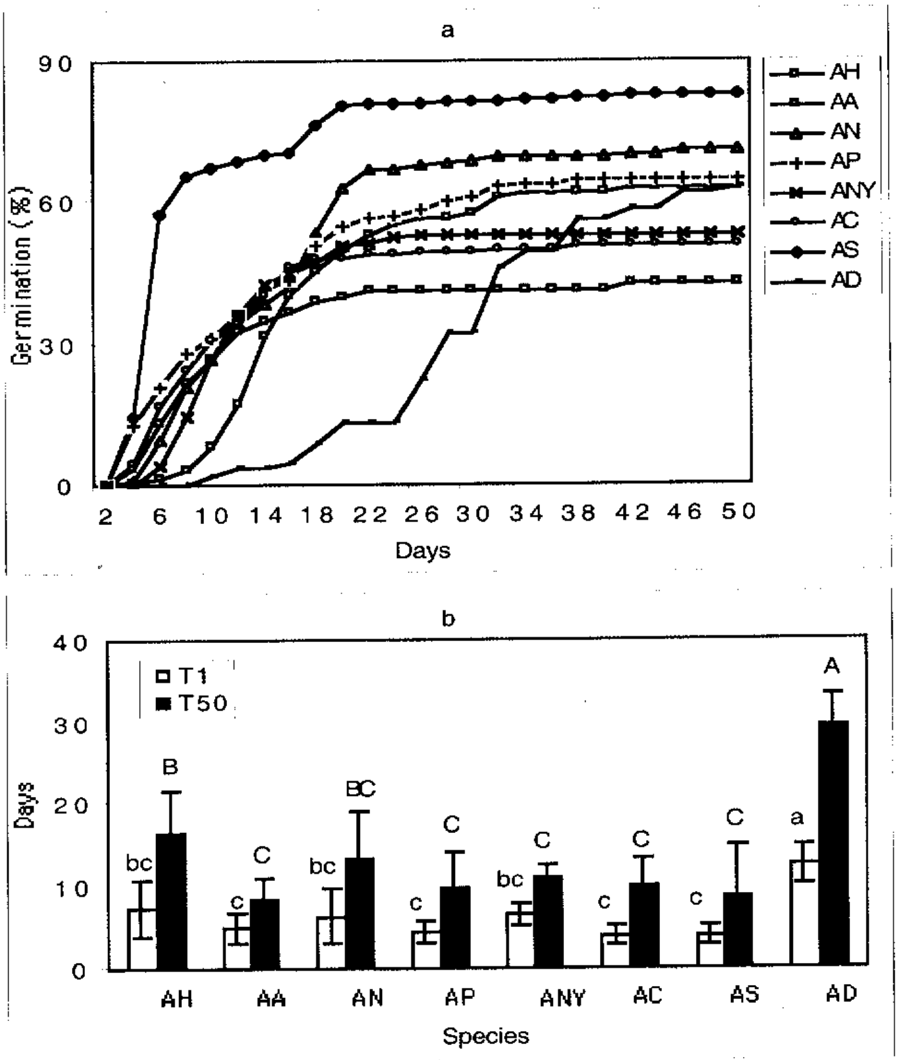

Figure 30. Comparison of germination in 8 *Acacia* species (data from 8 petri dishes representing 4 temperature cabinets of 50 seeds/dish, except *A. prainii* and *A. coolgardiensis* of 6 dishes). a. Cumulative percentage of germination. b. Time to germinate. T1 = days to first germination, T50 = days to 50% final germination. Species legend as in Table 33. Entries with different letters among species indicate a significant difference between means for T1 and T50 using Tukey's family error rate (Figure 30b). Standard error bars shown.

A. steedmanii was seen to have a pattern of simultaneous germination with the majority of seed developing in a relatively short period. In contrast, *A. neurophylla* had rapid, steady germination. *A. densiflora* had a quite different pattern and seed seemed to germinate slowly and periodically. All others species had continuous development, initially with slow activity, followed by a more rapid period and then germinating slowly towards the end. According to the days required for 50% germination, species could be divided into 3 categories as fast, medium or slow germination. Species with fast germination were *A. steedmanii*, *A. acuminata*, *A. coolgardiensis*, *A. prainii*, *A. nyssophylla* and *A. neurophylla*, with 8-11 d to 50% final germination. A species with a medium speed was *A. hemiteles* with 16 d to 50% final germination. The species with slowest germination was *A. densiflora,* with 29 d to 50% final germination.

5.2.3.2. Seedling characteristics

Of the 8 species examined in section 5.2.3.1, seven were planted on to enable early seedling growth characteristics to be discovered. *A. densiflora* was not used as this seed batch took too long to germinate and few seedlings were available. All species had longer roots than shoot (Figure 31a). Root: shoot length ratio was greater in species with small seed (*A. coolgardiensis*, *A. nyssophylla*; Figure 31b). Species with heaviest shoots were *A. acuminata*, *A. hemiteles* and *A. steedmanii* (Figure 31c). These were species with heavier seed. Species with medium weight shoots were *A. prainii* and *A. neurophylla;* these were species with medium weight seed. Species with lightweight shoots were *A. nyssophylla* and *A. coolgardiensis*. These were the species with smallest seed. Using linear regression, species with larger seed were associated with heavier shoots ($F = 5.315$, $P = 0.0690$). Of the 7 species, seedling of largest mass were attained by *A. acuminata* and *A. hemiteles*. The smaller seedlings were *A. nyssophylla* and *A. coolgardiensis*. Species with larger seed had heavier seedlings ($F = 7.975$, $P = 0.0369$); species with larger seed also had heavier roots ($F = 20.51$, $P = 0.0062$).

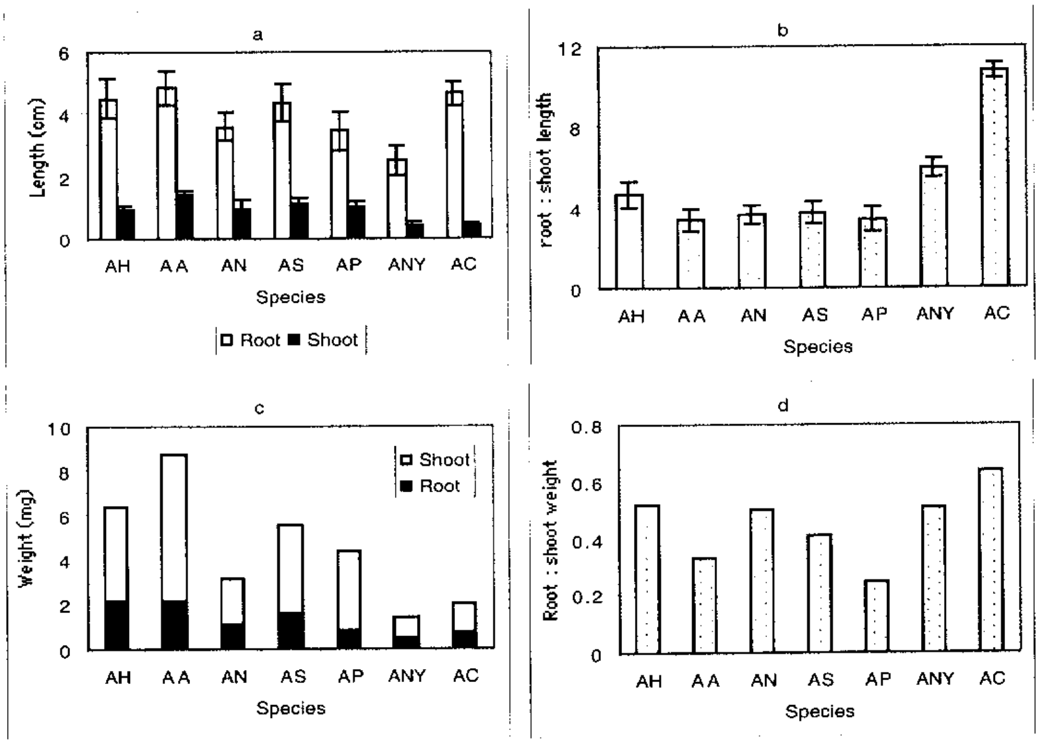

Figure 31. Seedling characteristics of 7 *Acacia* species, 14 d-old (n = mean of 8 seedlings). a. Length of root and shoot; b. Root: shoot length ratio; c. Root and shoot weight. d. Root: shoot weight ratio. Species: AH = *A. hemiteles*, AA = *A. acuminata*, AN = *A. neurophylla*, AS = *A. steedmanii*, AP = *A. prainii*, ANY = *A. nyssophylla*, AC = *A. coolgardiensis*. Bars represent standard errors (Figure 31 a and b).

A. prainii and *A. acuminata* had lowest root: shoot weight ratios (Figure 31d). Of the 7 species examined, *A. prainii* and *A. acuminata* tend to occur in relatively moist habitats compared to the other species (Chapter 3). Species that occur mainly in relatively drier areas tend to have a greater root: shoot weight ratio, while species grown in seasonally wet areas (high soil moisture) had a higher shoot: root ratio. There was also a tendency for heavier root : shoot weight ratio in those species with smaller seeds. Of the 7 species studied, *A. prainii* and *A. coolgardiensis* had the best growth. As 14-d old seedlings, seedling dry weights of both species were already heavier than the seed dry weight. In contrast, *A. steedmanii* and *A. hemiteles* are slow-growing species, with seedling mass only 34 and 54% of seed mass respectively. In those species with slow growth, no seedling recruitment was observed in the field.

5.2.4. Discussion

Westonia experiences a Mediterranean climate, characterised by a long hot, dry summer (7-8 months) with a short cool winter. Much of the annual rainfall occurs over the winter months (May-August). Mean maximum summer temperatures range from 35-45°C and winter temperatures ranged between 0-27°C. Due to the typically short period of rain, the best time for seed germination here is presumably as early in the growing season as possible to gain resources for growth and avoid the probability of encountering poor growing conditions coinciding with rainfall coming to an end. Species need to avoid germination after small falls of rain during the dry season, as mortality can be complete during the subsequent dry season. For successful seedlings, seeds need to germinate early in the wet season, as later-established seedlings are less likely to survive competition from vegetation already present.

For the species of *Acacia* studied, the best germination was in the cool winter temperature range (15-25°C), when seasonal moisture is more likely available. Mott (1972) was the first to note the existence of complementary suites of species in the arid/semi-arid zone that tend to germinate either following summer rain (mainly annual grasses) or with winter rain (especially the daisies: family, Asteraceae). Similarly, Jurado & Westoby (1992) report that Central Australian graminoids are mostly summer germinators whereas forbs are mainly winter-germinating. The tendency for graminoids (Poaceae) to be summer germinators is also found in Baskin & Baskin (1988). Most species are not restricted to a narrow temperature range for germination and seed of the species *Acacia estropholiata* F. Muell., *A. kempeana* F. Muell., *A. ligulata* A. Cunn. ex Benth., *A. tetragonophylla* F. Muell. and *A. victoriae* Benth. are said to germinate equally well at 12, 20 or 28°C (Jurado & Westoby 1992). However, seed of *A. aneura* F. Muell. ex Benth. is said to germinate better at 12°C, whereas *A. farnesiana* (L.) Willd and *A. murrayana* F. Muell. ex Benth. germinate equally well at either 20 or 28°C.

Barrett (1995) reports seed of *A. acuminata* incubated at 20°C as giving 100% germination. For *A. hemiteles*, using seed pre-treated with moist heat (80°C), Barrett

(1997) found the best incubation temperature was 20°C whereas both 15 and 30°C gave low germination. This level of incubation temperature is about that obtained in the present study. Although most *Acacia* species of SRNR had a tendency to germinate in cooler temperatures, the species were spatially varied in best temperature threshold for germination. Therefore, they were differentiated by time for seedling recruitment. This strategy presumably avoids competition among seedlings that may tend to become established at different times. For *A. hemiteles*, *A. acuminata* and *A. prainii,* the best germination was at 20-25°C, with both 15 and 30°C slightly unfavourable. For *A. neurophylla* and *A. coolgardiensis,* the best incubation temperature were at 15-25°C, whereas 30°C was unfavourable and for *A steedmanii* and *A. densiflora* the best were at 15-20°C, whereas both 25 and 30°C were unfavourable. *A. nyssophylla* had good germination over the range of temperature 15-30°C.

For Africa and Arabia, *Acacia* (*A. origena* Hundle and *A. pilispina* Pic.-Ser.), seeds are capable of germination over a wide range (10-30°C) of constant temperatures (Taketay 1998). Other studies with *A. origena* collected from south-western Saudi Arabia also show ability to germinate over a wide range (10-35°C) of temperatures (Abdulfatih 1995). Taketay (1998) suggests that the germination response of *Acacia* species over a wide range of constant temperatures has practical implications in countries like Ethiopia, where different temperature conditions prevail as a result of varied topography.

In *A. hemiteles, A. coolgardiensis, A. prainii* and *A. steedmanii,* the highest incubation temperature (30°C) results in lower and slower germination. In *A. acuminata, A. neurophylla* and *A. densiflora,* the highest incubation temperature (30°C) results in less germination but it is earlier. Therefore, both the level and speed of germination may have different responses to temperature of incubation.

Most of the species examined had rapid germination and germinated mainly in 2-15 days. The only species with a medium speed was *A. hemiteles* (16 d to 50%), while species with slow germination was *A. densiflora* (29 d to 50%). *A. steedmanii* had a pattern of "simultaneous germination", with all seed germinated over a relatively short period (2-6 days). *A. densiflora* had a pattern of slow, periodical germination. Variation in speed of germination among species suggests that they have different "depths" of dormancy and there could be large difference in establishment after rains sufficient for germination. Rapid germination in some species may particularly increase the likelihood of establishment in seasonally dry environments. Prolonged germination, small percentages of germination each day over a long period in some species will limit seed loss from seed-bank, because only a few seeds germinate to completion when conditions are favourable. However, the response of seed germination to field temperature would not necessarily be as in this study, as storage and germination conditions could be different. Exposure of soil-stored seed to the strong daily temperature fluctuation in the soil surface has been shown to increase germinability in some species (Mott 1974b). Fluctuating temperatures during germination might have different effects from the constant temperature used in the laboratory. Therefore, it may be difficult to predict the season in which seedlings of different species will appear in the field.

The boiling water treatment has traditionally been considered an effective agent for reducing seed impermeability in *Acacia* species. Harding (1940) reported that boiling accelerated germination considerably but that it became harmful when it lasted longer than 5 s. In a study of 3 *Acacia* species from the deciduous tropical forest of southern Mexico, Cervantes, Carabias & Vazquez-Yanes (1996) found the largest number of germinated seeds was obtained by applying scarification. Boiling was not very effective in promoting germination and long boiling periods had deleterious effects, the magnitude of which was species-dependent.

The application of boiling water in this study was effective in promoting germination, as most seed had a high germination level. Relatively low germination in some species was presumed a result of initial low seed viability. I presume, *Acacia* species from tropical areas are inappropriately pre-treated with boiling water, due to their possession of a thin seed coat, because there is no adaptive advantage of a hard coat. For species from arid environments boiling water treatment is required, due to possession of a thick seed coat. Such species have different adaptability to environmental conditions.

All *Acacia* species examined here had seeds that become mature in December, about 6 months before the beginning of the next rainy season (in May). Soft seed may then germinate readily during the rainy season, while hard seed, buried under sand, may be left unable to imbibe water and absorb oxygen. If their environment becomes humidified in the following rainy season, germination may occur under a protective layer of sand. Some seeds may be lost to predation by ants or birds.

Early seedling characteristics of *Acacia* species that grow naturally in drier habitats were different from those of more moist habitats. Seedling characteristics of particular species may be taken to reflect their presence in particular habitats. The highest root: shoot weights were attained by species that grow naturally in dry areas and in those species with small seed. This biomass partitioning is a presumed strategy to obtain water. There is also a tendency for greater root: shoot ratios in species with smaller seed. Of the 8 species examined, generally species with larger seed produce larger seedlings (root or shoot).

In comparing seedling mass to seed mass, greatest growth was in *A. prainii* and *A. coolgardiensis*. In both, seedling mass was more than seed mass. The slower growing species were *A. steedmanii* and *A. hemiteles* with seedling mass only 34 and 57% of seed mass. Both species, of slow growth, had no recruitment observed in the field. Whether slow growth of these species has any relation to failure of recruitment awaits further investigation.

5.3. Study No. 2. Germination and seedling characteristics of grass species of Sandford Rocks Nature Reserve (SRNR)

5.3.1. Introduction

At SRNR a number of grass species occur. Seven of the most dominant species are: *Amphipogon strictus, Aristida contorta, Eriachne ovata, Neurachne alopecuroidea, Austrostipa elegantissima, Austrodanthonia caespitosa and Spartochloa scirpoidea. S. scirpoidea* plants occur in rocky areas; it is a perennial species that may partially dry off when rains are absent and produce new growth in winter. *A. elegantissima* has quite a wide distribution, generally growing in fairly dry areas as an understorey species in Eucalyptus woodland. *A. caespitosa* is common in sites of relatively high soil moisture, however, it is sometimes present in relatively dry areas in Eucalyptus woodland or shrubland. All other species are mainly grown at entrance site at SRNR, and are generally adapted to some extent on relatively high soil moisture (Chapter 2, 2.3.2). *A. strictus* is a common understorey species in *Acacia jennerae* shrubland, of brown, fine sandy loam and sandy clay loam of relative depth. *N. alopecuroidea* was observed as an understorey in wandoo woodland, in seasonally flooded, dark, fine texture loamy soil. *E. ovata* is an understorey in *Acacia saligna* thicket, in seasonally flooded, dark, fine texture, sandy clay loam or sandy loam. *A. contorta* is in low open grassland of sandy soil. All these 7 grass species produce seeds in December.

Westonia experiences a Mediterranean climate. The region has 7-8 months of hot, dry summer, with a short cool wet winter. Much of the annual rainfall occurs over the winter months of May to August (Chapter 1, 1.3). Summer temperatures range from 35-45°C and winter temperatures 0-27°C. Therefore, plant growth (especially annual) is presumed limited to the periods of high soil moisture content following rain. Response of seed germination to temperature generally follows that of a temperature threshold. Too high or too low temperature generally results in low or no germination. For annuals, timing of seed germination in the field is considered to be roughly regulated by soil temperature. Fluctuating temperatures generally promote seed germination (Mott 1974b).

A series of germination tests was conducted under various conditions of incubation and pre-treatment temperatures to identify germination characteristics of grass species at SRNR. The main aims of this study were to investigate: Does hot water pre-treatment improve germination of these species? Under what temperature regime do most seeds germinate? How do germination and seedling characteristics vary between species?

5.3.2. Methods

5.3.2.1. Experiment 1: Effect of hot water (40°C) pre-treatment on germination.

All seeds used were collected from SRNR or nearby areas. Seeds were stored at room temperature (~ 21°C) under dry conditions until required for use. Two germination studies were undertaken. In this first study (October 1999), I used seed collected in December 1998 to examine the effect of hot water pre-treatment in 7 species *(A. strictus, A. contorta, E. ovata, N. alopecuroidea, A. elegantissima, A. caespitosa* and *S. scirpoidea)*. Pre-treatment was soaking of seeds in either hot water (40°C) or ambient (~20°C) temperature for 20 min. Each treatment was represented by 250 seeds, with 2 replicates ($\sum n = 500$ seeds), except for *S. scirpoidea,* where 150 seeds were used per treatment ($\sum n = 300$ seeds). After soaking, all seeds were surface sterilised with sodium hypochlorite, then rinsed with deionised water. Each batch was spread across the surface of a punnet, three-quarters filled with sterile coarse sand, then covered with 2 mm of sand. The punnets were maintained in a glasshouse. Any germinants were recorded and removed. Germination was defined as the time of emergence of the green cotyledon of the seed through the punnet surface soil.

To investigate variation in seedling characteristics between the species over the first two weeks, 8 seedlings of each of the seven grass species were grown from germinated seed in pots (10 cm diam. and 15 cm depth) in a mixture containing 1:1:1 coarse sand: fine sand: peat moss, with no fertiliser applied. At 14 d after transplanting, seedlings of each species were harvested. Seedlings were carefully removed from the pots and any adhering peat washed away from the root. Lengths of shoot and root were measured. Root and shoot were separated, placed in envelopes, dried at 60°C for 4 days and weighed to the nearest 0.1 mg. Root and shoot ratio were determined.

5.3.2.2. Experiment 2: Effect of incubation temperature on germination.

A year later, in the second study (October 2000), the effect of incubation temperature (15, 20, 25 and 30°C) on 5 species *(A. contorta, N. alopecuroidea, A. elegantissima, A. caespitosa* and *S. scirpoidea)* was investigated. Each treatment was represented by 200 propagules, with 3 replicates ($\sum$ n = 600 seeds). Each batch was spread across the surface of punnets, three-quarters filled with sterile coarse sand. The punnets were then placed in dark, incubation cabinets. Seeds were observed at daily intervals. Water was replenished as necessary. Any germinants were recorded and removed. Seeds of *S. scirpoidea* were collected in December 1999. All other seeds were collected in December 1998.

From the germination tests (experiment 1 and 2), percentage of germination and number of days to first and to 50% final germination were subjected to analysis of variance. Tukey's test was used to detect any significant difference in comparisons between treatments. Data were transformed to Arcsine to meet normality of data. The experiment was carried out at the laboratory of Environmental Biology, Curtin University of Technology.

5.3.3. Results

5.3.3.1. Experiment 1: Effect of hot water (40°C) pre-treatment on germination.

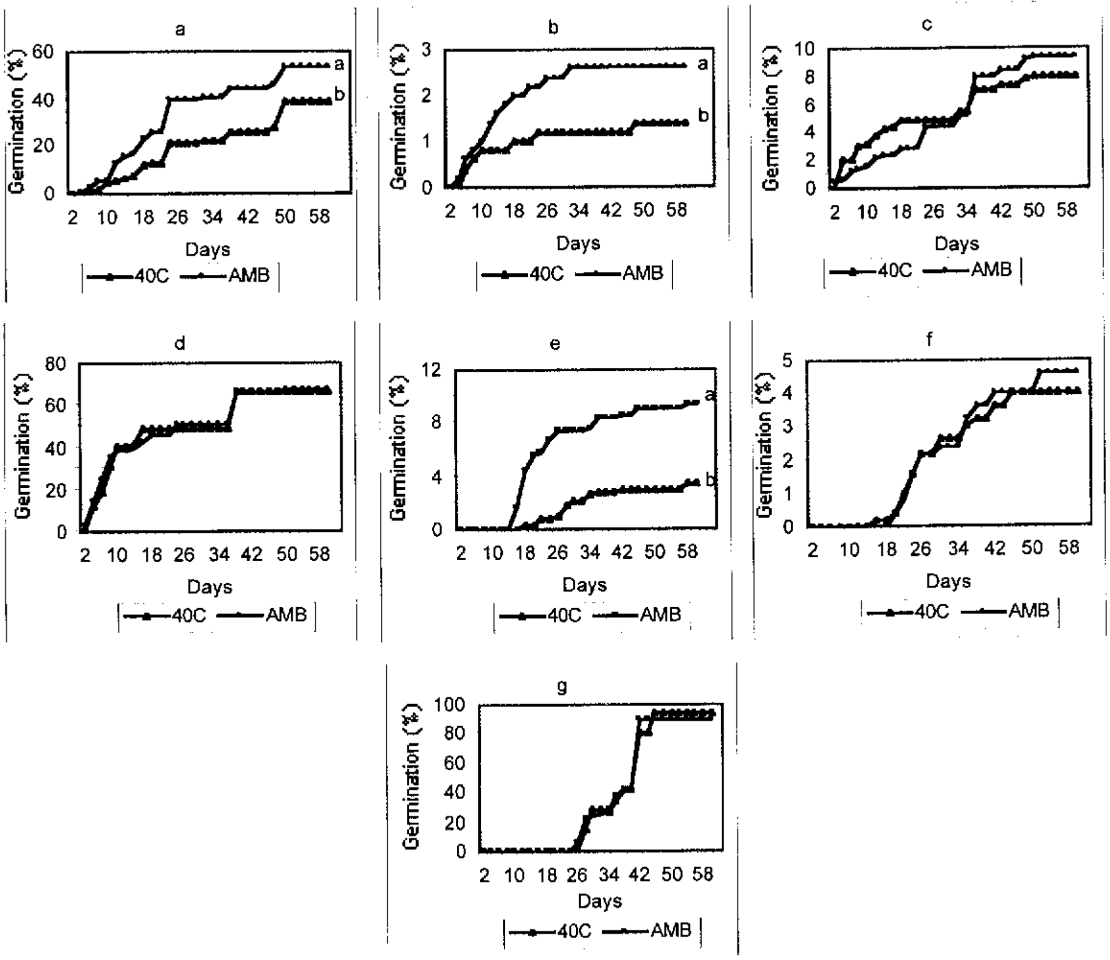

Figure 32. Effect of hot water (40°C) pre-treatment on germination of: a. *A. elegantissima*; b. *A. contorta*; c. *A. caespitosa*; d. *N. alopecuroidea*; e. *E. ovata*; f. *A. strictus*; g. *S. scirpoidea*. Species with different letters against temperature treatment indicate a significant difference between the means using Tukey's family error rate. No letters = analysis not significant.

Hot water treatment did not improve germination in any of the 7 species tested. In *A. elegantissima, A. contorta* and *E. ovata* (Figures 32 a, b and e), hot water pre-treatments reduce germination (all $P<0.001$). Germination of *E. ovata* was reduced from 10% at ambient temperature to only 4% after the 40°C treatment. In *A. caespitosa* and *A.*

strictus (Figures 32c and f), hot water pre-treatments did not affect germination but not significantly ($P = 0.750$ and 0.673). In *N. alopecuroidea* and *S. scirpoidea* (Figure 32 d and g) both pre-treatments gave about the same germination level ($P = 0.9740$ and $P = 0.920$).

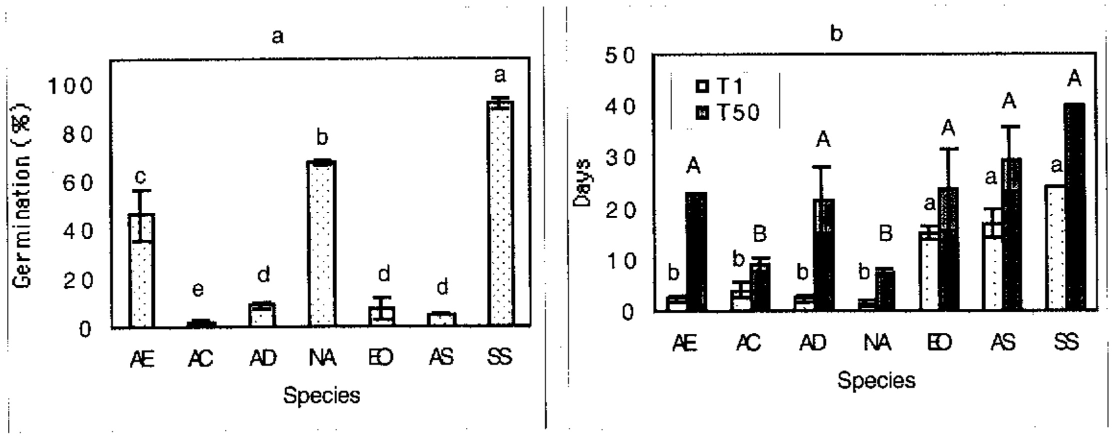

Figure 33. Comparison of germination between the species (mean data from all treatments). a. Germination (%). b. Day to first (T1) and 50% (T50) final germination. Species: AE = *A. elegantissima*, AC = *A. contorta*. AD = *A. caespitosa*, NA = *N. alopecuroidea*, EO = *E. ovata*, AS = *A. strictus*, SS = *S. scirpoidea*. Entries with different letters in species indicate a significant difference between the means using Tukey's family error rate. Bars represent standard errors.

Of all species, *S. scirpoidea* attained the highest germination level, with 92% seeds germinated (Figure 33a). The second highest level was attained by *N. alopecuroidea* with 67% germination. The third was *A. elegantissima* which gave 46% germination. All other species had less than 10% germination. The lowest level was *A. contorta* with only 2% germination.

The two most rapidly germinating species (*N. alopecuroidea* and *A. contorta*) required 1.5-4 d to first germination and 7.5-9 d to 50% final germination (Figure 33b). *A. elegantissima* and *A. caespitosa* commenced germination rapidly (2.5 d) but required three weeks (21.5-23 d) to give 50% final germination, suggesting a pattern of slow, steady germination. Three species (*S. scirpoidea, E. ovata* and *A. strictus*) required longer times to germinate, with 15-24 d to first germination and 24-40 d to 50% final germination. Of the 7 species, *S. scirpoidea* took the longest time to germinate. My observations suggest that *S. scirpoidea* has a particularly relatively hard seed covering, as of all the grass species studied, only in this species did a hot water pre-treatment improve germination, albeit slightly.

5.3.3.2. Experiment 2: Effect of incubation temperature on germination.

Germination in *A. contorta* was very poor at all incubation temperatures (not shown). Two species (*A. caespitosa* and *A. elegantissima*) germinated poorly at 30°C incubation (Figure 34a and b). In two species (*N. alopecuroidea* and *S. scirpoidea*), germination at 30°C was slightly lower but not significantly different from 15-25°C (Figure 34c and d). For *A. caespitose,* more seed germinated at 15°C; in *A. elegantissima,* seeds germinated slightly better at 20°C. In *N. alopecuroidea,* slightly more germination occurred at 25°C, while in *S. scirpoidea,* seed germinated equally well at 15 and 20°C incubation.

In *A. caespitosa* and *A. elegantissima,* there was no pronounced effect of incubation temperature on time to germinate (days to first and 50% final germination). For *N. alopecuroidea* and *S. scirpoidea,* germination was earlier at higher incubation temperatures (Figure 35a and b). In *N. alopecuroidea,* at 15°C incubation temperature seeds required 21 and 25 d to first and 50% final germination compared with only 7 and 12 d at 30°C. In *S. scirpoidea,* at 15°C incubation temperature seeds required 15 and 28 d to first and 50% final germination, compared with only 9 and 17 d at 30°C incubation temperature.

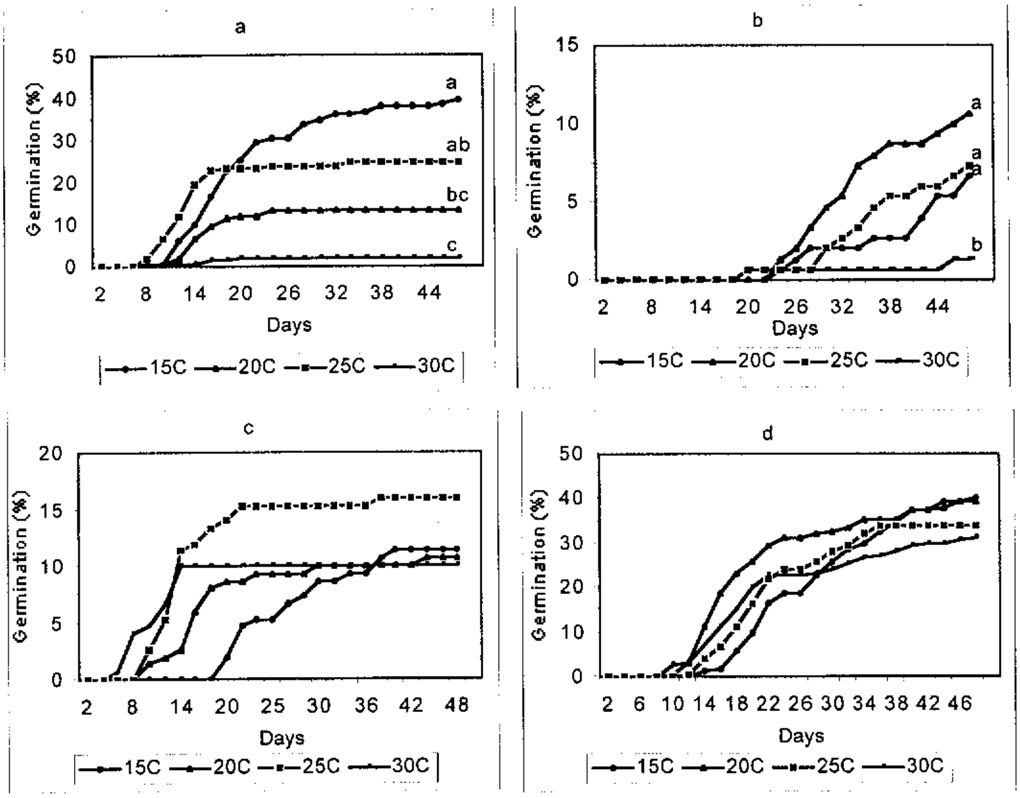

Figure 34. Germination in a range of incubation temperatures, of 4 grass species. a. *A. caespitosa*; b. *A. elegantissima*; c. *N. alopecuroidea*; d. *S. scirpoidea*. Entries with different letters in a treatment indicate a significant difference between means using Tukey's family error rate. No letters = analysis not significant (50 d).

The percentage of seed that germinated (50 d) was different between the species ($P<0.001$). The best level was attained by *S. scirpoidea* with 37% germination (Figure 36a). The second level was attained by *A. caespitosa* with 20% germination and the third level was attained by *N. alopecuroidea* with 12% germination. The poorest germination was attained by *A. contorta* with only <1% germination (not shown).

Of the 5 species, *A. elegantissima* required the longest time to germinate, with 24 and 36 days to first and 50% final germination (Figure 36b). The pattern was of low, steady germination. All other species had about the same speed and pattern of germination, initiated by slow germination, followed by more rapid germination and then slow germination at the end. In *A. contorta*, speed of germination was obscured due to very poor germination.

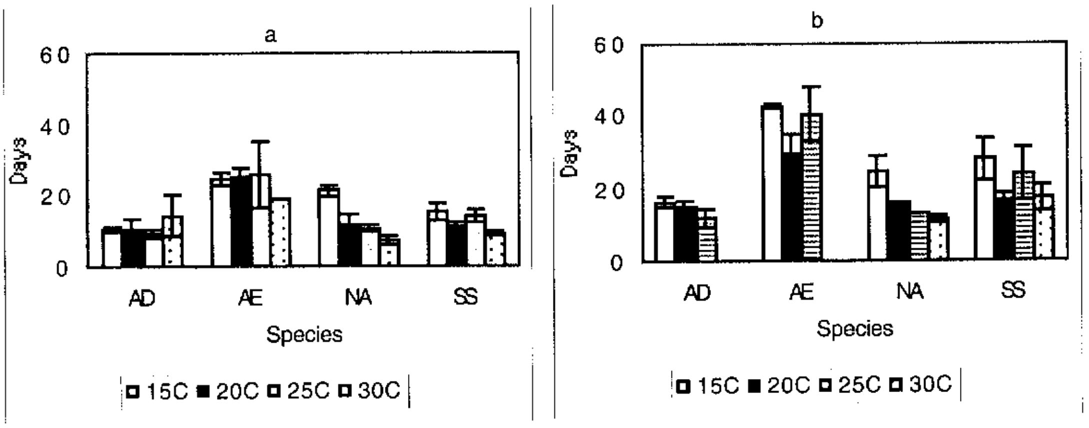

Figure 35. Days required for germination between the treatments. a. Day to first germination, b. Days to 50% final germination. Species: AD = *A. caespitosa*; AE = *A. elegantissima*; NA = *N. alopecuroidea*; SS = *S. scirpoidea*. Standard error bars shown.

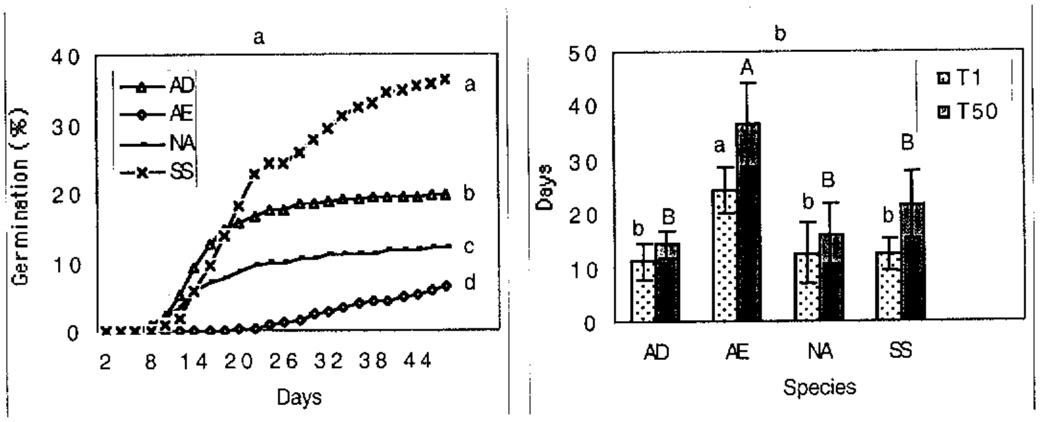

Figure 36. Comparison of germination between species after 50 days (mean data from all treatments). a. Germination (%). b. Days to first (T1) and to 50% (T50) final germination. Species legend as in Figure 35. Entries with different letters in a species indicate a significant difference between means using Tukey's family error rate. Bars represent standard errors (Figure 36b).

5.3.3.3. Comparison of experiments 1 and 2.

A comparison of germination in 1999 (glasshouse) and 2000 (incubation cabinet) found that of the 5 species examined in both years (except *A. caespitosa*), germination in the glasshouse was greater than in the incubation cabinets (Figure 37a). Factors responsible may have been: firstly, (except for *S. scirpoidea*) lower germination in 2000 than in 1999 may have been affected by reduced seed viability after 22 months storage (December 1998-October 2000). Secondly, fluctuating ambient temperatures in the glasshouse may have promoted germination. Lower germination in the dark incubation cabinet may indicate seeds require light for germination. Germination of *A. caespitosa* was greater in 2000 (19.8%) than in 1999 (8.7%). This may be explained by a storage period of more than one year being required to effectively break seed dormancy. Covering of seed by sand in the glasshouse treatment may also have reduced germination of *A. caespitosa*.

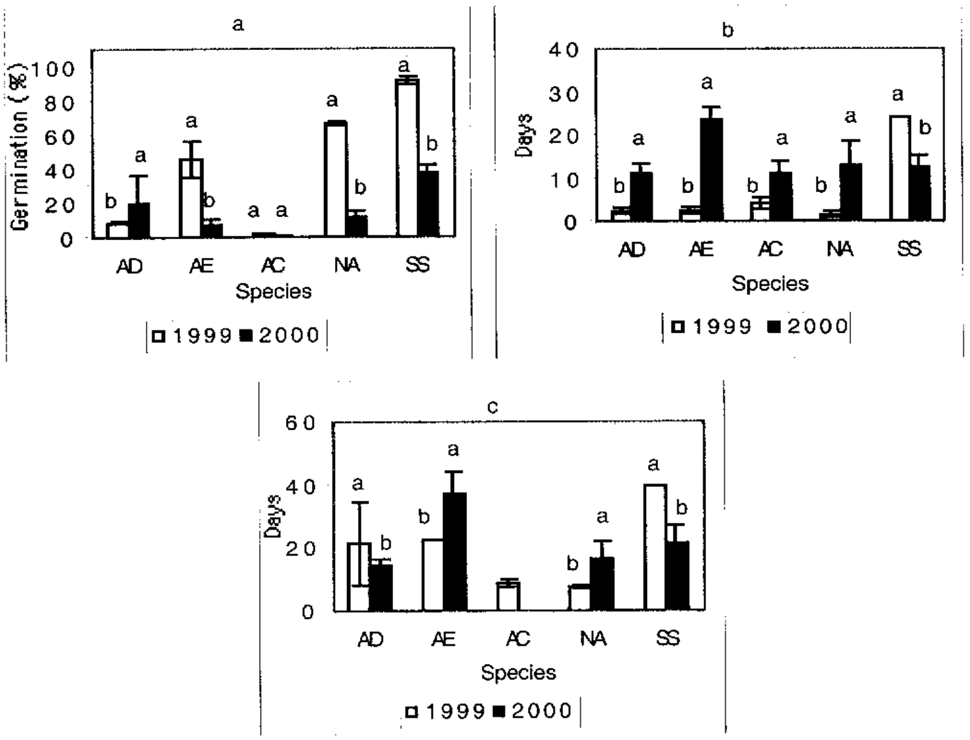

Figure 37. Comparison of germination in 5 grass species, germinated in glasshouse (1999, n=2) and incubation cabinet (2000, n=8). a. Percentage of germination. b. Days to first germination. c. Days to 50% final germination. Species legend is as in Figure 35. Entries with different letters in years indicate a significant difference between means using Tukey's family error rate. Bars represent standard errors.

Except in *S. scirpoidea*, and for days to 50% final germination of *A. caespitosa* (Figure 37b and c), germination required a shorter period in 1999 (glasshouse) compared to 2000 (incubation cabinet). In the glasshouse, 1.5-4 d were required for first germination compared to 11-24.4 d in the incubation cabinet. Fluctuating temperatures and/or presence of light in the glasshouse are presumed to have promoted earlier germination. Alternatively, longer storage time did not increase times to germination.

S. scirpoidea required 24 and 40 d to first and 50% final germination in the glasshouse, while in the incubation cabinet the periods were 12 and 22 d. Longer germination of *S. scirpoidea* in the glasshouse may have been affected by sand burial obscuring the result. As the *S. scirpoidea* seeds were from different years, they may have differed in viability. *A. caespitosa* seed gave more germination in the incubation cabinet than in the glasshouse and less time was necessary to finalise germination in the incubation cabinet then in the glasshouse.

5.3.3.4. Seed and seedling characteristics

Seed weight was obtained for caryopses, except in *S. scirpoidea* where seeds were naked. Of 7 grass species examined, *A. contorta* and *N. alopecuroidea* had the heaviest seed (Figure 38a) while the lightest seed was of *A. strictus*. Most seed weight is contributed by caryopsis, not cotyledon. Therefore, seed mass may not reflect seed size. The heaviest seedling shoot was found in *A. strictus* (Figure 38b). The heaviest root was attained by *E. ovata*. Of 7 species, only *E. ovata* had greater root than shoot. In all other species, shoot weight was greater than root weight (Figure 38c). In *A. strictus,* shoot weight was much greater in comparison to root weight.

The longest shoots and roots were attained by *A. elegantissima* (Figure 38d). *E. ovata* had a long root but a short shoot. *A. strictus* and *S. scirpoidea* both had short root and shoots. Comparing root to shoot length, *E. ovata* had the longest root : shoot ratio (Figure 38e). Root lengths were more than twice shoot length.

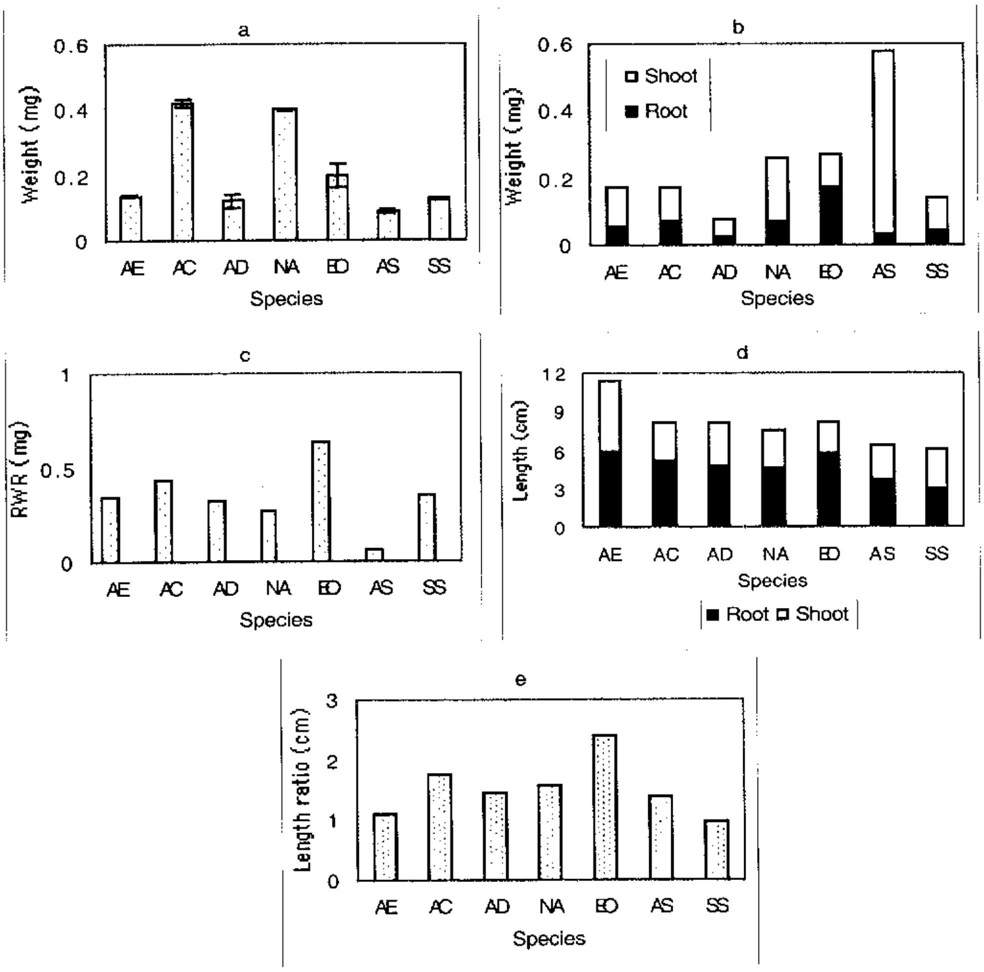

Figure 38. Seeds and seedling characteristics of 7 grass species. a. Seed weight (mean of 4 batches of 250 seeds/batch, except *S. scirpoidea,* 75 seeds/batch). b. Root and shoot weight. c. Root/shoot weight (RWR). d. Seedling length. e. Root per shoot length. Species: AE = *A. elegantissima*, AC = *A. contorta*, AD = *A. caespitosa*, NA = *N. alopecuroidea*, EO = *E. ovata*, AS = *A. strictus*, SS = *S. scirpoidea* (n = 8 seedlings per species).

5.3.4. Discussion

Germination values obtained generally reflect the dominance/abundance of each species at SRNR. *S. scirpoidea* attained the best germination (to 92%). Occupying the next level were *N. alopecuroidea* (to 67%), *A. elegantissima* (to 46%) and *A. caespitosa* (to 20%). Three species (*E. ovata, A. strictus* and *A. contorta*) gave relatively poor germination, with less than 10%. *A. contorta* seed germinated poorly. This species is said to have an obligate requirement for light at germination (Mott 1972). In the pastoral areas of WA it is a summer germinating grass, with incubation at 30°C giving optimum germination (Mott 1973). Jurado & Westoby (1992) classified *A. contorta* as a species of intermediate germination, in that little viable seed of this species remains after any rainfall sufficient to result in germination. Mott (1973) reported that less than 3% of *A. contorta* seed was still viable after being in the soil for one wet summer.

Mott (1974a) proposed two dormancy mechanisms are involved in *A. contorta* seed. One is associated with the embryo and is broken by storage at ambient temperatures : this mechanism is an after-ripening requirement. The second is associated with the enclosing palea and lemma and can be broken by their removal, by prolonged dry storage at high temperatures, by oxidising agents, such as hydrogen peroxide, or by removal of a small piece of the lemma over the embryo of the caryopsis. Mott & Tynan (1974) found that a lipid-containing layer covering the inside of the lemma was intact in dormant grain but was fractured in non-dormant grain.

Of the 5 grass species examined for best temperature regime for germination, all except *A. contorta,* all had more germination at 15-25°C than at 30°C. Therefore, they are more likely to germinate in the cool winter season. Presumably, these species are adaptive to germinate in winter when more moisture is available, and thus more seedlings are likely to survive. The same trend is shown in germination of *Acacia* species (section 5.2). However, the response of seeds to temperature in the field would likely differ. Exposure of soil-stored seed to the strong daily temperature fluctuation at the soil surface has been shown to increase germination in some species (Mott 1974b). Similarly, fluctuating temperature during germination in the field might have different effects from constant temperature.

The annual flora of the arid region of Australia has been described in various studies (Mott 1972; Baskin & Baskin 1988; Jurado & Westoby 1992) which note that the typical flora which occurs after winter rains is predominantly of dicotyledons, whereas Monocotyledons (especially grasses) make up a large proportion of summer germinating annuals. In this study however, most species at SRNR are seen to germinate in the cooler winter period. The flora is thus more similar to the typical flora areas of the southwest.

In 7 grass species subjected to pre-treatment, hot water (40°C) pre-treatment did not improve the level or rate of germination; indeed, hot water reduced germination. Hot water pre-treatment is not appropriate to break dormancy in grass seeds in this environment. Dormancy is a survival strategy that delays germination until conditions are favourable for growth. Baskin and Baskin (1998) claim that of the various types of dormancy available to plants, grasses only exhibits physiological dormancy. This can often be overcome by manipulating dry storage condition, via duration of storage, by injury to the seed covering layer or with application of gibberellic acid.

Generally, germination in glasshouses is greater and quicker than in incubation cabinets. Presumably in grass seed, fluctuating temperatures promote germination. In the 3 species, germination in 1999 was greater than in 2000. Lower germination in 2000 may be due to reduced seed viability after ~2 years storage. This syndrome may become more intense as seed gets older. This deterioration is usually termed physiological aging. In perennial rye grass (*Lolium perenne* L.), seed aging reduces the rate of germination and also extends mean germination time and reduces final percentage germination (Arachchi, Naylor & Bingham 1999). Seed ageing can also delay and reduce the emergence of the coleoptile and produce a higher proportion of abnormal seedlings. Soil temperature and moisture content at sowing determines the rate and success of seed germination and emergence.

Generally, *S. scirpoidea* and *A. elegantissima* required longer times to germinate, however *S. scirpoidea* germinated over a short time "window", suggesting that most seed had the same depth of dormancy, while *A. elegantissima* appears to show steady, slow germination. The different germination patterns among species indicates unequal dormancy. A variety of germination responses may be affected by the period of storage. Depth of dormancy varies with time in different ways, although the most frequent trend is a gradual reduction and ultimately loss. The duration of dormancy is genetically controlled, but environmentally regulated. This variability may induce the production of seeds with different depths of dormancy at the time of dissemination; this may be expressed as a high genetic variability among crops of a single species or among individuals of a single crop. These differences may be related to the duration of seed viability.

Seedlings that establish earlier than others in the same cohort will be at an advantage. This is mainly because such seedlings may be able to capture more resources, especially scarce resources (Harper 1977). In a study of three species of *Danthonia* (*D. linkii, D. tenuoir, D. richardsonii*), Lodder, Groves & Muller (1994) found that *Danthonia* seedlings failed to emerge when seed was sown at depths greater than 25 mm. Fewer germination obtained in the glasshouse treatment may have resulted from seed being covered with sand. Optimal temperature for germination of *Danthonia* was 20/10°C and this is nearly optimal for the genus generally (Hagon & Groves 1977; Lodder *et al.* 1994). This level is about that obtained in the present study. *Danthonia* did not require light for germination. This supports the results of this study with more germination in the dark incubation cabinet than in the glasshouse. Presumably, the inability of *Danthonia* to emerge from depth arises because of the relatively small seed reserve combined with a poor ability to elongate the sub-coleoptile inter-node (Whalley 1987). The sub-coleoptile elongation allows some grasses to emerge from deeper sowing. *Danthonia* caryopses should be sown as shallow as possible for maximum field emergence. Nutrient addition is suggested as not affecting establishment or germination in *Danthonia* (Hagon & Groves 1977).

In the more arid areas, *A. contorta* requires higher temperature for germination, normally germinating after summer rain and setting seed in autumn. However, in the milder southwest, germination occurs in the winter where rain is normally predictable. The mechanism responsible for dormancy in *A. contorta* is generally mechanical, residing in the glumes. The autumn seeds of *A. contorta* would remain dormant during the cool winter, before a short period of high soil surface temperature with summer break of dormancy and thus allowing germination to take place during the summer rain. Only a small amount of viable seed remains after germination, either in the field or laboratory, so that little is available for subsequent germination. However, in the southwest, germination occurs in the winter where rain is normally predictable. Thus, the life cycle varies with different climatic zones, with conditions unfavourable for completion of the life cycle (Mott 1974b). *A. contorta* has an obligate light requirement for germination. Seeds must occur near the surface and the surface must be moist during the germination period.

Germination of *Austrostipa compressa* is higher in light than darkness (Smith, Bell & Loneragan 1999). In this study, germination of the related *A. elegantisima* was reduced from 46% in the glasshouse to only 6% in the dark incubation cabinet. The ability to detect light quality is a mechanism that differs between the buried and the unburied state. There is no increase in germination of seeds after simulated fire-heating. This study also found that germination of *A. elegantissima* was reduced by the heat pre-treatment. Seeds of *A. compressa* germinated well at temperatures of 13-28°C (Smith *et al.* 1999). The optimum temperature obtained in this study for *A. elegantissima* (20°C) was in the range obtained for *A. compressa*. *A. compressa* maintains dormancy at high temperatures, preventing germination occurring until after summer rainfall events. Seeds that germinate in summer face a limited chance of survival as a result of water stress in the environment. Seed of *A. compressa* is significantly affected by temperature and light. Germination is greater in low temperature and with a light treatment. No seed germinated in complete darkness. Germination of *A. compressa* decreased with increased duration of heating and with increased temperature (Smith *et al.* 1999).

Of the 7 species examined, *A. strictus* appears to have the fastest growth compared to the other species. *E. ovata* had the heaviest roots. Only *E. ovata* had greater root mass than shoot mass. This rhizomatous perennial grass seems to be a strong competitor. In all other species, shoot ratio was greater than root ratio. This is characteristic of species growing in moist habitats. The longest shoot and roots were attained by *A. elegantissima*. This may be characteristic for this species as an understorey species in *Eucalyptus* woodland. *E. ovata* had long roots but a short shoot. *A. strictus* and *S. scirpoidea* both had relatively short roots and shoots. *E. ovata* had the highest root/shoot ratio. Root length was more than twice the shoot length.

CHAPTER 6

EFFECT OF SEED SIZE ON GERMINATION AND SEEDLING CHARACTERISTICS IN *ACACIA* SPECIES

6.1. General introduction

The seed of *Acacia* species is characterised by a thick or "hard" seed coat. This is responsible for seed coat-imposed dormancy. It is a barrier that must be broken to enable the embryo to obtain water needed to reactivate its metabolism and start growing. Therefore, before imbibition and germination can occur, the seed coat must be rendered permeable. In general, by virtue of their hard seed coat, which minimises moisture exchange and the loss of stored reserves through respiration, *Acacia* seeds retain their viability well for many years and present few storage problems. Seeds of some species can remain viable after 50 years in the field (Moffett 1952).

The possession of a hard seed coat has some ecological advantages; it favours the accumulation of persistent seed banks in the soil by preventing germination of viable seed in the soil for long periods. This spreads germination over time, increasing the chance that some seeds will germinate, establish, and complete the life cycle successfully (Bewley & Black 1994). The hard seed coat is waxy and water repellent. It can also be considered as having evolved to withstand unfavourable conditions such as heat caused by fire, strong teeth of dispersing animals or passage through the gut, severe drought and mechanical damage. In unpredictable environments, such as those of arid Australia, germination is often a high-risk event; possession of a hard seed coat reduces the risk of germination by avoiding depletion of the seed bank following a single large rainfall event. The hard seed coat has value in maintaining the population of plants.

Cavanagh (1985) describes the seed coat (testa) as effectively providing an impermeable barrier to water penetration. Anatomically, he defines it as a continuous layer of tightly packed, elongate Malpighian cells, directly below the water permeable cuticle. This Malpighian zone varies in thickness both within and between species. Under natural conditions, and after most artificial treatments, the first site at which water penetration occurs is at the lens (the strophiole), which blocks the hilum (a scar where the developing seed was attached). The lens is a site of structural weakness in the seed coat, comprised of shortened Malphigian cells which rupture under the stress induced by heating (Tran & Cavanagh 1984).

Numerous techniques have been used to render *Acacia* seeds permeable. Of all techniques, the boiling water treatment appears to give better results for many Australian *Acacia* species, whereas soaking in concentrated sulphuric acid is frequently more effective for African *Acacia* species (Doran *et al.* 1983; Cox *et al.* 1993; Danthu *et al.* 2002). Placing *Acacia* seeds in boiling water damages the cuticula and sometimes parts of the palisade layers of the seed coat and thus can effectively break dormancy. For several Australian *Acacia* species, soaking the seed at 80°C for 1-10 minutes is effective (Clements *et al.* 1977). The nature of the hard seed coat is species specific. Some species are sensitive to prolonged heating but germination is enhanced with a moderate heat pre-treatment. There are several *Acacia* species which have soft seed coats so pre-treatment before sowing is unnecessary or even lethal (Doran *et al.* 1983). Different responses may be obtained if seeds are divided into different size classes (Moffett 1952). The direct and indirect effects of seed size on seed coat thickness, seed coat permeability and the surface-volume ratio may determine both the speed and probability of successful germination.

The size of a seed is extremely variable; it varies across plant species, both among and within species (Wulff 1986; Westoby, Jurado & Leisman 1992). In many species, seed weight is phenotypically one of the least flexible characteristics (Fenner 1985). Seed weight is an internal trait that may affect different juvenile and adult characters and is probably one of the earliest indicators of offspring quality (Wulff 1986). The size of a seed depends on the form of the ovary, the condition under which the parent plant is growing during seed formation, on the species, size of the embryo, the amount of endosperm present and to what extent other tissues participate in seed structure and determination of seed size.

The wide differences in seed size among species has been related to the ecological conditions in which the plant is established. Species from open habitats tend to have lower mean seed mass than species from more closed habitats (Bonfil 1998). Species whose seedlings become established in shade tend to have heavier seed than those that can establish in the open. Species that grow in more advanced seral stages have heavier seeds than those that grow in early successional stages (Baker 1972). There is a tendency for increased seed weight when seedlings are likely to be exposed to drought after germination and where a rapidly developing root system is advantageous. There is an increase in seed weight from mesic to xeric environments, and this may be due to either or both of increased thickness of seed coat and greater seed content. Another trend is a decrease in seed weight with altitude. This may be associated with less moisture and lower temperatures (Baker 1972).

Seed and seedling size are often positively correlated. Seed size may be an important factor in seedling survival as it is likely to be affected by the quantity of metabolic reserves in the seed. A difference in seed size or weight may in turn affect any of the following: seed distribution (dispersal); seed water relations; persistence in the soil seed bank; seedling establishment; and, plant fitness (Bonfil 1998; Seiwa 2000). Small seeds are characteristic of species that have persistent, dormant, seed banks in the soil. Small size may facilitate burial, escape from predation, assist in dispersal and enhance germination rate. Small seeds tend to have a higher surface-volume ratio than larger ones (Wulff 1986).

One of the most effective adaptations for ensuring successful seedling establishment is the possession of large seeds. Seedlings from large seeds draw on greater metabolic reserves in the embryo and endosperm and thus can attain a larger initial seedling size (Westoby *et al.* 1992). The larger reserve in heavier seeds may allow more pre-photosynthetic growth of the seedling and thus better initial growth and survival. Larger food reserves will enable a seedling to establish its leaf system more quickly, thus allowing photosynthesis to proceed as soon as possible.

Larger seeds germinate earlier and achieve greater germination than smaller seeds, and this has been found in many species. Examples include pines e.g. Radiata pine (Griffin 1972); *Pinus taeda* (Dunlop & Barnett 1983); other forest trees e.g. *Virola surinamensis* (Howe & Richter 1982); *Lithospermum caroliniensis* (Weller 1985); *Quercus* (Tripathi & Khan 1990); and *Lobelia inflata* (Simons & Johnston 2000). Protein and carbohydrate concentration factors have been linked to size-specific variation in germination.

Variability in seed size may also affect the size of resultant seedlings. Large seeds contain more mineral nutrients and carbon-based reserves. A larger storage reserve allows for more extended pre-photosynthetic growth and greater attained size in early life. Therefore, large seeds may produce competitively superior seedlings that are more likely to tolerate adverse conditions (Black 1955; Weller 1985; Eriksson 1999; Seiwa 2000; Vaughton & Ramsey 2001). Large seed mass is highly advantageous for seedling establishment on nutrient poor soil (Vaughton & Ramsey 2001).

Although many studies have reported the role of seed size in influencing germination and seedling characteristics, very few have examined *Acacia* species. In this chapter, the possible effects of variation in seed size on germination and seedling size and the possible effects of variation in seed size on seed coat thickness were investigated in *A. fauntleroyi* and *A. prainii* (studies No. 1, 2 and 3). The aim was to develop a better understanding of recruitment in these species. These species are obligate seeders; they rely on seeds for recruitment and I have observed no evidence of suckering.

6.2. Study No. 1. Effect of seed size on germination and seedling characteristics in *Acacia fauntleroyi*

6.2.1. Introduction

A. fauntleroyi is an erect shrub, 1.8-5.0 (-7) m high. The bark is red and fibrous, stringy or shaggy. Plants are sometimes single stemmed but commonly have more than one stem (at 20 cm above ground level). Phyllodes are several nerved, grey-green or yellowish-green, more or less resinous and aromatic; flowers are yellow. At SRNR, it generally flowers in September and seed becomes mature in December. However, in March 2001 *A. fauntleroyi* was observed flowering (after previously flowering in September 2000).

Plants are found at the base of the main granite rock. They grow in shallow, coarse granitic sand, forming a well drained soil. Populations are few in number, plants form occasionally narrow groves with dense canopy shrubs. It is sometimes present with *Acacia lasiocalyx* and common with large clumps of the perennial grass *Spartochloa scirpoidea.* A population study of *A. fauntleroyi* at SRNR and its associated species was presented in chapter 3 (Section 3.3.3).

The Australian flora has evolved a wide range of germination responses that ensure survival. Environmental cues for germination and ecological conditions that occur in the habitat of the plants and seeds are often strongly correlated. In WA, germination response in a wide range of species is, as yet, largely unknown. A major limitation to the germination of native species is the mechanism of seed dormancy. Many leguminous seed have long dormancy periods determined by the presence of a hard, waterproof seed-coat. The hard-seeded species often present considerable problems in nursery production, where rapid and uniform germination is desirable. The following mechanisms are known to prevent seed germination in legumes (Cervantes *et al.* 1996): interference with water absorption and gas exchange; presence of chemical inhibitors; modification of the light spectrum, impinging upon the embryo; and, mechanical restriction of the hard seed coat. Of these, the impedance of water entrance into the seed is the most common cause of delay in seed germination (Cavanagh 1980).

Exclusion of water from penetrating the seed is determined by the presence of two structures: a water-proof layer of suberised sclereids in the seed coat, and the lens or strophiole, which blocks the hilum. Both can become worn by mechanical damage with the passage of time. Both can be artificially damaged by heating or abrasion, thus allowing seed rehydration and germination. Among legumes, damaging the coat or the strophiole usually results in the breakage of dormancy. The most widely used pre-germination treatments are short-lasting immersion of the seeds in boiling (or hot) water, exposure to dry heat and mechanical abrasion (scarification) or piercing of the coat.

The experiment reported here investigated to what extent are germination and seedling characteristics affected by seed size. Does pre-treatment improve germination? Under what temperature regime does most seed germinate?

6.2.2. Methods

Mature pods were collected in December 1999. Seeds were removed from the pods and sorted to enable removal of aborted, dry or infected seeds. Sound seeds were then stored at room temperature (21°C) under dry conditions until ready to use. Seeds were individually weighed to the nearest milligram using an electronic balance (AND, ER-180A). The mean mass per seed was determined, then seeds were placed in containers, categorised according to size.

6.2.2.1. Seed water content of seed of different size

Three seed size classes: small, medium and large (4<5.5 mg, 7<8.5 mg and 10<11.5 mg, respectively) were chosen to represent seed size variation among seeds. For each seed size class, 25 air-dried seeds ($\sum$ 75 seeds) were weighed individually every 24 hours (for 4 days) before and after attaining constant weight by drying in a 60°C cabinet. Percentage of seed water content (W) was calculated by dividing seed water content by seed dry weight (S) and seed water content [W (%) = W / (S + W) x 100].

6.2.2.2. Effect of seed size, pre-treatment and incubation temperature on germination.

The experimental design took three seed size classes (small, medium or large). These were subjected to conditioning in water adjusted to one of four pre-treatment temperatures (ambient, 50°C, 75°C or 100°C). Seeds were then incubated at one of two temperatures (15°C or 30°C). A total of 24 treatments were applied. Each treatment was represented by 3 replicates and each replicate was represented by 20 seeds (Σ n = 1440 seeds). Lots of 60 seeds for each treatment were prepared by pouring 30 ml of water into a glass beaker (50 ml volume capacity) containing the seeds at temperatures of 50°C, 75°C or 100°C, then left to cool to room temperature. Seeds were also covered with water at ambient temperature (~20°C) for the control.

After pre-treatment, all seeds were surface sterilised by shaking in sodium hypochlorite (3%), then rinsed with deionised water. Seed lots were than divided to three petri dishes, with 20 seeds per dish. Seeds were placed on two Whatman No. 3 filter papers (9 and 11 cm) in plastic petri dishes (diameter 11 cm). Petri dishes were partially filled with sterilised vermiculite (approximately 0.5 cm from the bottom). The vermiculite and filter paper were then moistened with the fungicide "previcure" (Hoescht Schering Agrevo, Glen Iris, Vic. Australia) to reduce fungal growth, and deionised water was added to maintain a humid environment within the dish. For each treatment, three petri dishes were then placed in dark, incubation cabinets at 15°C and 30°C.

Seeds were observed at daily intervals. Additional water and previcure was applied in the petri dish when required. Radicle emergence (~2 mm) was the criterion for deciding if germination had taken place. Any germinants were recorded and removed; counting of the germinated seeds was continued until no more germination occurred for 14 successive days. Parameters recorded were number of seed germinated and speed of germination (number of days to first germination and number of days to 50% final germination). Numbers of seeds that germinated and speed of germination were subjected to one way analysis of variance, and the general linear model (GLM) was applied to determine the interaction effect between treatments (Ott 1993). Tukey's test was used to detect any significant difference in the comparison within the treatments. Data were transformed to Arcsine, to meet normality criteria. Distributions of seed mass were examined using descriptive statistics. Kurtosis and skewness of seed mass were obtained. Kurtosis is a measure of how different a distribution is from the normal distribution. A negative value indicates a distribution with more peaks than normal. A positive value indicates a distribution flatter than normal. Skewness is a measure of asymmetry. A value more or less than zero indicates skewness in the data.

6.2.2.3. Effect of seed mass on seedling mass.

Germinated seeds from small (4<5.5 mg) and large (10<11.5 mg) size categories were planted into 5 x 5 x 5 cm cells with a mixture containing 1: 1: 1 coarse sand: fine sand: peat moss, with no fertiliser applied. The trays were maintained in a glasshouse and watered daily. The transplant date were recorded for each seedling to enable individuals to be harvested as 50 day-old seedlings. At this age, 30 seedlings from small and large seeds were harvested. Seedlings were carefully removed from the trays and any adhering peat washed away from the roots. Shoots and roots were separated, dried at 60°C for 4 days and weighed to the nearest 0.1 mg. Root and shoot ratios were determined and compared using analysis of variance.

6.2.3. Results

6.2.3.1. Seed mass variation and seed moisture content

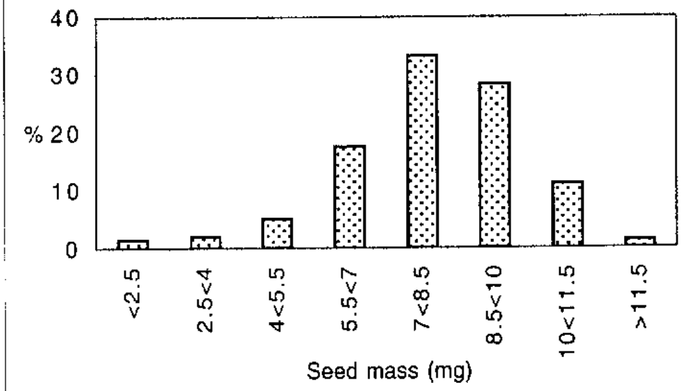

Figure 39. Distribution of seed mass (%) of *A. fauntleroyi* (n = 650 seeds) collected in 1999.

Seed mass spanned the range from 0.8-14.3 mg (mean = 8.3 ± 2.0 mg, n = 650). Distribution was skewed to the left (-0.727); there were more seeds with mass more than the mean than would be expected for a normal distribution. The distribution also exhibited positive kurtosis (1.385); there were more seeds near the mean than expected for a normal distribution (Figure 39). Seeds attained a constant weight after drying for 72 hr in the 60°C oven. Larger seeds had significantly more water per seed than smaller seeds (P = 0.004). Small seed had a mean of 0.48 mg water or 9.90% of dry weight, medium seed had 0.66 mg or 8.05% and large seed had 0.80 mg or 8.08%. These percent moisture values did not differ significantly between seed weight classes.

6.2.3.2. Effect of seed size, pre-treatment and incubation temperature on germination.

Of the 1440 seeds sown, 1014 germinated (70.42%); with 318 (66%), 361 (75%) and 335 (70%) in small, medium and large seed size classes respectively. Small seeds produced fewer germination than medium and large seeds. The general linear model (GLM) applied to numbers of seed germinated (days 20, 40 and 60) reveals seed size, pre-treatment temperature, incubation temperature and interaction all affected the number of seed that germinated (Table 34). Of the treatments applied, pre-treatment (conditioning) temperature affected germination more than incubation temperature. Incubation temperature affected germination more than seed size. The interaction of seed size and pre-treatment temperature was stronger than between seed size and incubation temperature (shown by *F* value).

Table 34. *F* and *P* values of general linear model on numbers of seed germinated by seed size, pre-treatments and incubation temperature, at 20, 40 or 60 days from setting out.

Source of variation/days	20		40		60	
	F	*P*	*F*	*P*	*F*	*P*
Seed size (S)	50.58	<0.001	15.03	<0.001	7.52	0.001
Pre-treatment (P)	186.11	<0.001	125.76	<0.001	174.39	<0.001
Incubation (I)	91.14	<0.001	30.12	<0.001	17.39	<0.001
S X P	34.68	<0.001	19.65	<0.001	30.06	<0.001
S X I	10.46	<0.001	6.79	0.003	13.00	<0.001
P X I	3.93	0.014	8.40	<0.001	11.85	<0.001
S X P X I	7.64	<0.001	7.27	<0.001	6.73	<0.001

Table 35. Mean number of germinated seed as affected by seed size (n = 24 for replicates, 20 seeds per replicate), pre-treatments (n = 18 for replicates, 20 seeds per replicate) and incubation temperature (n = 36, for replicates, 20 seeds per replicate).

Seed size	Days 20	Days 40	Days 60	Pre-treatment	Days 20	Days 40	Days 60	Incubation	Days 20	Days 40	Days 60
Small	11.54a	12.67a	13.17	Ambient	3.44c	4.94c	7.00c	15°C	7.75b	11.11b	12.17
Medium	9.38ab	12.75a	13.91	50°C	5.39c	9.44c	10.83b	30°C	11.42a	13.11a	13.97
Large	7.83bc	10.92b	12.21	75°C	13.72b	17.78a	18.47a	*F*	91.14	30.12	1.67
F	50.58	15.03	0.49	100°C	15.78a	16.28b	16.33a	*P*	<0.001	<0.001	0.200
P	<0.001	<0.001	0.616	*F*	186.11	125.76	32.48				
				P	<0.001	<0.001	<0.001				

Entries with different letters in a column indicate a significant difference between means using Tukey's family error rate. No letters = analysis not significant.

Over a 60-day period, seed of all seed size classes (small, medium and large) produced about the same final germination level (Figure 40a), however smaller seed germinated sooner (Table 35). Of the range of pre-treatments applied, optimum pre-treatment for seeds of *A. fauntleroyi* was soaking in water at 75°C, which gave more than 90% germination (Figure 40b). Soaking at ambient or 50°C gave lower germination, while soaking in boiling water gave slightly reduced germination.

Of the incubation treatments applied, 30°C gave greater and faster germination than 15°C incubation (Figure 40c). Speed of germination (days to first and 50% final germination) between seed sizes (Figure 41a), pre-treatment (Figure 41b) and incubation temperatures (Figure 41c) were clearly varied (all $P<0.001$).

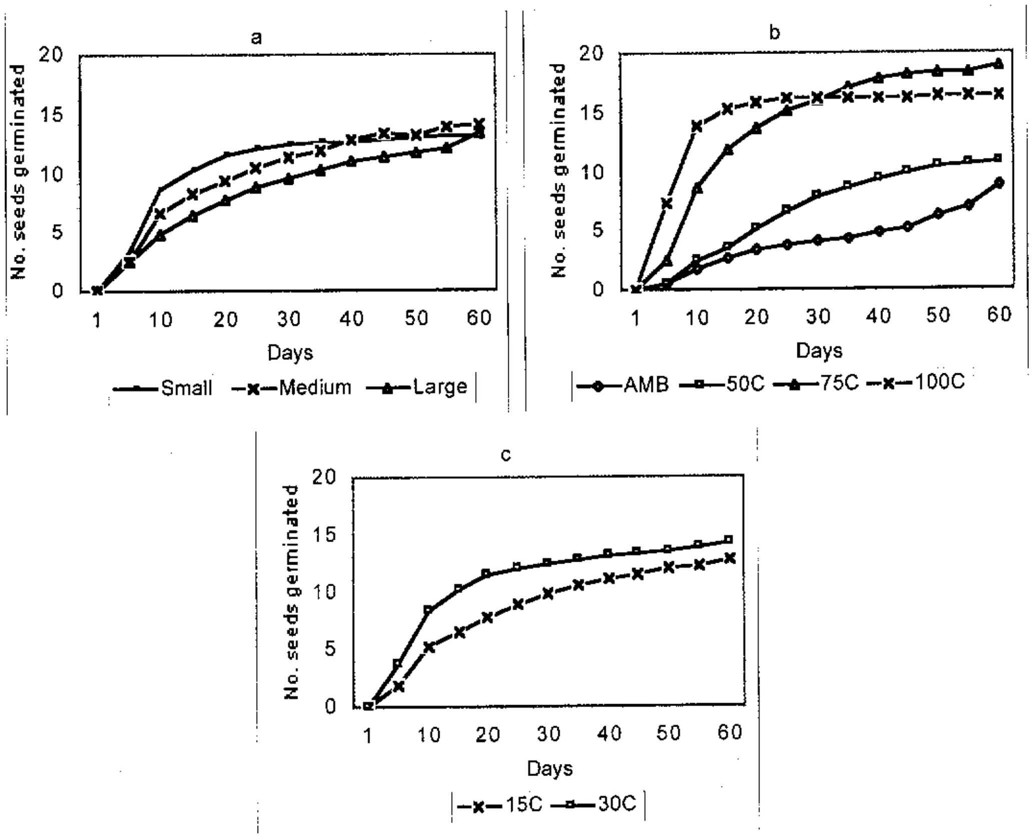

Figure 40. Germination by: a. Seed size. b. Pre-treatments. c. Incubation (n = as in Table 35). AMB = ambient temperature.

With the interaction of seed size and pre-treatment temperature (Table 36), at ambient pre-treatment, smaller seeds produce greater germination than larger seed (Figure 42a). The proportion of soft seed was clearly related to seed size. Following soaking at 50°C, germination by 20 days was greater in small seeds. However, after 40 days, small and medium seeds attained about the same germination level, more than with large seeds (Figure 42b). Soaking at 50°C, plus prolonged exposure to moisture improved germination in medium seeds but not to the same extent as in large seeds. This suggests that medium seeds have a thinner seed coat and are more easily damaged than large seeds.

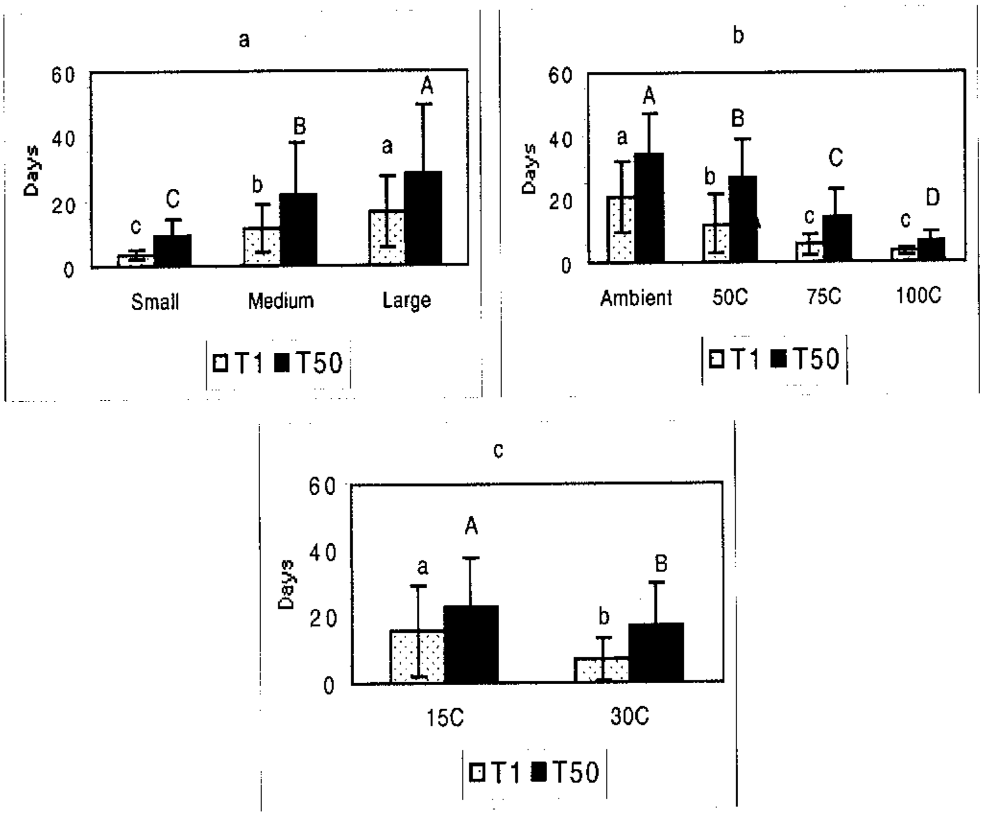

Figure 41. Speed of germination by: a. Seed size; b. Pre-treatment; c. Incubation: T1 = days to first germination; T50 = days to 50% final germination. Entries with different letters among treatments indicate a significant difference between means using Tukey's family error rate. Bars represent standard error.

Table 36. Mean numbers of germinated seed at 20, 40 and 60 days by seed size and pre-treatment temperature (n = 6, for replicates, 20 seeds per replicate).

Seed size/	20				40				60			
days	AMB	50°C	75°C	100°C	AMB	50°C	75°C	100°C	AMB	50°C	75°C	100°C
Small	7.50a	10.67a	17.67	10.33b	8.83a	13.00a	18.00	10.83b	10.17a	13.50a	18.00	11.00b
Medium	2.33b	3.50b	13.50	18.67a	4.33b	10.17a	18.00	18.50a	7.33ab	12.00a	18.50	18.50a
Large	0.50b	2.00b	10.00	18.83a	1.67bc	5.17b	17.33	19.50a	3.50b	7.00b	18.83	19.50a
F	11.59	18.42	3.15	49.04	6.23	7.88	0.40	63.56	3.55	7.81	1.28	71.94
P	<0.001	<0.001	0.072	<0.001	0.011	0.005	0.677	<0.001	0.065	0.005	0.306	<0.001

Entries with different letters in a column indicate a significant difference between means using Tukey's family error rate. No letters = analysis not significant. AMB = ambient temperature.

After soaking at 75°C, all seeds attained greater germination (Figure 42c). Of some interest is that small seed peaked sooner, with most germinating in less than 20 days. At 20 days, medium seeds exceeded 65% germination, whereas large seeds had exactly 50%. After 40 days, small and medium seeds attained the same germination, slightly greater than large seeds, so it may be concluded that as seed size increases, a longer time is necessary for germination to finish.

The boiling water treatment resulted in greater germination in large and medium seed than in small seed (Figure 42d). Exposure to boiling water may have killed ~50% of the small seeds. This is the reverse of ambient pre-treatment, in which ~50% germinated without any heat stimulus. It is presumed that all small soft seeds are killed by the boiling water treatment while all small hard seeds cannot germinate in ambient pre-treatment. Therefore, in total, most of the small seeds are viable. Boiling water treatment also causes medium and large seeds to germinate sooner, with most germination in 10 days.

Of the pre-treatments applied, it was found that soaking small seeds in water at 75°C was the best treatment to improve germination (Table 37 and Figure 43a), with both soft and hard seed germinating equally well. In medium and large seeds, in which most seeds were hard-seeded, soaking at 75°C and 100°C were the best method (Figure 43b and c). For medium and large seeds, seed germinated faster from boiling water than the 75°C pre-treatment. Some 95% of medium seeds germinated by 20 days from the boiling water treatment. This level was not attained until 45 days after soaking seeds at

75°C. Some 94% of large seeds germinated by 20 days from the boiling water treatment. Fifty days was required to reach this level after soaking at 75°C. Thus, incubation requires longer times for germination after less severe pre-treatment.

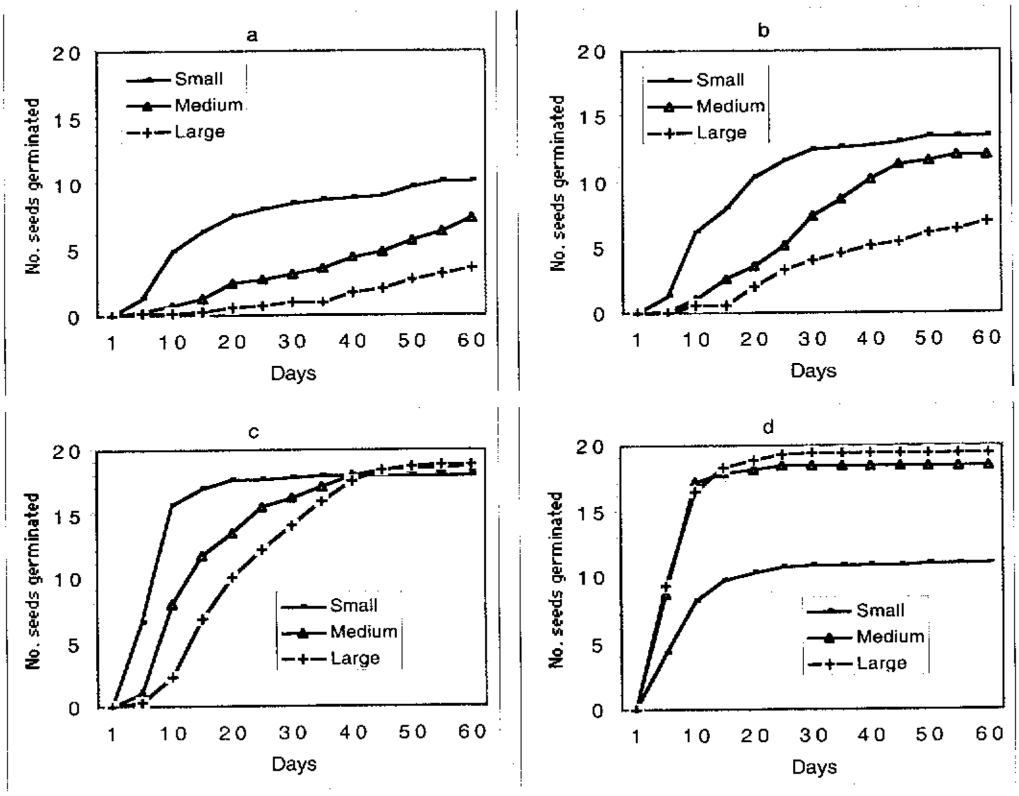

Figure 42. Germination by seed size, separate graphs for each of the 4 pre-treatments. a. Ambient temperature; b. 50°C; c. 75°C; and d. 100°C (n = as in Table 36).

Table 37. Mean numbers of germinated seed at 20, 40 and 60 days by pre-treatments and size of seed (n = 6, for replicates, 20 seeds per replicate).

Days/	20			40			60		
Pre-treatment	small	medium	large	small	medium	large	small	medium	large
Ambient	7.5 c	2.3 c	0.5 c	8.8 c	4.3 c	1.7 b	10.17b	7.33b	3.50b
50°C	10.7 b	3.5 c	2.0 c	13.0 b	10.2 b	5.2 b	13.50b	12.00b	7.00b
75°C	17.7 a	13.5 b	10.0 b	18.0 a	18.0 a	17.3 a	18.00a	18.50a	18.83a
100°C	10.3 bc	18.2 a	18.8 a	10.8 bc	18.5 a	19.5 a	11.00b	18.50a	19.50a
F	19.763	30.09	26.827	16.403	36.432	55.26	13.98	16.29	60.69
p	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Entries with different letters in a column indicate a significant difference between means using Tukey's family error rate. No letters = analysis not significant. AMB = ambient temperature.

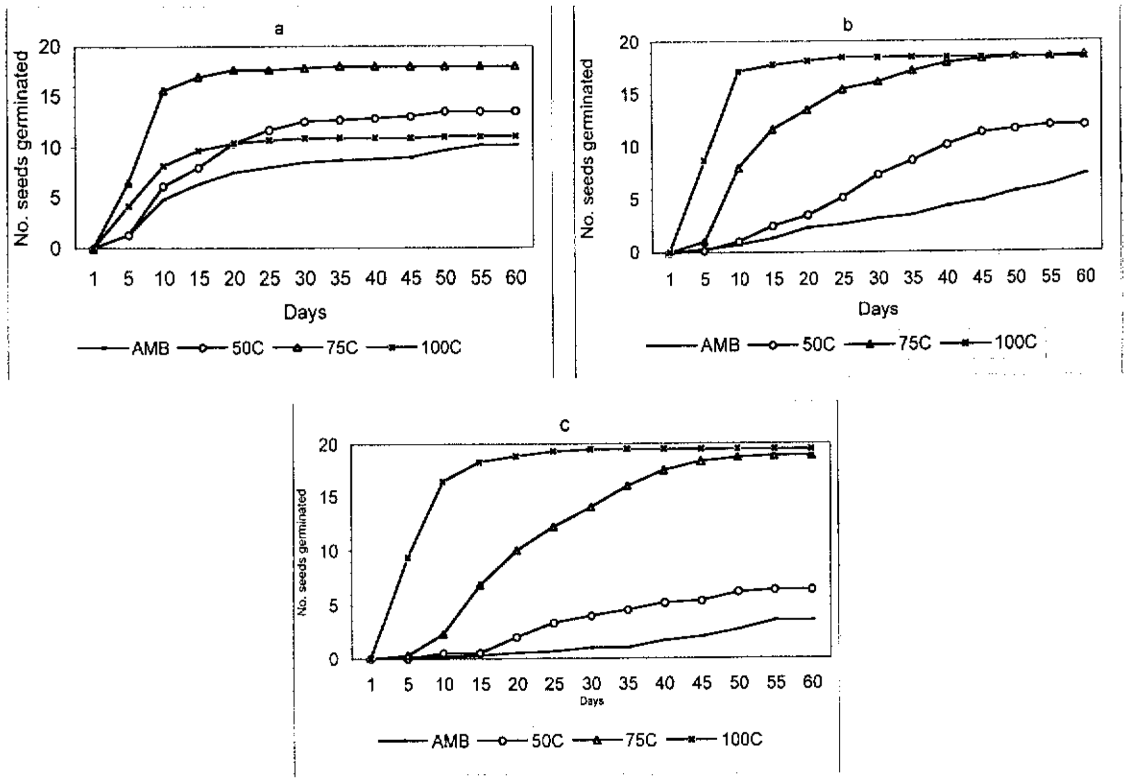

Figure 43. Germination by pre-treatment, separate graphs for each of the seed sizes. a. Small; b. Medium; and, c. Large seed (n = as in Table 37). AMB = ambient temperature.

Table 38. Mean number of germinated seed at 20, 40 and 60 days by incubation temperatures and size of seed (n = 12, for replicates, 20 seeds per replicate).

Days/	20			40			60		
Incubation	small	medium	large	small	medium	large	small	medium	large
15°C	10.7	6.9	5.7	12.8	11.3	9.3	13.75	12.42	10.83
30°C	12.4	11.8	10	12.6	14.3	12.5	12.58	15.75	13.58
F	0.937	2.745	1.667	0.009	1.282	0.877	0.56	2.14	0.78
p	0.346	0.112	0.21	0.924	0.27	0.359	0.462	0.158	0.388

With the interaction of seed size and incubation temperature (Table 38) in small seeds, 30°C incubation gave a slightly lower final germination than at 15°C (Figure 44a), while for medium and large seeds (Figure 44b and c), more germination occurred at 30°C incubation. Therefore, it may be concluded that 30°C incubation was slightly unfavourable for small seeds. However, in all seed size classes, germination was more rapid at the highest incubation temperature (30°C) than at the lowest (15°C).

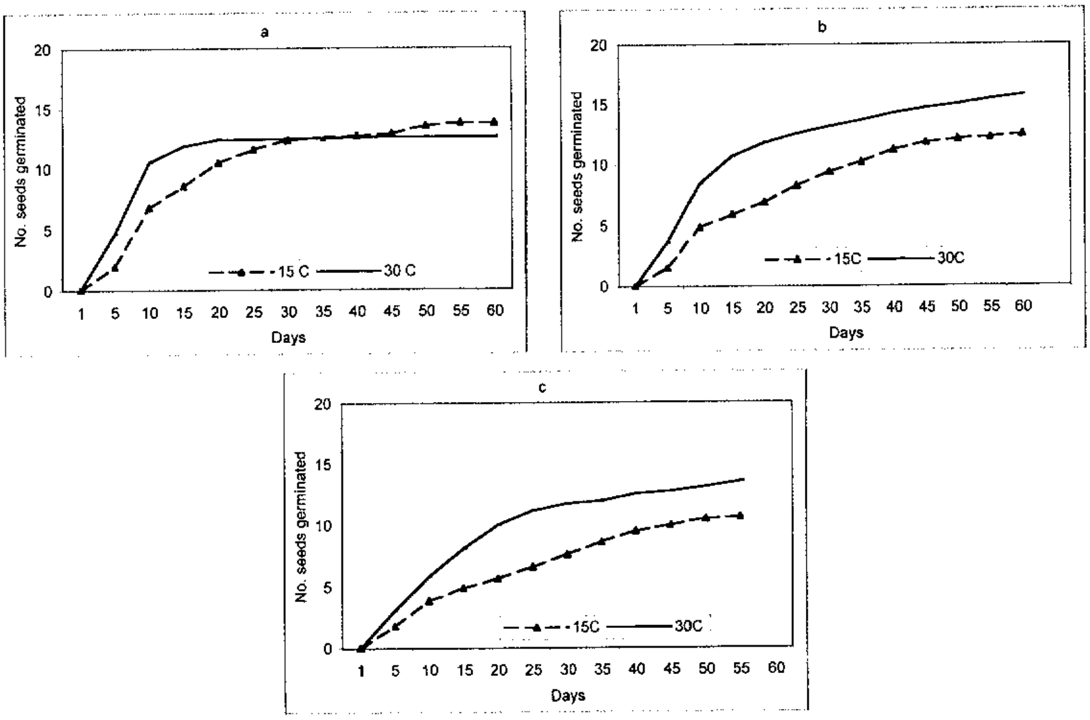

Figure 44. Number of germinated seed by temperature of incubation: a. Small seed. b. Medium seed. c. Large seed (n = as in Table 38).

After 60 days of germination at 15°C incubation (Table 39), small seeds produce slightly greater germination than medium and large seeds (Figure 45a), while at 30°C incubation (Figure 45b), germination is slightly greater in large and medium than in small seeds, although not significantly different. Larger seeds appear to take longer to germinate and require a higher incubation temperature. This suggests that smaller seeds are more likely to germinate in a cooler season and to germinate more rapidly than the larger seeds, while larger seeds require longer times.

The interaction of pre-treatment and incubation temperature on number of seed that germinated reveals that pre-treatment at high temperatures (75°C and 100°C) does not require high temperature incubation to improve the level of germination (Figure 46c and d). Both 15°C and 30°C incubation gave the same germination level. For seed pre-treated at low temperatures (ambient and 50°C), high temperature incubation (30°C) was needed to improve the level of germination (Figure 46a and b).

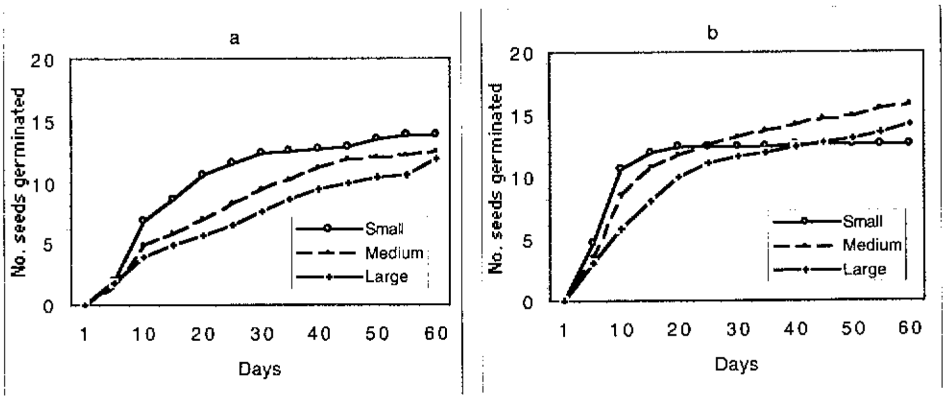

Figure 45. Effect of seed size and incubation temperature on number of seed germinated. a. Incubated at 15°C; b. Incubated at 30°C (n = as in Table 39).

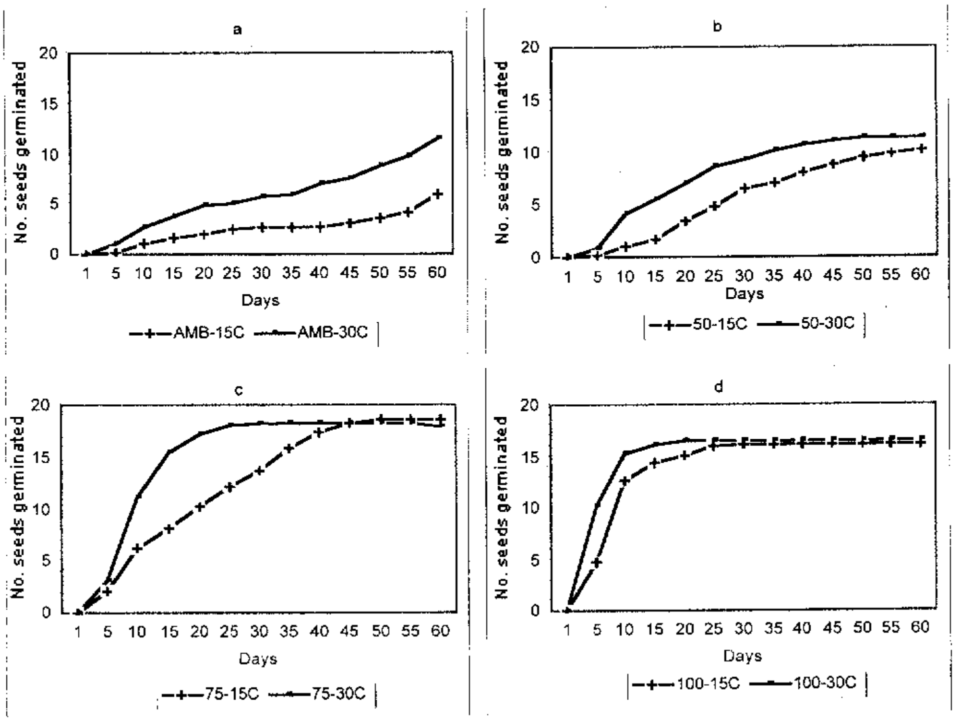

Figure 46. Effect on number of seed germinated by the pre-treatment. a. Ambient; b. 50°C; c. 75°C; d. 100°C; and incubation temperature 15°C or 30°C. AMB = ambient temperature. Each line represent the germination from 20 seeds in 6 dishes (=120).

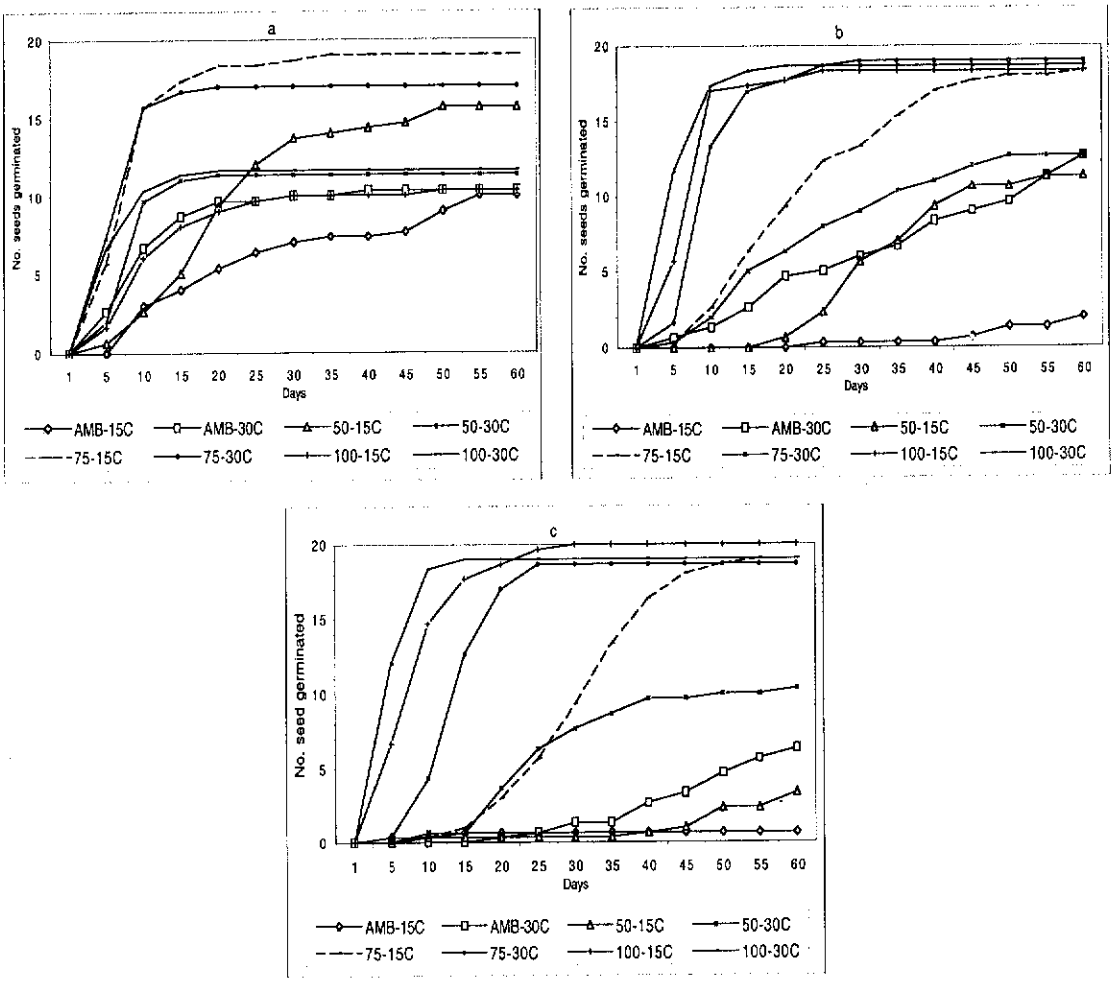

Figure 47. Effect of seed size, pre-treatment and incubation temperature of *A. fauntleroyi* seeds on number of seeds germinated; separate graph for each of seed size. a. Small seed. b. Medium seed. c. Large seed. AMB = ambient temperature. Each line represents the mean germination of seed from 3 petri dishes (n =3). Each replicate had 20 seeds.

Table 39. Mean number of germinated seed at 20, 40 and 60 days by seed size and incubation temperatures (n = 12, for replicates, 20 seeds per replicate).

Days/	20		40		60	
Seed size	15°C	30°C	15°C	30°C	15°C	30°C
Small	10.67	12.42	12.75	12.58	13.75	12.58
Medium	6.92	11.83	11.25	14.25	12.42	15.75
Large	5.67	10.00	9.33	12.50	10.83	13.58
F	1.62	0.44	0.62	0.40	0.50	1.72
P	0.213	0.646	0.542	0.675	0.611	0.194

Entries with different letters in a column indicate a significant difference between means using Tukey's family error rate. No letters = analysis not significant.

Considering the interaction of seed size, pre-treatment and incubation temperature on number of seed that germinated, the best treatment for small seeds is pre-treatment at 75°C and incubation at 15°C (Figure 47a). This gives more than 90% germination. For small seeds pre-treated and incubated at high temperatures, germination is reduced. This is because small seeds possess thinner seed coats which are more easily damaged. In medium and large seed, the best combination is pre-treatment at 75°C and incubation at 30°C or pre-treatment at 100°C and incubation at either 15 or 30°C. In all these combinations, seed gave more than 90% germination (Figure 47b and c). For medium and large seeds, due to their thicker seed coats, higher pre-treatment or incubation temperatures are required. For the two heavier seed size classes (medium and large), pre-treatment at 75°C and incubation at 15°C also gave a high germination level (>90%), however seeds require a longer time to germinate. Slightly less germination of small seeds in 30°C incubation and 100°C pre-treatment temperature suggests the susceptibility of small seed to damage by high temperature. High temperature may promote denaturation of enzymes.

6.2.3.3. Effect of seed mass on seedling mass.

Under controlled conditions, seedlings of *A. fauntleroyi* (50 d old) had about three times more shoot than root mass. This may be a consequence of this species having an epigeous germination mode and growing naturally in a relatively moist habitat (at the edge of the granite rock). Seedling mass of seedlings raised from large seed was more than two-fold that of small seeds (Figure 48a). Seedlings of large seeds had significantly heavier root and shoots (all $P<0.001$).

Although not significantly different, small seedlings had a slightly higher root ratio (RWR) than large seedlings ($P = 0.142$). Large seedlings had a slightly greater shoot ratio (SWR) than small seedlings ($P = 0.219$). Thus, there was slightly greater early investment of seed reserves to roots in small seedlings than in large seedlings (Figure 48b). Linear regression analysis reveals there were significant relationships between root mass (Rm) and seedling mass (Sdm): $\text{Sdm} = 0.145 + 2.29\ \text{Rm}$, $P = 0.001$

(for small seedlings); and Sdm = 0.497 + 1.71 Rm, $P<0.001$ (for large seedlings). The relationship was slightly stronger in seedlings raised from large seed than those from small seed.

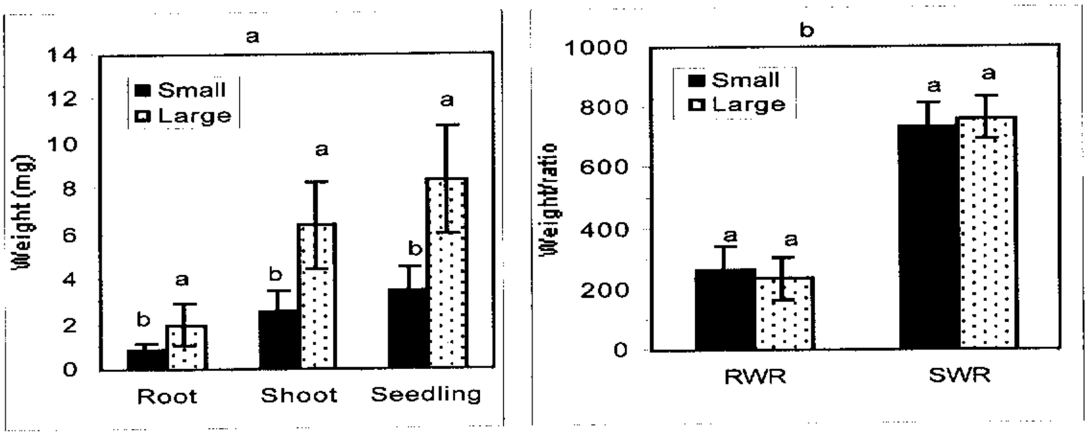

Figure 48. Comparison of mean seedling dry mass of *A. fauntleroyi* raised from small and large seeds, 50 d after germination (n = 30 seedlings per seedling size). a. Root, shoot and seedling weight. b. Root/shoot weight (RWR) and shoot/root weight (SWR). Entries with different letters in a character indicate a significant difference between means using Tukey's family error rate. Bars represent standard error.

By comparing mean seedling weight (n = 30) with mean seed weight (n =100), this suggests that seedlings grown from small seeds are less efficient in the use of stored resources than those from large seeds. At 50 d after germination, small seedlings used 32% of mean seed mass for respiration, compared to only 25% in large seedlings. Seedlings raised from large seeds have the potential for greater pre-photosynthetic growth.

6.2.4. Discussion

6.2.4.1. Distribution of seed size and seed water content.

The pattern of distribution in seed mass in 1999 indicated the population was skewed to the left and had positive kurtosis. Most seeds collected belonged in the heavier size categories with only a few poorly formed, light-weight seed. The heavy rainfall in 1999 (597.2 mm) presumably promoted seed production in that year. Seed sizes are rarely considered in *Acacia* species, however, the 1999 results revealed the range of seed weight was from 0.8-14.3 mg. Seed sizes clearly affected the germination patterns. A range of seed sizes gives plants an advantage in seed dispersal. After ripening, seeds disperse by falling to the ground. They may then be moved in flood water, washed by rain run-off or stream action. It is presumed that seed of different seed masses will disperse to different distances and become buried at different depths. Such dispersal would give greater chances of seeds finding favourable habitat.

Witkowski & Garner (2000) found that mean depth of seed burial is more or less inversely proportional to seed mass in *Acacia nilotica, A. tortilis* and *Dichrostachys cinerea*. Size and shape of seeds is also considered important in determining characteristics of the seed bank. Large seeds and seeds with a large surface/volume ratios are less likely to be incorporated into the soil seed bank. Such seeds have less chance of finding their way passively down cracks in the soil or of being buried by soil animals. Therefore, seed size tends to affect the persistence of seed in the soil seed bank.

In *A. fauntleroyi,* seed moisture content was 8.5%. In 22 *Acacia* species collected from Argentina, Chile and Paraguay, Lamarque *et al.* (2000) found that seed moisture spanned the range from 4.2-10.0%. In *A. fauntleroyi* seed collected in 1999, the larger seeds had greater water content than smaller seeds. Larger seeds also required a slightly longer time to lose water than smaller seeds. This suggests that larger seeds would be more likely to retain water longer for germination. Wilson & Witkowski (1998) found an inverse correlation between imbibition rate and seed mass in four African savanna species. So it may be presumed that larger seeds require longer times to imbibe and also to lose water than smaller seeds. Impermeable seeds normally have lower water contents than permeable seeds. In *A. fauntleroyi,* there were more soft seeds in the smaller seeds, however these had lower water contents. Therefore, it is presumed that in *Acacia* species, hard-seededness is less affected by initial seed moisture content and more by seed coat structure or thickness.

6.2.4.2. Effect of seed size, pre-treatment and incubation temperature on germination.

Seed germination is the most important event in the life cycle of a plant. Two related seed traits affecting fitness are seed size and time required for seed germination. As heavier seeds contain more food reserves they may germinate faster and achieve greater germination than lighter seeds. In *A. fauntleroyi,* heavier seeds generally gave more germination than lighter seed. Of the 1440 seeds, 66% germinated in small seeds, 75% in medium seeds and 70% in large seeds. Presumably, some small seeds (~5%) are not fully developed which results in less germination. However, germination was slower in heavier seeds. Small seeds germinated twice as quickly as medium seeds and medium seeds about twice as quickly as large seeds (Figure 41a, section 6.2.3.2). It is presumed that in *Acacia* species, germination per seed is related to food reserves but speed of germination is related to seed coat thickness. Larger seeds, with thicker seed coats, take longer to imbibe and hence to germinate than seeds with thinner seed coats or smaller seeds. This phenomenon is also seen in the weedy species *Alliaria petiolata* (Brassicaceae) (Susko & Lavett-Doust 2000), in which smaller seeds germinate significantly earlier than larger seeds.

Seed of *A. fauntleroyi* had quite a high proportion of soft seeds (0.35). Soft seed may be defined as that proportion of seed that germinates after ambient pre-treatment, but is killed by exposure to 100°C. Seedlings may germinate from this soft seed coat fraction at any time when adequate soil moisture is available. The proportion of hard-seed varied between seed sizes with the highest proportion of soft-seed in smaller seeds (small seed, 0.5; medium seed, 0.35; and, large seed, 0.18). Perhaps due to the possession of a thinner seed coat, many small seeds do not require any damage to the seed coat prior to water imbibition.

Increasing pre-treatment temperature from ambient up to that of boiling water improves germination in *A. fauntleroyi.* However, for small seeds, the boiling water treatment reduces germination. In small seeds (with thinner seed coats), boiling water may more readily give access to the embryo resulting in death. Of the pre-treatments applied, the best treatment for small seeds was soaking in water at 50-75°C, while for medium and large seeds soaking it was at 75-100°C. Therefore, the best pre-treatment to break dormancy for seeds of *A. fauntleroyi,* irrespective of size, was soaking in water at 75°C, as this effectively breaks dormancy in all size classes. Increasing pre-treatment temperature to promote germination in legumes is widely reported in the literature with many different patterns (Doran *et al.* 1983; Cox *et al.* 1993; Danthu *et al.* 2002).

Seed sizes may be related to seed quality in terms of genetic identity. Larger seeds may have a better genetic identity. The presence of fire for recruitment of *A. fauntleroyi* is important for a greater chance of more large seeds germinating. In the absence of fire for a long period, recruitment may depend more on small seeds and this could lead to some loss in quality. The requirement of heat treatment for germination of Australian *Acacia* is presumed as an adaptation to fire (Gill 1975), that frequently occurs in sclerophyllous vegetation types.

After seeds are released from dormancy by a suitable pre-treatment, they require an appropriate temperature environment in order to germinate successfully. Incubation treatments applied reveal that seed of different sizes have different responses to incubation temperature. At the coolest temperature used (15°C incubation), germination was greater and sooner in smaller seeds than in larger seeds. However, at the warmest temperature (30°C incubation), germination was greater in larger seeds. Larger seeds appear to respond better to higher incubation temperatures, however higher incubation temperature is slightly detrimental for small seeds. The difference of response to incubation temperature between seed of different sizes is presumably related to difference in metabolic rate and enzyme effectiveness. Extrapolating to the natural environment in the cooler winter season, smaller seeds are more likely to germinate, while larger seeds would take a longer time to complete germination. The variation in temperature requirements for germination between different (extremes) seed sizes may imply that seeds of different sizes could give rise to seedlings establishing in different seasons, depending on the range of current temperatures in the environment. This type of characteristic may be considered as an adaptive strategy if it could be shown that seed from different parents contributes to different seedling cohorts.

Reduced seed germination at warmer temperatures is presumably caused by molecular dysfunction due to membrane degradation and denaturation of enzymes (Bewley & Black 1994). Higher temperatures may promote more rapid water influx into seeds and lead to cracked cotyledons and damage to cell membranes. It can also cause imbibition injury in embryos by rapid water influx.

Pre-treatment temperatures had a greater effect on germination than incubation temperatures. The interaction effect of seed size and pre-treatment temperature was stronger than between seed size and incubation temperature. This suggests that the main barrier for germination was seed dormancy. Hard seed coats protect seeds from germination until moisture can enter the seeds in sufficient amounts to initiate the metabolic process that defines the onset of germination. In small seeds, the interaction of pre-treatment and incubation temperature had less effect on germination than it did in medium or large seeds. This is primarily due to small seeds having thinner seed coats that are more easily damaged and thus allow moisture ingress to promote germination sooner. Thicker seed coats, on medium and large seeds, require higher pre-treatment and incubation temperatures to give high levels of germination and increased speed of germination.

This study reveals that the best treatment for small seed was pre-treatment at 75°C and incubation at 15°C. For medium and large seeds, the best treatments were pre-treatment at 75°C and incubation at 30°C or pre-treatment at 100°C and incubation at either 15 or 30°C. In these treatments, all viable seeds successfully germinated. For medium and large seed, pre-treatment at 75°C with incubation at 15°C also gave good germination, however seed took a longer time to germinate. In several *Acacia* species, treatment at 120°C for 5 min resulted in death of the entire seed lot (Auld & O'Connell 1991). Pre-treatment at 70°C is commonly effective for many Australian *Acacia* species

(Herranz, Ferandis & Martinez-Sanchez 1998). As *A. fauntleroyi* seeds are sensitive to pre-treatment, incubation and prolonged germination (as with most Australian *Acacia* species), it presumably has a persistent soil seed bank.

Pre-treatment by immersion in hot water clearly improves germination of *A. fauntleroyi*. Similar responses are recorded for many other *Acacia* (Larsen 1964; Preece 1971b; Shea *et al.* 1979; Glossop 1980). The requirement of a heat treatment prior to germination in legumes is presumed to be a fire adaptation trait (Gill 1975). High temperatures generated by fire stimulate germination by inducing rupture of the seed coat. It is common to find massive germination of *Acacia* after wild fires. In nature however, there are many other mechanisms that promote seed permeability. Expansion and contraction due to temperature oscillation, alternate dry and wet periods, movement of seed by wind and/or water on sandy surfaces, micro-organism action, scarification in the gut of vertebrates or herbivore digestive systems, and unsuccessful seed predation can all render seed permeable.

Different requirements of heat treatment for germination among seed sizes is a natural, indirect consequence of selection and evolutionary forces. It leads to varied patterns that tend to reduce competition among seedlings since it allows differing establishment patterns for cohorts of regeneration. In contrast, a uniform heat requirement would cause simultaneous germination of seeds and lead to massive competition among seedlings. The variation in proportion of hard-seed among seeds of different size probably reflects the inherent germination strategy of *Acacia*. Some seeds will be stimulated to germinate readily (especially small soft seed) but may then fail due to lack of adequate follow up rains. Remaining seeds (large hard seed) will germinate over varied lengths of time as adequate moisture and oxygen penetrates through the testa to the seed. Seeds are likely to remain dormant, perhaps for several years until there has been adequate scarification that is sufficient to crack the seed coat. This hard seed coat allows *Acacia* species to use a range of seedling establishment 'windows' provided in arid environments, while at the same time ensuring the presence of a persistent seed bank (Letnic, Dickman & McNaught 2000)

Although good seed production and germination were found, seedling establishment of *A. fauntleroyi* at SRNR appears to fail frequently, as few seedlings were observed in the field over 3 years (1998-2001) and plants only form small populations (Chapter 3, section 3.3.3). Some population control factors are presumably: seed predation and herbivory may be high; root competition from established vegetation may constrain seedling recruitment; soil moisture may be rarely sufficient to promote seedling establishment; and periods of long drought (>100 d) may result in mass death of plants.

6.2.4.3. Effect of seed mass on seedling mass.

In *A. fauntleroyi,* larger seeds produced larger seedlings (root and shoot). This has also been found for many other species (Wulff 1986, in *Desmodium paniculatum*; Moegenburg 1996, in Sabal palmetto; Bonfil 1998, in *Quercus rugosa* and *Q. laurina*; Eriksson 1999, in *Convallaria majalis*; Vaughton & Ramsey 2001, in *Banksia*). The general effect of seed size on seedling size may be reflected by more carbon or nutrient reserves in large than small seeds.

Large seeds have the capacity to contain large embryos and substantial food reserves, which enable a seedling to achieve growth of both root and shoot before it becomes dependent on it own photosynthesis. Enhanced nutrient reserves in large seeds and their translocation from cotyledons to elsewhere in the seedling during early growth can reduce the reliance of the seedling on external supplies of nutrients, a distinct advantage on infertile soil (Vaughton & Ramsey 2001). Black (1955) found that seed size determines the initial area of cotyledons; the area of the cotyledons determines the extent of the difference in the early vegetative growth stage between plants from different seed sizes. In addition, embryo weight has been shown to determine early size differences, seedling vigour and emergence time (Gross & Soule 1981). Therefore, it is more advantageous to raise seedlings from large seeds when seedlings are exposed to competition with neighbours. Westoby, Leisman & Lord (1996) suggest that seedlings from large seeds often have an advantage under a variety of adverse conditions including shading, burial under litter, drought and defoliation.

Seedlings from small seeds had slightly greater root/shoot ratios than did seedlings from large seeds. This suggests that small seedlings expend more energy in developing roots than larger seedlings. Root ratio is a measure of biomass allocation to capture water and nutrients. Shoot ratio is a measure of biomass allocation to capture carbon (Hunt 1982). Slightly higher root/shoot ratios may be developed in small seedlings than large seedlings, thus permitting sooner acquisition of nutrients and water, and avoiding drought effects. As small seeds contain fewer resources (giving less pre-photosynthetic growth), it depends more on external resources than seedlings from larger seeds.

Although large seeds produce large seedlings, larger seedlings are not always more advantageous than small seedlings. Photosynthetic rates per unit area have sometimes been found to be negatively related with seedling leaf areas. The initial differences in seedling size, produced by different seed size, may soon disappear owing to different growth rates among seedlings (Zimmerman & Weis 1983). Seed size may have no effect in dense stands where seedling success is largely determined by order of emergence (Howell 1981). Seed size may only affect seedling survival if it affects both emergence time and seedling size. Advantages of seedlings from one seed size could change in different environmental conditions.

6.3. Study No. 2. Effect of seed size on germination and seedling characteristics in *Acacia prainii*

6.3.1. Introduction

A. prainii or Prain's wattle is generally a compact shrub, 2-4 m tall. Bark is dark grey or red-brown and fibrous on the main trunk and branches. Branching occurs at ground level. Phyllodes are narrow, erect, sub-glaucous, pungent to sub-pungent, quadrangular (nerves resinous), with an impressed mid-nerve. Phyllodes are dark yellowish green or light green. Flowers are very bright yellow, in loose balls 5-7 mm diameter on reduced racemes. The flowers are prolific, pods are reddish brown and papery.

Over 3 years of observation (1998-2001) at SRNR, *A. prainii* flowered consistently in September, with seed becoming mature in December. Plants are mainly found at the winter-wet areas around the main rock and form a dense or concentrated population in an open low shrubland, growing in moist sandy loam along the creek line. This species is an obligate seeder, with no evidence of suckering; it relies on seeds for recruitment. *A. prainii* almost certainly has annual recruitment and many seedlings were found. Some 15% of measured plants were less than 0.5 m tall and thus can be classified as seedling or sapling stages. A population study of *A. prainii* at SRNR and its associated species was presented in chapter 3 (Section 3.3.2).

Variation in seed mass occurs within and between species. It is commonly interpreted as a trade-off between quantity (seed number) and quality (mass) (Wulff 1986). Although large seeds have an increased chance of establishing to give a seedling, they are produced in fewer numbers than small seeds when resources are finite (Westoby *et al.* 1996). Seed size is an important variable affecting seed dispersal, persistence in the soil, seedling establishment and fitness. Larger seeds give rise to better competitors, particularly under resource-limited or competitive conditions. Germination date and hypocotyl length of *Pithecellobium pedicellare* are affected by initial seed mass (Kang, Jaschek & Bawa 1992). Timing of emergence also plays a critical role in seedling establishment, particularly under competitive conditions. Early germination and emergence usually have an advantage over later germination, in that early seedlings capture a disproportionate share of environmental resources (light, nutrients and water) and receive ephemeral light for longer before canopy closure (Seiwa 2000).

In the present work, possible effects on germination and seedling characteristics of variation in seed size were studied for a better understanding of recruitment in *A. prainii*. The main aim was to investigate to what extent are germination and seedling characteristics affected by seed size. Does pre-treatment improve germination? Under what temperature regime does most seed germinate?

6.3.2. Methods

Mature pods were collected in December 1999. Seeds were removed from the pods and sorted to enable removal of aborted, dry or infected seeds. Sound seeds were then stored at room temperature (21°C) under dry conditions until ready to use. Seeds were individually weighed to the nearest milligram using an electronic balance (Section 6.2.2). The mean mass per seed was determined, then seeds were placed in containers and categorised according to size.

6.3.2.1. Seed water content of seed of different size.

Three seed size classes: small, medium and large ($3<5$ mg, $7<9$ mg and $11<13$ mg) were chosen to represent the range of seed size variation within the batch of seeds. For each seed size class, 30 air-dried seeds (Σ 90 seeds) were weighed individually every 24 hours (for 4 days) before and after attaining constant weight by drying in a 60°C cabinet. Percentage of seed water content (W) was calculated by dividing seed water content by seed dry weight (S), that is, seed water content [$W (\%) = W / (S + W) \times 100$].

6.3.2.2. Effect of seed size, pre-treatment and incubation temperature on germination.

6.3.2.2.1. Experiment 1 : Effect of seed size and pre-treatment temperature on germination.

To investigate the effect of seed size and pre-treatment temperature conditioning on germination, the three seed size classes, defined in section 6.3.2.1. were used. The experimental design involved replicates (3) from the three seed size classes being subjected to one of four pre-treatment temperatures (ambient, 50°C, 75°C or 100°C). Each replicate was represented by 20 seeds (Σ n = 720 seeds). After appropriate pre-treatment, all seed was incubated at 30°C.

6.3.2.2.2. Experiment 2 : Effect of seed size and incubation temperature on germination.

To investigate the effect of seed size and incubation temperature on germination, seed from two other seed-size classes, 5<7 mg (small) and 9<11mg (large) were used. A different design was necessary due to fewer seed. The experimental design subjected seed from two size classes to one of three incubation temperatures (20°C, 25°C or 30°C), with 3 replicates. Each replicate was also represented by 20 seeds (Σ n = 360 seeds). All seed was pre-treated with boiling water (100°C).

Lots of 60 seeds for each treatment in experiment 1 and 2 were pre-treated by placing them with 30 ml of water in a glass beaker (50 ml volume) at temperatures of 50°C, 75°C or 100°C; they were then left to cool to room temperature. The control involved soaking in water at ambient temperature (~20°C). All seeds were surface sterilised with sodium hypochlorite, then rinsed with deionised water. Seed lots were then placed in 3 petri dishes with 20 seeds per dish. Seeds were placed in plastic petri dishes (diameter 11 cm) lined with two Whatman No. 3 filter papers (9 and 11 cm). Petri dishes were partially filled with sterilised vermiculite (approximately 0.5 cm from the base). The vermiculite and filter paper were then moistened with "previcure" (Hoescht Schering Agrevo, Glen Iris, Vic. Australia) to reduce fungal growth, and deionised water to maintain a humid environment within the dish. Seeds were then placed in dark, incubation cabinets.

Seeds were observed at daily intervals. Additional water and previcure were added to the petri dishes when required. Radicle emergence (~2 mm) was the criterion for deciding if germination had taken place. Any germinants were recorded and removed; counting the germinated seeds was continued until no more germination occurred for 14 successive days. Parameters determined were number of seed germinated and days required for germination (number of days to first and to 50% final germination). Numbers of seeds that germinated and time to germinate were subjected to one way analysis of variance, and the general linear model (GLM) was applied to determine interaction effects between the treatments (Ott 1993). Tukey's test was used to detect any significant difference between means in comparisons within the treatments. Number of seeds that germinated was transformed to Arcsine to meet normality of data.

6.3.2.3. Effect of seed mass on seedling mass

Germinated seeds from the seed size classes 5<7 mg (small) and 9<11 mg (large) in experiment 2 (section 6.3.2.2.2) were planted into 5 x 5 x 5 cm planting cells, which contained a 1: 1: 1 potting mixture of coarse sand: fine sand: peat moss, with no fertiliser applied. The trays were maintained in a glasshouse and watered daily. The transplant dates were recorded for each seedling to enable individuals to be harvested as 50 day old seedlings. At this age, 20 seedlings each from small and large seed were harvested. Seedlings were carefully removed from the trays and any adhering peat washed away from the roots. Shoots and roots were separated, dried at 60°C for 4 days to obtain dry weights and weighed to the nearest 0.1 mg. Root and shoot ratios were determined and compared using analysis of variance.

6.3.3. Results

6.3.3.1. Distribution of seed mass and seed moisture content.

Seed mass spanned the range from 1.4-15.7 mg (mean = 8.0 ± 3.4 mg, n = 200). Distribution was skewed to the left (-0.135); there were more seeds with a heavier mass than the mean, than would be expected for a normal distribution. The distribution however exhibited negative kurtosis (-1.321); fewer seeds with a mass near the mean mass than would be expected for a normal distribution (Figure 49). Therefore, seed mass was highly variable.

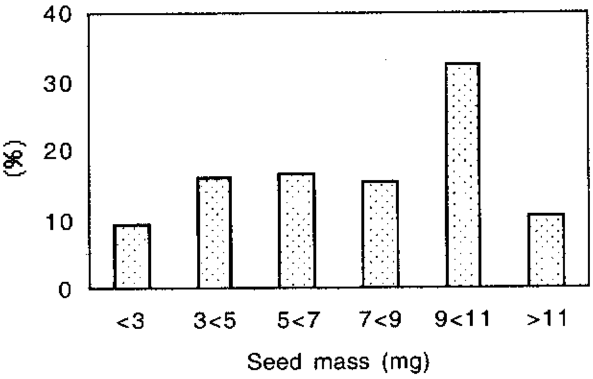

Figure 49. Distribution of seed mass (%) of *A. prainii* (n = 200 seeds) collected in 1999.

Seeds attained a constant weight after drying for 72 hr in the 60°C oven. Heavier seeds had significantly more water than lighter seeds ($P = 0.002$). Small seeds had a mean of 0.34 mg water or 8.90% of seed dry weight, medium seeds had 0.63 mg or 6.67% and large seeds had 0.81 mg or 6.79%. These percent moisture values did not differ significantly between seed weight classes.

6.3.3.2. Experiment 1 : Effect of seed size and pre-treatment temperature on germination.

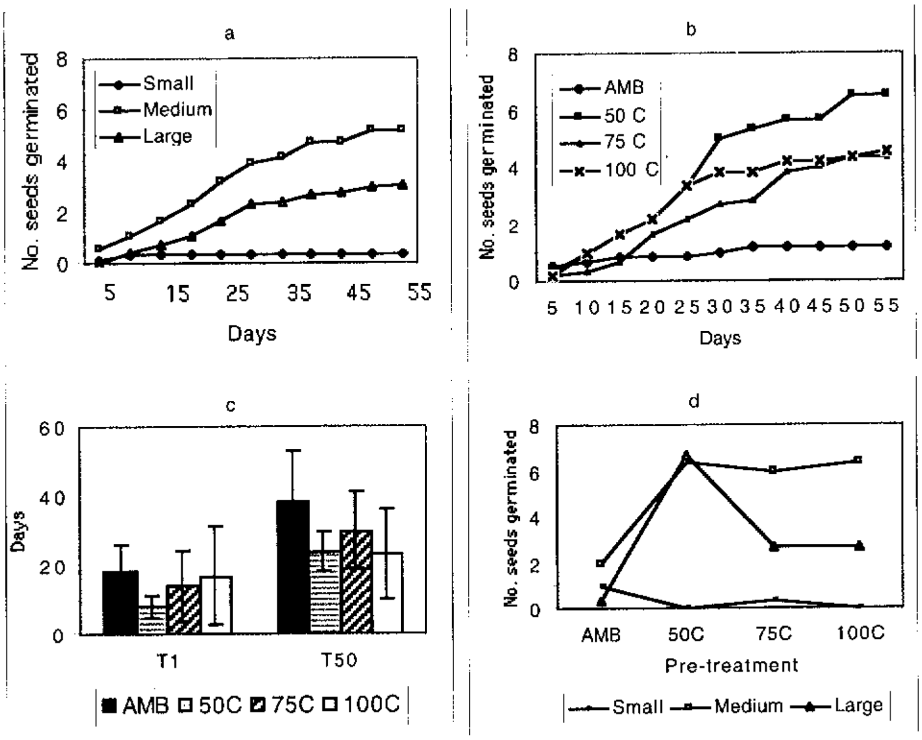

Figure 50. *A. prainii* experiment 1. Number of germinated seed by: a. Seed size (n = 12, for replicates, 20 seeds per replicate); b. Pre-treatment (n = 9, for replicates, 20 seeds per replicate); c. Days required for germination by pre-treatment (data pooled from medium and large seeds only). T1 = days to first germination, T50 = days to 50% final germination. AMB = ambient temperature; d. Effect of seed size and pre-treatment on germination at 55 d (n = 3 for replicates, 20 seeds per replicate).

Germination from this batch of seed was poor. Of the range of treatments applied, the maximum was 33%. Small seeds at all treatments had less than 6% germination. The general linear model applied to the number of seeds germinated (55 d) reveals that seed size ($F = 37.90$, $P<0.001$), pre-treatment ($F = 8.42$, $P <0.001$) and their interaction ($F = 5.12$, $P = 0.002$) all significantly affected the number of seed that germinated. Germination was greater in medium than in large or small seeds (Figure 50a); and greater after 50°C than other pre-treatments, but not before 25 d where both 50 and 100°C pre-treatment gave similar germination (Figure 50b). Due to the very poor germination, there was no pronounced difference in the mean numbers of days required for first germination and 50% germination among the seed sizes. However, large seeds took a slightly longer time to germinate than medium seeds. There was also no pronounced effect of pre-treatment on times of germination. However, although not significantly different, exposure of seed to any level of warm water reduced the times taken to germinate after ambient exposure only (Figure 50c).

The interaction of seed size and pre-treatment temperature (Figure 50d) with the ambient pre-treatment produced no significant difference in germination ($P = 0.229$). The population of soft seed was some 5% in small seeds, 10% in medium seeds and 3% in large seeds. Following the 50°C pre-treatment, the medium and large seeds attained similar germination levels but there was no germination in small seeds ($P = 0.002$). After 75°C pre-treatment, germination was greater in medium than in small and large seeds and greater in large than in small seeds ($P = 0.014$). After the boiling water treatment, germination was greater in medium than in large seeds but no germination was found in small seeds ($P = 0.004$). Therefore, at all pre-treatments, small seeds had poor germination. Of the pre-treatments applied, the best pre-treatment for small seeds was at ambient temperature, while for medium and large seeds most seeds germinated after the 50°C treatment. Poor germination suggests that 30°C incubation is unfavourable for germination of *A. prainii.* High temperature incubation may have promoted denaturation of enzymes.

6.3.3.3. Experiment 2 : Effect of seed size and incubation temperature on germination.

The general linear model (GLM) applied to the number of seeds germinated (55 d) reveals that seed size ($F = 224.07$, $P = <0.001$), incubation temperature ($F = 14.09$, $P<0.001$) and their interaction ($F = 23.64$, $P = <0.001$) all significantly affected the number of seeds that germinated. Large seeds produced most germination with more than 70% (mean > 14 seeds) and less than 10% in small seeds (Figure 51a). Variation in time taken for germination between seed sizes was not obtained due to few small seeds germinating. The best incubation temperature was 25°C, which gave most germination; germination was equally poor at 20 and 30°C (Figure 51b). Germination time (days to first and 50% final germination) was also more rapid at 25°C incubation, while both 20°C and 30°C gave slower germination (Figure 51c).

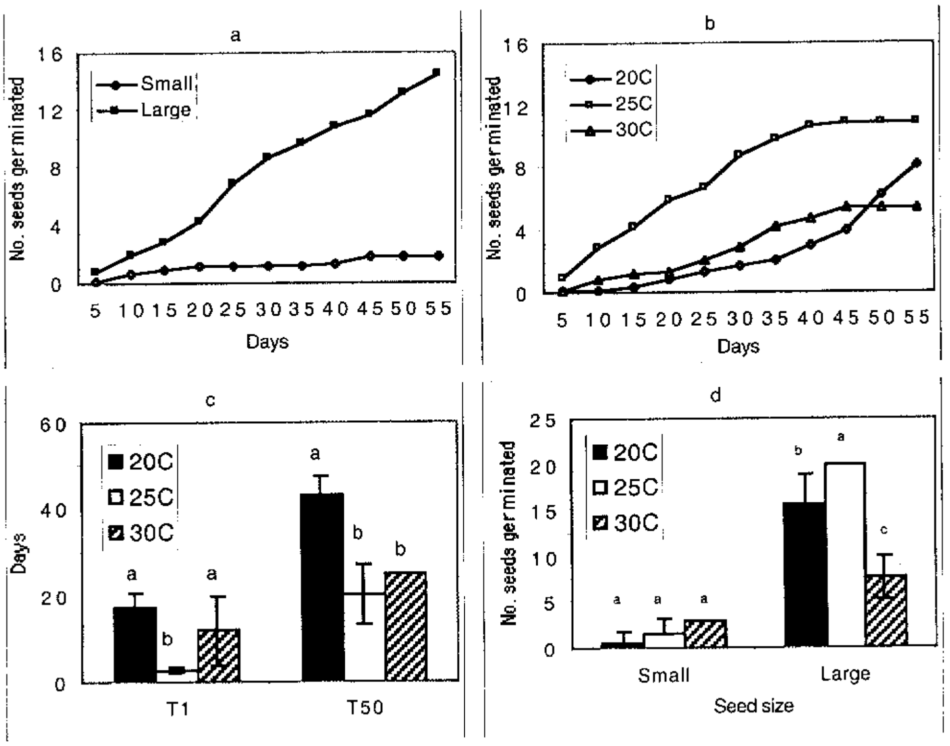

Figure 51. *A. prainii* experiment 2. Number of germinated seed by: a. Seed size (n = 9, for replicates); b. Incubation temperature (n = 6, for replicates) 20 seeds per replicate throughout; c. Time to germinate. T1 = days to first germination, T50 = days to 50% final germination (data from large seeds only); d. Interaction of seed size and incubation temperature (n = 3 for replicates). Entries with different letters among treatments indicate a significant difference between means using Tukey's family error rate (Figure 51c and d). Bars represent standard errors.

Interaction of seed size and incubation temperature reveals (at 55 d) that 25°C incubation gave more germination than 20°C, and 20°C gave more germination than 30°C (Figure 51d). All large seeds germinated (mean of 20 seeds or 100%) at 25°C incubation compared with only 38% at 30°C incubation. Therefore, incubation at 30°C may have killed some 62% of large seeds. Thus, the poor germination obtained in experiment 1 (section 6.3.3.2) was more affected by incubation temperature (30°C) than by the pre-treatment applied. Seeds incubated at 20°C also produced relatively high germination (78%), but germination took longer. Thus, reduced temperature lengthens the time for germination. In large seeds, 80% of germination had occurred after only 30 d at 25°C incluation. This level required 55 d when incubated at 20°C. For small seeds, possible effects of incubation temperature on both amount and time taken for germination were obscure as very few seeds germinated. For large seeds, mean days to first germination within the incubation range of temperatures (20, 25 and 30°C) were 17, 3 and 12 d respectively. Days to 50% final germination were 43, 20 and 25 d respectively, suggesting that 25°C is near the optimum temperature for germination of *A. prainii.*

6.3.3.4. Relationship between seed mass and seedling mass.

Seedling mass of seedlings grown from large seeds were significantly heavier than those grown from small seeds ($P = 0.003$). However, shoot mass was not significantly different between seedling sizes ($P = 0.232$). Both seed sizes produced seedlings with greater shoot mass than root mass (Figure 52a). Root ratio (RWR) was significantly heavier in large than small seedlings ($P<0.001$) and shoot ratio (SWR) was significantly heavier in small than in large seedlings ($P<0.001$). This data suggests that there is greater early investment of seed reserves in shoots by seedlings from smaller seed (Figure 52b).

By comparing mean seedling weight (n = 20) with mean seed weight (n = 100), it is noted that seedlings from small seed were less efficient in use of seed resources than those of seedlings from large seed. At 50 d after germination, small seedlings had lost 24% of mean seed mass to respiration compared with only 15% in large seedlings. Seedlings from large seed have a greater potential for pre-photosynthetic growth. Linear regression between root mass (Rm) and seedling mass (Sdm) for small seedlings reveal: Sdm = 4.89 + 1.58 Rm, $P = 0.013$. For large seedlings, the relationship is: Sdm = 4.86 +

1.49 Rm, $P < 0.001$. Apparently, the relationship between root mass and biomass produced was slightly stronger in seedlings from large than in seedlings from small seeds.

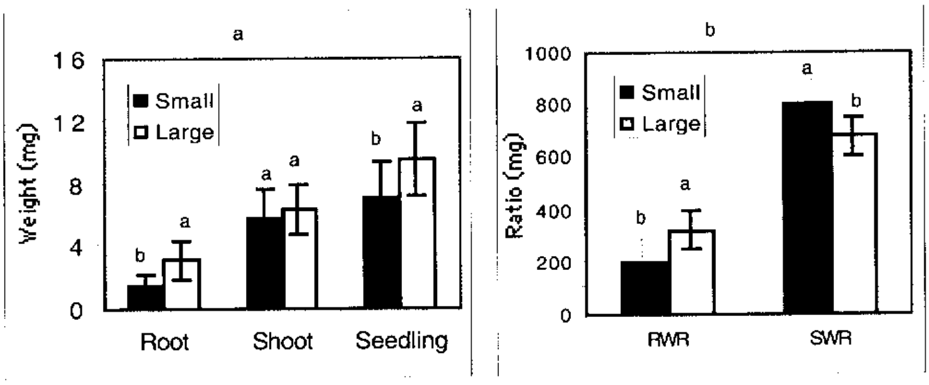

Figure 52. Comparisons of mean seedling dry mass of *A. prainii* raised from small and large seeds, 50 d after germination. a. Root, shoot and seedling weight; b. Seedling weight ratios. RWR = root ratio; SWR = shoot ratio. Legend as in Figure 48 (n = 20 seedlings per seedling size). Entries with different letters among characters indicate a significant difference between means using Tukey's family error rate. Bars represent standard errors.

6.3.4. Discussion

Seed mass distribution of *A. prainii* reveals that it is not quite normal, being skewed to the left, indicating negative kurtosis. That is, more seeds with mass heavier than the mean and fewer seeds with mass near the mean than expected for a normal distribution. The range in seed mass is quite variable (1.4 –15.7 mg). My experiments show that seed size, pre-treatment, incubation and interaction all affected the number of seeds that germinated. Larger seeds produced more germination and I suggest that fitness is positively related to seed size. Seeds in the size class 5<7 mg gave less than 10% germination (section 6.3.3.3). Of the seeds produced in 1999, a high percentage was less than 7 mg in weight (Figure 49). Seeds in the size class 9<11 mg gave more than 70% germination (up to 100%) when incubated at favourable temperatures (section 6.3.3.3). It may be hypothesised that *A. prainii* seeds which weigh ± 9 mg is required to give good germination.

Seed size is limited either directly or indirectly by the availability of resources for current photosynthesis. One explanation for seed mass variation is that resources for seed provisioning are limited and plants are not able to supply all seeds to the optimum level. Defoliation and the general availability of resources can affect seed size (Stephenson 1980; Willson & Price 1980; Wulff 1986). Many ungerminated seeds of *A. prainii* were presumably affected by limited resource availability during seed development, mainly caused by metabolic derangement by rust fungus infection. At SRNR, most large plants of *A. prainii* were observed to be infected by the rust fungus; this infection reduces the capacity of phyllodes to synthesise resources for seed development.

The best pre-treatment temperature conditioning for seeds of *A. prainii* was exposure of seed to boiling water (100°C), suggesting that seed of this species are particularly hard-seeded. The best incubation temperature of those used was 25°C. The combination of boiling water pre-treatment and incubation at 25°C gave 100% germination. At 20°C incubation, seeds also gave relatively high germination, however germination was slower. At 30°C incubation, more than 60% of seeds were presumed killed as they failed to germinate.

In most *Acacia* species at SRNR, seeds do not germinate quickly after shedding. Only a small fraction have soft seed and generally these are of small size. The remainder will await the reduction in hard-seededness, which occurs after some time, precisely how long is not known (Preece 1971b). When the seed is soft, the coincidence of rain and temperature in the optimal range will allow germination. The seeds will not all germinate together, there will be some staggering as a result of the variation inherent in the seeds. After seed shedding, seeds will be gradually covered by layer of soil, perhaps aided by insect mediation. This will not prevent germination through the absence of light, as long as burial is not so deep that water fails to penetrate or that emergent cotyledons cannot push aside the material that covers the seed (Preece 1971b). In the shrubby legumes, *Acacia lateriticola*, *A. drummondii* and *A. extensa*, germination is apparently suppressed by light compared with darkness. Germination responses are also reduced by exposure to red and far-red light (Bell, King & Plummer 1998). In *Acacia origena* and *A. pilispina*, seeds germinate well in dark or light (Taketay 1998), suggesting that seed will germinate well either buried or on the soil surface. Response of *Acacia* seed to light seems to vary considerably among species. It is suggested that with soft seed, germination will be more rapid if the seed is in an atmosphere rich in carbon dioxide, in decaying litter or in animal dropping (Preece 1971b).

A. prainii seedlings produced higher shoot mass than root mass. Production of more photosynthetic biomass may be a consequence of possessing an epigeous germination mode. Larger seeds produced larger seedlings. This could have been a consequence of higher levels of remobiliseable mineral nutrients and/or carbon-based reserves in the larger seeds. Seedlings raised from small seed had higher shoot ratios than seedlings raised from large seed, and seedlings raised from large seed had higher root ratios than seedlings raised from small seeds. Thus, seedlings raised from smaller seed had a strategy to obtain more carbon resources, while those raised from larger seed had a strategy to obtain water. In the use of food reserves, there was a tendency for seedlings raised from small seed to be less efficient than seedlings raised from large seed. Large seed-seedlings have potential for more extensive pre-photosynthetic growth. The advantages of large seeds are presumably in the capacity to provide more energy and nutrients, enabling seedlings to achieve greater root and shoot growth prior to photosynthesis kicking in.

Intra-specific variation in seed sizes have been shown to affect several fitness components, such as successful seed germination, seedling growth and intra-specific variation in germination requirements. Because mortality at germination and in the seedling state is often high, variation in seed mass is likely to have strong effects on plant fitness (Vaughton & Ramsey 1998). Large and well-resourced seeds have been shown to provide an advantage when seedlings are competing with neighbours (Eriksson 1999; Turnbull, Rees & Crawley 1999). Larger seeds contain more mineral nutrients and carbon based reserves than small seeds. Young seedlings from large seeds are therefore more likely to tolerate adverse conditions. They may establish better in the shade, under drought when buried beneath soil or litter, in established vegetation (Westoby *et al.* 1996) and in nutrient poor soil (Stock, Pate & Delfs 1990). Soil nutrient levels may be less critical in affecting their early growth.

6.4. Study No. 3. Effect of seed coat thickness on variation in seed size in the species *Acacia fauntleroyi* and *Acacia prainii*

6.4.1. Introduction

The impermeability of seed coats to water (hard-seeded-ness) occurs in several plant families (Leguminosae and Malvaceae). Their seed coats contain a layer of tightly packed, thick-walled columnar cells that, except for a few locations (hilum, micropyle, and chalazal pore), completely enclose the embryo. The seed coat becomes impermeable to water during the later stages of seed development, concomitant with seed dehydration and onset of dormancy (Egley 1976).

The palisade cell layer (Malpighian, macrosclereid) of the seed coat is suggested as a major barrier to water diffusion. Impermeability of *Pisum sativum* seeds is due to a combination of a continuous layer of hard, pecticeous caps on the palisade cells of the seed coat, quinones in the cells and the tightly-packed arrangement of the cells (Werker, Marbach & Mayer 1979). Abundant tannin in the Malpighian cells of *Glycine max* (L.) Merr. and cutin in the hilum also cause impermeability; palisade cell walls that contain a callose deposit were proposed as causing impermeability in *Sesbania punicea* (Cav.) Benth. seeds (Egley 1989). However, Werker *et al.* (1979) emphasised that a layer of tightly packed cells is not by itself a barrier to water because water could permeate the cellulosic fibrils of the cell walls. A water-resistant substance could be impregnated into the cell walls. Bhalla and Slattery (1984) found that seed coat impermeability in *Trifolium* (clover seeds) is caused by deposition of callose in the cells of the parenchyma cell layer of the seed coat. Therefore, callose acts as the barrier to movement of water into the seeds.

Various chemical constituents of the testa have also been suggested as being responsible for causing seed-coat impermeability, including the waxy surface layer, cuticulae and the suberised Malpighian cell caps. Another suggestion is that impermeability resides in the lumen of the Malpighian cell (Marbach & Mayer 1974). The cuticle on the seed surface is no longer considered to be the sole barrier to water entry into the seed because removal of the cuticula of many hard seeds does not always result in imbibition of water. However, the surface cuticle may function as a first-line barrier to water diffusion and may act in combination with other barriers deeper within the seeds.

Natural loss of testa impermeability may occur at various sites on the seed (Egley 1979), but it usually occurs at a specific area. A number of studies on papilionoid legumes found that the primary site of water entry into the seed is the lens (Quinlivan 1971; Ballard 1973). The lens is a site of inherent weakness in a testa otherwise very resistant to ambient influence. For *Sida spinosa* (Malvaceae), the primary site of water entry is the chalazal area (Egley & Paul 1982). In *Albizia lophantha* or *Paraserianthes* (leguminous tree), it is the strophiolar plug (Dell 1980). For *Acacia* species, the term strophiole is used to refer to a specialised region of the seed coat, where the first site of water entry occurs (Tran & Cavanagh 1980). The external appearance of the strophiole is very variable. It can be circular, elongated or even triangular. Internally, the strophiole is characterised by shortened macrosclereid cells and is the area where the vascular bundles most closely approach the surfaces of the seeds. Therefore, the lens is situated at a position most sensitive to rapid uptake of water and is also more sensitive to rapid hydration.

The lens is sensitive to changes in temperature. One of the treatments which has proved effective in rupturing the lens is immersing the seed in hot water (Egley 1979; Manning & Staden 1987). Placing *Acacia* seeds in hot water damages the cuticle and sometimes parts of the palisade layers of the seed coat and can effectively break dormancy. Under natural conditions, temperature fluctuations can cause a split at the lens, resulting in seed permeability. From that theory, the site of initial water entry and subsequent pathways of water movement, and the rate of water entry are crucial aspects of water uptake in legume seeds. Therefore, seed coat thickness must have a role in germination.

In previous sections, it has been shown that seed of different size had different germination characteristics in *A. fauntleroyi* (section 6.2) and *A. prainii* (section 6.3). In the present work, possible effects on seed-coat thickness of variation in seed sizes in both those species are studied. The aim was to investigate whether seed coat thickness differs among seed of different size.

6.4.2. Methods

Five seeds representing each of small, medium and large seed sizes (5, 8 and 11 mg for *A. fauntleroyi* and 4, 8, 12 mg for *A. prainii*) were selected, and then fixed in 2.5% glutamate in 0.05M PO_4, buffer pH 6.8 (4 days). Seed were then washed in 0.05 M PO_4, buffer pH 6.8 for 2 hour (2 times). Seeds were dehydrated in ascending order of different alcohol concentration including 50% ethanol (2 hours), tertiary-butyl alcohol (TBA) 1, TBA 2, TBA3, TBA 4, TBA 5 (for 2 hr in each treatment) and pure TBA (twice, 1 hr each). During the second pure TBA treatment, seeds were transferred to a heating oven (60°C) until no bubble exited from the seeds. Then the seed were embedded in paraffin wax.

Seeds were softened by immersion in "Bakers softening solution" (distilled water, 95% ethanol, glycerol) for 2 hr. The seed tissue in the paraffin block was sectioned (12 μm) using a sledge microtome. Sections were dewaxed through alcohol dehydration and rehydration. Sections were counter-stained with alcoholic safranine (1% in 50% ethanol) for 4 minutes and fast green (0.2% in 95% ethanol) for 40 s each. As the seed coat thickness varied along the circumference of the seed, each section was measured 2 times for seed coat thickness (using a Nikon light microscope, 1000 x magnification). One reading was from the maximum thickness region and another from the minimum thickness, along the circumference of the seed. Seed coat thickness was taken as a mean of the maximum and minimum readings. Data for seed coat thickness were subjected to analysis of variance. Tukey's test was used to detect any significant difference in the comparison within the means.

6.4.3. Results

Table 40. Seed coat thickness, Malpighian + mesophyll cell layers (μm) by seed size.

Species	Seed size	N	Malpighian	Mesophyll	Malpighian + mesophyll
A. fauntleroyi	Small (5 mg)	44	33.98c	136.14b	170.12b
	Medium (8 mg)	52	38.65b	202.55a	241.20a
	Large (11 mg)	74	47.26a	185.54a	232.80a
	F		55.88	35.46	38.76
	P		<0.001	<0.001	<0.001
A. prainii	Small (4 mg)	80	35.56b	178.19c	213.75c
	Medium (8 mg)	80	36.34a	209.69a	246.03a
	Large (12 mg)	48	37.66a	195.78ab	233.44ab
	F		5.20	17.98	18.39
	P		0.006	<0.001	<0.001

Entries with different letters in a species, in a column indicate a significant difference between means using Tukey's family error rate. No letters = analysis not significant. N= number of observations for each seed size category.

Table 41. Comparison of thickness (μm) of Malpighian and mesophyll cell layers between of *A. fauntleroyi* and *A. prainii.*

Seed coat		*A. fauntleroyi*		*A. prainii*	*F*	*P*
	N	Mean (SD)	N	Mean (SD)		
Malpighian	170	42.49 (6.65)	208	36.35 (3.63)	130.07	<0.001
Mesophyll	170	177.96 (47.29)	208	194.36 (35.90)	14.69	<0.001
Malpighian + mesophyll	170	220.44 (48.13)	208	230.71 (36.58)	5.55	0.019

N = all measurements including small, medium and large seed categories for each species.

In both species, seed coat thickness varied among seed sizes. Thinner seed coats occur in smaller seeds, rather than larger seeds (Table 40). Using linear regression, in *A. fauntleroyi* there was no relationship between thickness of the Malpighian (Mp) and mesophyll (M) cell layers (Mp = 41.043 + 0.0081 M, $P = 0.455$). In *A. prainii*, a thicker Malpighian cell was associated with thicker mesophyll cells layer (Mp = 33.588 + 0.01419 M, $P = 0.043$). The Malpighian cell layer was thicker in *A. fauntleroyi* than *A. prainii*, but the mesophyll cell was thicker in *A. prainii* than in *A. fauntleroyi* (Table 41). Generally, seeds of *A. prainii* had a thicker seed coat than *A. fauntleroyi*.

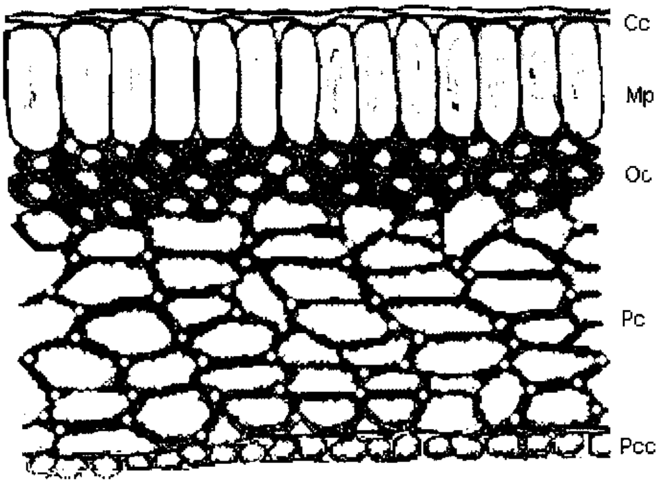

Figure 53. Diagram of the cross-section of *A. fauntleroyi* seed observed under the microscope (1000 x magnification). a. Cuticula (Cc); b. Palisade layer/Malpighian cell (Mp); c. Osteosclereids of collenchyma (Oc); d. Parenchyma cell (Pc). e. A single layer of cell parenchyma close to cotyledon (Pcc).

Both species observed under the microscope (100 x magnification) possessed a similar seed coat structure. There is no discernible difference in the form of the cells that construct the seed coat layer, presumably as these species are growing in relatively similar habitat conditions (Chapter 3). The outer layer of the seed coat is the cuticle. The cuticle layer was removed while the seed was heated during dehydration in the preparation of sections. Three layers of the seed coat under the cuticula can be differentiated by differences in cell structure that presumably contribute to seed dormancy in both species (Figure 53). The first is a palisade layer of sclereids or macrosclereids (Malpighian cells) with fluted wall thickening. The second is a sub-epidermal layer (osteosclereids) of collenchyma, with cell walls very thick and suberised. The third layer is of parenchyma, with cell walls also tightly suberised. The inner-most layer consists of a single layer of small-celled parenchyma close to the cotyledon.

6.4.4. Discussion

This study found that seeds of different size differed in seed coat thickness. This morphological pattern is presumed to affect seed coat permeability and determine both speed and probability of successful germination. Variation in seed coat thickness between seed sizes explains the variation in quantity and speed of germination between seed of different sizes obtained in previous tests (sections 6.2 and 6.3). Generally, the seed coat of *A. prainii* is thicker than in *A. fauntleroyi*. Therefore, seed of *A. prainii* requires a longer time to imbibe water than does *A. fauntleroyi*. This characteristic may explain why more soft seed is found in *A. fauntleroyi* (35%) than in *A. prainii* (6%).

In both species, cell parenchyma also appears to contribute to hard-seeded-ness, as cell walls are thickly suberised. Therefore, all cell layers that comprise the seed coat contribute to hard-seeded-ness. Seeds need to be pierced below the Malpighian layer for imbibition. Collapsed parenchyma cells below the Malpighian cells of *Acacia auriculiformis* seed were proposed to form a dense barrier to water diffusion (Pukittayacamee & Hellum 1988). Experiments on the depth of relative impermeability were made by Tran and Cavanagh (1980) on *Acacia farnesiana*. They found that seeds remained impermeable when a hole is made as far as the macrosclereid layer. Seed will be permeable if the hole penetrates past the boundary between the macrosclereid and osteosclereid cells.

In both species, cells at outer side had thicker cell walls than those of the inner side. Therefore, the main barrier to water penetration was cell palisade or Malpighian cell. Doran *et al.* (1983) claim that about 36% of the total thickness of the seed-coat (testa) is of Malpighian cells; in both species studied here it is about 20%. They also suggest that the Malpighian zone varies in thickness both within and between species. The second barrier was cell osteosclereid, directly under the Malpighian cells, and the third barrier is of cell parenchyma, with thinner cell walls.

The hard seed coat of legume species has been suggested as having many advantages. It contributes to the accumulation of persistent seed banks in the soil by rendering the seed viable in the soil for long periods. Persistent seed banks spread germination over time, increasing the chance that some seeds will germinate, establish and complete the life cycle successfully (Bewley & Black 1994). This hard seed coat can also be viewed as an adaptation that enables plants to withstand unfavourable conditions such as heat caused by fire, strong teeth of dispersing animals, severe drought and mechanical damage. In unpredictable environments, such as those of arid Australia, germination is often a high-risk event; possession of a hard seed coat reduces the risk of germination following marginal rainfall events and increases the chance of germination during any major rainfall events, which are more favourable for the establishment of new seedlings.

CHAPTER 7

GENERAL CONCLUSIONS

7.1. Introduction

An ecological study of plant species at Sandford Rock Nature Reserve (SRNR) was conducted. The study area is an important nature reserve that has more or less pristine natural vegetation (Muir 1979). The reserve incorporates one of a number of significant granite outcrops within the Western Australian wheatbelt. The granite rock dominates the reserve, with 20% of the land area. Its rims may have only 2% of the land area but receive much water from redistribution of rainfall that falls on the rock. Water shed from the massive complex of granite (occupying the centre of the reserve) fills rock pools in winter, drives an ephemeral stream and probably contributes to underground aquifers that supply water to woodlands and shrublands of the area through the drier months (Fox 1997).

Vegetation consists of a mosaic of associations (woodland and shrubland) with patches dominated by various species (Chapter 2). Some plant associations are related to the large granite outcrop that has been extensively eroded, particularly by wind, rain, lichens and mosses. These forces have exposed and shaped the granite outcrop, contributing to the formation of the surrounding soil; determining a range of seasonally wet sites; and the assemblage of distinct vegetation types is related to the topographical heterogeneity of the landscape (Hopper *et al.* 1997).

Natural vegetation that remains in the WA wheatbelt has a high conservation value since all remaining natural habitats are required as genetic resources for maintaining biodiversity, and as reference areas (Moran & Hopper 1987). The southwest botanical province of WA is recognized as one of 25 biodiversity hotspots in the world, in terms of endemism and level of threat (Myers *et al.* 2002). A large number of species have geographically restricted ranges and naturally disjunct distributions (Gibson, Keighery & Keighery 2000). Composition of vegetation and natural regeneration of selected component species of the natural vegetation at SRNR are the main concerns of this study. It provides information that should be useful in determining the fate of individual species and management strategies that may be taken to effectively conserve the reserve as a whole.

7.2. Vegetation type and *Acacia* population

Distribution and occurrence of a total of 85 species from 20 families of woody perennial plant species was collated. All sites were dominated by the Myrtaceae, Mimosaceae and Proteaceae families. There was considerable variability in the structure and composition of vegetation between areas. Of all species collated, only 10.6% were in the common and 2.4% in the very common categories, suggesting that few species occur in more than a few particular habitats. Similarities among the 5 areas of vegetation described were only 0.18-0.29; that is some 71-82% of component woody plants comprise different species. The four most common and widely distributed species were *Acacia acuminata* Benth. (jam wattle), *Allocasuarina huegeliana* (Mi.) L. Johnson (rock sheoak), *Grevillea paradoxa* F. Muell. and *Acacia hemiteles* Benth. (tan wattle).

Composition of communities is related to the heterogeneity of habitat within the reserve. Soils derived from the granite rocks are predominantly sandy. Other more loamy soils are associated with various types of seasonally wet areas. Within different areas, the associated soils, micro-topographic variation and hydric regimes control the local patterns of plant distribution, association, and the performance of different plant species. Such patterns may be affected by differential seed accumulation, variation in species germination requirements and differences in growth and mortality in different microhabitats. Soil characteristics and moisture availability are presumably the most important factors which govern vegetation structure and functioning.

Based upon the physiognomy and cover of the ecologically dominant stratum of particular species, three vegetation types were observed to occur in the northeast corner area at SRNR (Chapter 2, 2.3.1): *"Allocasuarina huegeliana* woodland", commonly forms a more or less pure stand in relation to woody species, especially in black or brown dry shallow sandy soil; *"Grevillea paradoxa* low shrubland" occur on dry rocky soil or reddish yellow shallow soil; and, *"Acacia neurophylla* medium shrubland" is found on reddish yellow dry shallow soil that appears very dry in summer. *A. huegeliana* (sheoak) is one of the most common trees at SRNR; it usually reaches 6-8 m tall. Pure stands of this species sometimes occur in deep pockets of soil on edges of the granite rocks.

The entrance area mainly comprises seasonally moist areas (Chapter 2, 2.3.2); vegetation types present include *"Acacia jennerae* low open shrubland". This forms almost a pure stand in relation to woody perennial species. This species reproduces from suckers, a mode that presumably results in only a few spaces available to other woody species. Associated species are mainly the perennial grass (*Amphipogon strictus*) and a perennial herb (*Borya constricta*). "Low open grassland" mainly comprises grass species: *Neurachne alopecuroidea*, *Eriachne ovata* and *Aristida contorta,* and many seedlings of *Hakea invaginata*. Relatively deep (44.1 cm) soils with high soil moisture content allow continuous recruitment of *H. invaginata*. "Wandoo woodland" consists of the tall tree *E. capillosa* and over shrubs *Dodonaea viscosa* and *Alyxia buxifolia*. The understorey is mainly grown cover of the grass *N. alopecuroidea*. Wandoo woodland is seasonally flooded and has a dark, fine-textured loamy soil. *"Acacia saligna* thicket" has much grass understorey, mainly *E. ovata*, and seedlings of *H. invaginata*. It is also a seasonally flooded site, with soil of dark fine texture, well-drained sandy clay loam or sandy loam.

Sites in the West corner area tend to have deep dry sandy soils. These promote the formation of Myrtaceous thickets. Most plants are medium shrubs of *Acacia* and *Melaleuca* species. The deep sandy soil that becomes very dry in summer may be a typical edaphic environment for myrtaceous thickets. Vegetation associations present include (Chapter 2, 2.3.3): "*Phebalium tuberculosum* shrubland", with the main association with *Acacia* species and a few *Eriostemon tomentellus*. "*Acacia acuminata* thicket", with co-dominant *Acacia coolgardiensis*, *Phebalium tuberculosum*, *Baeckea behrii*, *Allocasuarina acutivalvis* and *Hakea invaginata*. "*Acacia coolgardiensis* thicket", with the main association with *Melaleuca eleuterostachya*, *Acacia hemiteles*, *Eriostemon tomentellus* and *Baeckea behrii*.

At the CK-3 area, the vegetation mainly consists of tall, open woodland of *Eucalyptus* species and Myrtaceous thickets (Chapter 2, 2.3.4). Most plants are *Eucalyptus* species. Vegetation types include "*Eucalyptus salmonophloia* woodland", mainly comprised of *Eucalyptus* species (*E. salmonophloia*, *E. loxophleba* and *E. capillosa*) as an upper canopy; and *Acacia acuminata*, *Dodonaea inaequifolia* and *Allocasuarina huegeliana* as components of an intermediate canopy, and very few understorey species. This vegetation type is confined to the most well-developed vegetation at SRNR. "*Kunzea pulchella* shrubland" is on the periphery of the *Eucalyptus* woodland, relatively close to the rock and characterised by prominent cover and high density of *K. pulchella* (granite Kunzea), with *A. acuminata* and *A. huegeliana* co-dominant and some annual grasses as ground cover in season.

Soils in the rock area are high in soil moisture, with the soil relatively shallow and mainly of sandy loam or clay loam and relatively rich in humus. It promotes the formation of healthy shrublands or thickets. *Eucalyptus* species are uncommon, perhaps restricted by the relatively shallow soil. Vegetation types include (Chapter 2, 2.3.5): "Dense *Leptospermum erubescens* thicket", with *Acacia lasiocalyx* as upperstory and *L. erubescens* as understorey. This type of vegetation occurs at the large pockets of soil at the rock site. *L. erubescens* thicket did not develop to the broom-bush habit. "Open low *Acacia prainii* shrubland", with co-dominant *Dodonaea viscosa*, *Melaleuca macronichia* and *Dodonaea inaequifolia* and no upperstory; this type of vegetation often forms concentrated thickets at the creek line or run-off area near the rock. "Low open

Dodonaea viscosa shrubland" occurs on marginally flat sites at the base or edge of granite rocks. Co-dominant species include *Hibbertia verrucosa, Baeckea elderana, Acacia fauntleroyi* and some annual grass *Spartochloa scirpoidea.*

Most of the *Acacia* species at SRNR are present only in particular habitats (restricted distribution) and form relatively distinctive associations. Common associates of *Acacia lasiocalyx* are *L. erubescens* (Chapter 3, 3.3.1). These small tree species are characteristic of granite rock/edge site vegetation. These species seem well adapted to survive in coarse soil material derived from eroded rock. *Acacia prainii* is a common associates of *Dodonaea* species (both *D. viscosa* and *D. inaequifolia*), *Melaleuca macronychia* and *Hibbertia glomerosa.* These species are characteristic of seasonally wet areas at the base of the main rock site. They are all apparently species that do well in sites of seasonally high soil moisture. *Acacia fauntleroyi* grows with *Hibbertia, Baeckea* and the grass species *Spartochloa scirpoidea,* while *Acacia hemiteles* occurs with *Oleria muellerii, Acacia erinaceae* and several grass species e.g. *Austrostipa elegantissima.*

In this thesis, for convenience, I named four associations after four of the most common *Acacia* species. *A. prainii, A. lasiocalyx* and *A. fauntleroyi* associations occur in high moisture habitats, related to run-off from the granite rock, while the *A. hemiteles* association is mainly found in dry areas in *Eucalyptus* woodland. *Alyxia buxifolia, Santalum spicatum, Grevillea paniculata* and *Melaleuca macronychia* were present in both contrasting habitat types. These species presumably are adapted to persist in both wet and dry areas.

Of the populations examined, no seedlings of *A. lasiocalyx* were observed (Chapter 3, 3.3.1). Past recruitment may have been associated with local flooding of the gnammas where *A. lasiocalyx* is mainly found. A satisfactory reason as to why it occurs at small patches of water gaining fringe soil is obscure. An important concomitant strategy would be to promote new seedling establishment. The rock is characterised by a series of eroded "holes" (gnamma holes). Small ones are bare but filled with water. Larger ones have a lot of soil (granite sand and humus) and some *A. lasiocalyx* present.

A. lasiocalyx grows well in sandy loam and clay loam, and most commonly occurs in sandy loam. Soil depth are relatively shallow (mean depth 22 cm). The occurrence of seed must define whether *A. lasiocalyx* has been able to establish at a particular site.

A. prainii mainly occurs in an open, seasonally moist area that provides variable summer sustenance. Consequently, the turnover of this short-lived woody perennial is high. When examined, *A. prainii* was found to have good recruitment, with many seedlings and saplings present. Seed production is regular and some germination occurs each year. The main seasonally moist site has moisture available for long periods and in the absence of drought, some recruitment can occur every year. However, the population is severely infected by rust fungus (*Uromycladium tepperianum*), which reduces seed production. Little information is available on the effect of this rust fungus. In the long term, this disease may severely affect *A. prainii* regeneration. Further investigation is required to understand the long-term significance of rust infection on the population of *A. prainii* at SRNR. Some *Acacia saligna* are also observed to be badly infected by this rust fungus.

A. fauntleroyi forms small populations of limited distribution in narrow strips of land at the edges of the granite. Population size is limited by the extent of these sites and by drought that occurs at SRNR periodically. In long drought periods (>100 d), plants are severely affected, especially the larger trees. Local extinction is likely when summer rainfall is scarce. Although populations are small, distribution of plant size suggests that seedling recruitment occurs. It is hypothesised that as plants grow near the edge of the granite rock, apparently in relatively shallow soil, rain shed from the granite can promote growth of seedlings. *A. fauntleroyi* also appears to depend on material eroded from the rock, as no plant was observed far away from rock sites.

A. hemiteles forms large populations of wide distribution. It is not associated with the granite rock. It is present as an understorey species of eucalypt woodland. However, this type of vegetation is remarkably stable and no seedling stage was observed. As it is an understorey species, it is possible that shade from the canopy may inhibit seedling recruitment (or that seedlings are shade intolerant). Light may be required for germination or early establishment of seedlings of this species. Strong competition from high density of associated plants and high seed predation or herbivore activity in the area may also affect natural regeneration of this species. Barrett (1997) artificially germinated pre-treated and non-pre-treated seeds of *A. hemiteles* at SRNR (March 1997). After the winter rain (May 1997) she found that some 10% of seeds had germinated. Relatively high rainfall occurred in that year (385.1 mm) was presumably sufficient to promote seedling growth. However, by October 1997, no seedlings remained. It is hypothesised that root competition from surrounding plants (mainly *Eucalyptus*) have reduced the chance of survival. *Eucalyptus* species generally have high water needs. Kangaroos are also present in large numbers in the area and are suspected to eat small seedlings. In an other study, Yates & Broadhurst (2002) reported that grazing does inhibit seedling establishment of *Acacia* in southwest WA. Grazing may be a major effect only in a particular site.

Generally, most *Acacia* species at SRNR exhibit little recruitment and form only small populations. Of all species observed, only *A. acuminata* and *A. prainii* appear to be regular in recruitment, with many seedlings found. Failure in natural regeneration may be due to lack of seed, poor microsites or high herbivore activity on seedlings. In a study of natural regeneration of *Taxus baccata* L., Hulme (1996) found that both predation and microsites limited plant regeneration. He found that regeneration becomes increasingly microsite limited as the population develops and more intense predation occurs beneath shrubs compared to open sites.

The seeds of most *Acacia* fall close to the mother tree to be dispersed by the action of surface wash and possibly by seed collecting ants, or seed-eating birds. Seed predators include a range of insects, mainly larvae, birds, ants and mammals. Insects (*Bruchid beetles*: Bruchidae) are the main cause of damage as predators of seeds in *Acacia* savannas in Africa and the Middle East (Bond *et al.* 2001). Parrots, particularly galahs (*Kakatoe roseicapilla*) eat mulga seed (Preece 1971b). In Arava, Israel, Ungulates browse on pods of *Acacia raddiata* and *A. tortilis* and excrete seed in their faeces, thus dispersing the seeds. High seed predation will result in only a small portion of seed surviving soil storage in *Acacia cyclops* in Western Australia (Gill 1984).

Disturbance in the form of browsing significantly limits recruitment and survival in many African Acacias. Heavy browsing will prevent juvenile acacias moving into taller size classes and thus indirectly reducing seedling recruitment (Pellew 1983; Prins & Van der Jeugd 1993; Bond *et al.* 2001; Barnes 2001). Stem, rather than leaf removal is more important in preventing growth of juveniles into taller size classes. Black rhino are important browsers of African acacia trees, biting off branches up to 25 mm diameter (Bond *et al.* 2001). At SRNR, rabbits, kangaroos, galahs and parrots are suspected of defoliating *Acacia* foliage. Browsing is especially important in summer, when most grasses are not available. Barnes (2001) found that only *Acacia erioloba* and *A. hebeclada* had green leaves in open grass areas in the dry season and this increased the risk of predation.

In African *Acacia*, fire kills the shoots of juvenile acacias, also setting back the growth of juveniles to adults. Presence of grasses also suppresses the growth of *Acacia* (Bond *et al.* 2001). Grass layers may shade the establishment of woody seedlings and compete for water and nutrients. Smith and Goodman (1986) found that *Acacia nilotica* was unable to establish under canopy shade. As an understorey species, failure of *A. hemiteles* to regenerate at SRNR could be affected by canopy shade.

Successful recruitment of arid zone shrubs is typically intermittent and seedling mortality is high. In dry sclerophyll jarrah forest, in the absence of fire, legume stands decline after approximately 15 years, and no regeneration occurs (Shea *et al.* 1979). The general absence of fire at SRNR over much of the last century is probably a cause of poor recruitment in *Acacia*. However, the mechanism of natural regeneration for most *Acacia* species at SRNR is still unknown and it is therefore difficult to determine particular factors that affect poor recruitment.

Generally, the *Acacia* species of SRNR are present only in particular well-defined habitats. The adequacy of moisture is the most powerful control of species presence. Rainfall that falls onto the rock are then redistributed. Therefore, most water is likely to be available at the base around the rock. The highest soil moisture habitat with relatively rich humus promotes distinct plant association. Four *Acacia* species (*A. lasiocalyx*, *A. fauntleroyi*, *A. prainii* and *A. saligna*) were observed to occur at such sites.

In Arava, Israel, seedling survival of *Acacia* is mainly determined by water availability. Several years of high rainfall are necessary for successful establishment of young trees (Rochner & Ward 1999). The distribution of *Acacia* species in the Negev and Sinai was studied by Halevy & Orshan (1973). They found that adequate water supplies during the summer and high temperatures are the main factors that control the spatial distribution of *Acacia* species. *Acacia* trees are restricted to channel beds, forming a concentrated vegetation type. In Arava, much *Acacia* tree mortality was caused by insufficient water supply (BenDavid-Novak & Schick 1997). The trees are sustained by water present in the upper-most layer of the alluvium and are therefore predominantly dependent on surface flows. That conclusion was mainly supported by a survey of the *Acacia* tree root system. It is not deep but extends laterally up to 20 m from the trunk. Lack of recruitment is also affected by human disturbance by lowering of ground water level through the excessive water extraction for agricultural purposes and road construction.

As most of the *Acacia* at SRNR form small populations and have poor recruitment, it is suggested that until more is known about natural regeneration of these acacias, protection of those reserves in which they occur now should be given the highest priority. In this way, the long-term viability of the species in their natural habitats will be enhanced.

7.3. Aspects of reproduction in *Acacia* species

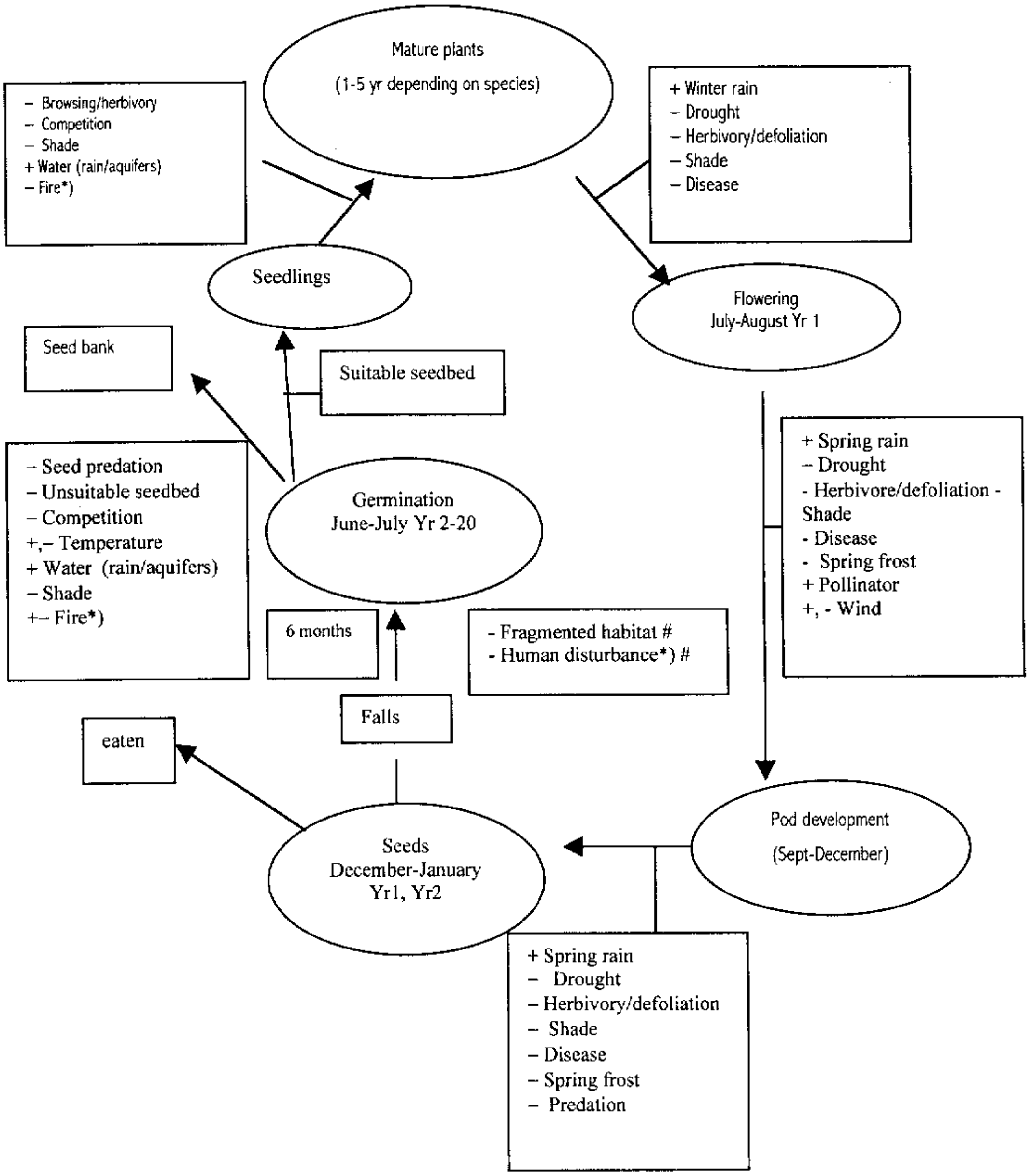

Figure 54. General life cycle of *Acacia* species and possible factors affecting natural regeneration. Plus and minus indicate positive and negative effects respectively. *) = Effect not seen at SRNR. # = Effect affects all plant life cycles (constant).

Reproductive success of *Acacia* is affected by rainfall in particular years (Chapter 4, 4.2). It appears that good rainfall is an important requirement for flowering and is critical for good fruit set. A wet winter is required to induce flowering and further rain is required after flowering to promote pod development and good seed set (Figure 54). Although all species suffered from drought in 2000, they differed in degree of susceptibility (Chapter 4, 4.2.3.1). *A. stereophylla* was severely affected and failed to develop pods. *A. hemiteles* did not flower and very few inflorescences developed a pod in both *A. lasiocalyx* and *A. saligna.* Some species developed relatively high pod numbers due to flowering earlier and therefore to some extent, can avoid drought. Only *A. neurophylla* is apparently drought tolerant. For some species (e.g. *A. steedmanii*), seed set appears sufficient to replace senescing adults but recruitment rarely occurs. Natural regeneration failure may be due to high seed predator or herbivore levels, unsuitable seedbeds and competition from established vegetation.

It is possible to place the *Acacia* species at SRNR into five different categories: 1) Species with large populations that flower and fruit regularly (e.g. *A. acuminata* and *A. prainii*). These species have good recruitment with many seedlings present. These species are relatively more susceptible to drought due to growing in relatively moist habitats; 2) Species with large populations but poor recruitment and irregular flowering (e.g. *A. hemiteles*). For this species, good winter rain is required to induce new shoots as flowers are confined to new shoots; 3) Species with relatively small populations and poor recruitment but flowering and fruiting regularly (e.g. *A. neurophylla, A. steedmanii, A. saligna, A. fauntleroyi* and *A. lasiocalyx*). All species, except *A. neurophylla* (which grows on yellow sand) are severely affected by drought; 4) Species with small populations, poor recruitment and which rarely set pods (e.g. *A. stereophylla*), and which may be constrained by poor pollination due to scarce individuals. This species is also affected by drought; 5) Species that have very few seed set at any time and are constrained genetically, regenerating vegetatively (*A. jennerae*). Most *Acacia* species at SRNR fit category 3 (small population and poor seedling establishment). In order to maintain or improve these populations, it may be necessary to provide conditions advantageous to seedling recruitment as an important component of any conservation management strategy. If not, local extinction of some of the small populations may occur.

Of pods collected in 1998, all species produced apparently mature seed of low weight (Chapter 4, 4.2.3.3). There were many immature and diseased seeds, and poor germination resulted. A late spring frost in 1998 is believed responsible for limited seed development. Of 13 species examined, only *A. neurophylla*, *A. nyssophylla* and *A. coolgardiensis* had relative tolerance to frost, with relatively high germination obtained. All others were very poor with little to no germination. The ecological and economic effects of frost are best known for crop plants. For native species, such as *Acacia,* information is very limited.

Leafiness affects *Acacia* plant reproductivity. Plants bearing more phyllodes initiate more inflorescences; more inflorescences set pods; and, fewer inflorescences dry off. These observations suggest that phyllodes donate nutrients to fruits (Hocking & Pate 1977) and resources tend to flow into fruits from the nearest phyllodes (Mooney 1972). Branch position also affects plant reproductivity. Generally, those branches in the upper part of the crown bear heavier inflorescences.

In two selected *Acacia* species (*A. saligna* and *A. lasiocalyx*), removal of phyllodes reduced the number of inflorescences initiated that develop into pods (Chapter 4, 4.3). It is presumed that removal of phyllodes reduced the production and availability of photosynthate. Therefore, competition among inflorescences (or pods) for resources was more intense; and subsequent abortions would have occurred. This confirms that the role of phyllodes as a donor of nutrients at reproduction time is critical in *Acacia* species. Therefore, herbivore activity and other defoliation, leaf shading or disease damage to phyllodes will all contribute to higher rates of inflorescence or pod abortion.

7.4. Germination and seedling characteristics of *Acacia* and grass species present at SRNR

Westonia experiences a Mediterranean climate. The region is characterised by a long, hot, dry summer with a short, cool, wet winter. Mean monthly summer maximum temperatures range from 35-45°C and winter temperatures from 0-27°C. For all *Acacia* species studied, the best germination corresponded with the cool season; none of them seem adapted to give high germination in summer (Chapter 5, 5.2). Although summer rain does sometimes occur, and that may be sufficient to promote germination, seedlings are unlikely to survive. Delayed summer germination will be of adaptive advantage in that it retains seed in the soil seed bank. Species need to avoid germination after small falls of rain during the dry season, as mortality can be complete during the subsequent dry period.

Of the 8 *Acacia* species examined, all show relatively high germination levels. Seedling establishment can actually replace senescing adults, however most species have poor recruitment and only small populations. *A. steedmanii* and *A. hemiteles* had no recruitment at all. Of all species, only *A. acuminata* and *A. prainii* had apparently good recruitment. Poor recruitment is not limited by poor seed production or germination, and there is no apparent effect of population size on germinability (e.g. in *A. steedmanii* very few present, however has relatively good seed production and good germination). Poor seedbed, strong competition, high predation or herbivore activity may have contributed.

Western Australia has a strongly seasonal climate. All WA natural vegetation can be said to be root saturated, where roots grow until no more water can be absorbed (Fox pers. comm). If some seed germinates in the period May-August, seedlings may perish from root competition. Thus, for a new plant to survive there must be a reduction in root competition. Reduction in root competition can occur by various agents in nature such as: fire from a lightning strike burns down a patch; lightning kills one or more large individuals or old age plants. Wind may blow over a tree; and rust fungus may kill an individual. All these factors can result in reduced root competition, thus promoting growth of new seedlings. In a saturated area, there may be a patch where in a very moist year, there is a surplus of water. Seedlings at these sites can survive until root competition sets-in in September/October. If good spring and summer rain occur, seedlings may persists and hang on independently.

Absence of fire for a long time is an obvious contributor to poor recruitment in most *Acacia* species at SRNR, since seeds of all species would appear to benefit from, and may be said to require, heat treatment to promote germination. In dry sclerophyll, jarrah forest, in the absence of fire, legume stands decline after approximately 15 years and no regeneration occurs (Shea *et al.* 1979). An obvious artificial strategy is to burn small areas in different places from time to time to promote seedling recruitment.

Distribution of *Acacia* species at SRNR appear mainly governed by moisture availability. Some species are well adapted to relatively moist habitats, whereas some species are well adapted to dry areas. Such specific habitat requirements apparently appear in characteristics of early seedling growth. Species that grow naturally in dry areas devote more resources to develop roots than those species that grow in moist areas. In dry areas, more resources may be used for root growth as an adaptation to the dry environment. Highest root ratios are also attained by species with small seed rather than those with large seeds. This biomass partitioning can also be viewed as a strategy that conserves moisture.

Of the grass species dominant in the reserve, with the exception of *Aristida contorta,* all had more germination in the winter than in the summer season. Seeds are unlikely to germinate after light summer rain (as there is little chance of seedling survival). The flora is thus more similar to the typical southwest flora. Of the 7 grass species, 4 gave relatively good germination. However, 3 species (*Eriachne ovata, Amphipogon strictus* and *Aristida contorta*) gave poor germination (<10%). Attention needs to be given to *A. contorta* as this species gave very low germination (2%). Generally, the germination values reflect relative abundance of the species at SRNR. Species with high germination levels are present in abundance and have a relatively wide distribution. Therefore, in any conservation strategy, those with poor germination should receive priority to avoid local extinction.

Hot water treatment is not recommended for stimulating germination in grasses. In some species, germination was reduced (Chapter 5, 5.3.3.1). Hot water pre-treatment is not appropriate to break dormancy in grass seed. Baskin and Baskin (1998) found that grass seeds tend to have physiological dormancy and this is not broken by hot water treatment. Other studies also suggest that at high temperatures, grass seeds tend to maintain dormancy (Smith *et al.* 1999). Therefore, except in *A. contorta*, grasses at SRNR may be capable of maintaining dormancy when subject to summer rain. Generally, germination in the glasshouse was greater and earlier than in incubation cabinets, suggesting that in most grasses, fluctuating temperatures promote germination. Storage of seed for more than 2 years also appears to reduce viability.

Of the 7 species examined, *A. strictus* had the fastest growth. *E. ovata* produced greater root than shoot mass, a characteristic of a strong competitor. In all other species, shoot mass was greater than root mass, characteristic of species that grow well in moist habitats. The tallest shoot and longest root were attained by *A. elegantissima.* This is an understorey species of eucalyptus woodland. *E. ovata* had a long root but a short shoot. *A. strictus* and *S. scirpoidea* both had short root and shoots. Both grow in sandy soils in fairly barren habitats.

7.5. Effect of seed size on germination and seedling characteristics

Both genetic and environmental factors might affect seed size. The environmental conditions to which the parental plant is exposed: temperature; nutrients; and water availability all affect final seed weight. Seed size is reduced with reduced nutrients or water, since both affect photosynthesis rates. Reduction in daily net carbon gain as produced by shortening of the photoperiod, competition for available resources or self-shading, also reduces seed size. In legumes, the leaves directly subtending the inflorescence may be the major source of carbohydrates for developing seeds, therefore leaf defoliation reduces seed size. Even small variations in seed size may affect dispersal, seed water relations, germination, size of the resulting seedling and seedling establishment and survival (Baker 1972; Wulff 1986; Westoby *et al.* 1992; Bonfil 1998; Seiwa 2000).

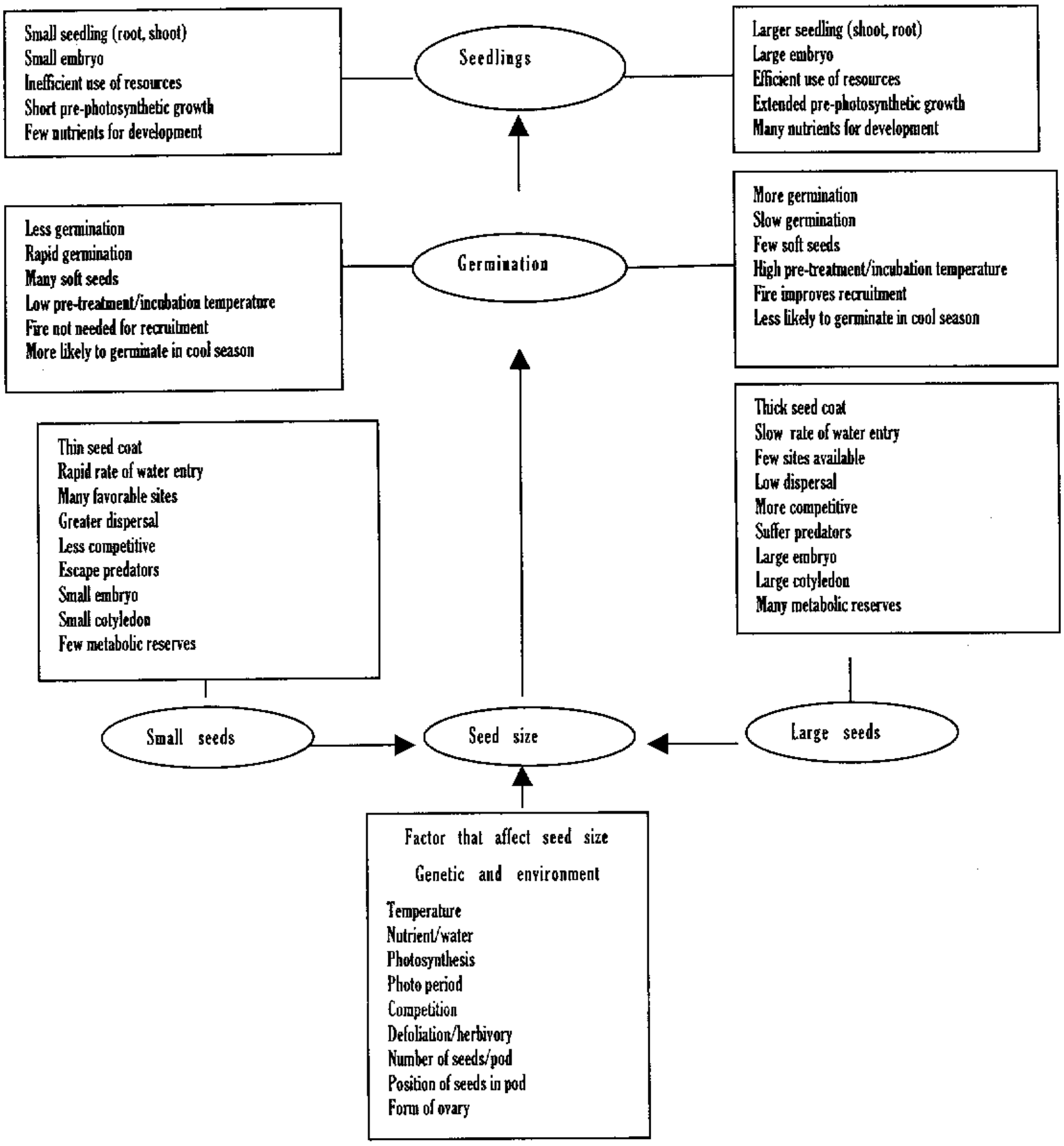

Figure 55. Proposed factors that affect seed size and the role of seed size in *Acacia* species.

In two selected *Acacia* species, both germination and seedling characteristics are shown to be affected by seed size (Figure 55). In *A. fauntleroyi,* heavier seeds attain more, but slower germination than light seeds (Chapter 6, 6.2). Less germination in small seeds is presumably affected by some small seeds being undeveloped. While more rapid germination of smaller seeds is due to thinner seed coats, this means water is imbibed sooner, thus, commencing germination. The degree of hard-seeded-ness varies between seed sizes, with a higher proportion of soft seed in smaller seeds. Smaller seeds have thinner seed coats and most of them do not require any surface damage to the seed coat prior to imbibition. Seed of different sizes show some responses to different pre-treatments and incubation temperatures for germination. Larger seeds generally germinate in greater numbers after higher pre-treatment temperatures. Therefore, the occurrence of fire for recruitment is important in that it could increase the chances of large seeds germinating. In the absence of fire, recruitment will depend much more on small seeds. Larger seeds also germinate better at higher incubation temperatures. Therefore, in the winter season, small seeds are more likely to germinate than large seed.

The interaction of pre-treatment temperature and seed size has a stronger effect on germination than the interaction between incubation temperature and seed size. This suggests the main barrier to germination in *A. fauntleroyi* is seed dormancy. The best treatment to promote germination of *A. fauntleroyi* for small seeds was pre-treatment at 75°C and incubation at 15°C. For medium and large seeds, best germination was from pre-treatment at 75°C and incubation at 30°C or pre-treatment at 100°C and incubation at either 15 or 30°C. This sensitivity to pre-treatment, incubation temperature and the prolonged germination period of *A. fauntleroyi* suggests that this species tends to develop persistent soil seed banks. However, this was not examined in the present study and would need further investigation for confirmation.

In *A. prainii*, germination numbers were affected by seed size, pre-treatment, incubation and their interactions (Chapter 6, 6.3). Larger seeds are more viable than smaller seeds. The best pre-treatment is soaking in boiling water (100°C) and the best incubation temperature is 25°C at which all seeds germinate. At 30°C incubation, more than 60% of seeds failed to germinate. Therefore, *A. prainii* is less likely to germinate in summer. Sensitivity of current *A. prainii* seeds to incubation temperatures suggests that after seed fall, following natural scarification and the entry of water, successful germination will depend greatly on the temperature of the environment.

Dormancy is considered to be an adaptation, preventing germination at unfavourable times for establishment and growth. In less predictable environments such as arid Australia, germination is a high risk event, since rainfall sufficient to allow germination may be insufficient for subsequent seedling establishment. Consequently, many species effectively spread the risks associated with germination in that depletion of the seed bank following a single large rainfall event is avoided by having a high proportion of hard seed in the seed bank.

In two selected *Acacia* species (*A. fauntleroyi* and *A. prainii*), seeds of different sizes differs in seed coat thickness. Larger seeds have thicker seed coats (Chapter 6, 6.4). This morphological pattern affects seed coat permeability and helps to determine both speed and success of germination. Variation in seed coat thickness between seed sizes explains variation in the values and speed of germination obtained between seed of different sizes. The seed coat of *A. prainii* is thicker than *A. fauntleroyi* and therefore requires a longer time to imbibe water. This variation explains the higher proportion of soft seed in *A. fauntleroyi* (35%) than in *A. prainii* (6%). In both species, all cell layers appear to contribute to hard-seeded-ness, as all layers are suberised. Cells at the outer layer (Malpighian cells) have a much thicker cell wall than that on the inner side (mesophyll cell). This characteristic is valuable in slowing the rate of water entry into the seed.

There have been numerous studies on the effect of heat treatment on *Acacia* seed. The effect generally could be "non", if the heat given is too weak; "destruction", if the stress is too great; and, "stimuli", if heat given removes an integument, an inhibitor or other stimulus. The response appears to vary between seed of different sizes and species. There are several *Acacia* from different regions that do not need scarification for germination because the seed is "soft". These include: *A. mangium* Willd. in tropical areas of Indonesia (Saharjo & Watanabe 1997); *A. constricta* in the Sonoran desert (Cox *et al.* 1993); *A. ataxacantha*, *A. dudgeoni*, *A. kamerunensis*, *A. senegal* and *A. erhenbergiana* in West Africa (Danthu *et al.* 2002) and in some Australian acacias: *A. argyrodendron* Domin, *A. cambagei* R.T. Baker, *A. cyperophylla* F. Muell. ex Benth., *A. georginae* F.M. Bailey, *A. harpophylla* F. Muell. ex Benth, *A. latzii* Maslin and *A. maconochieana* Pedley (Doran *et al.* 1983). For those species, heat treatment would not effectively induce germination. Thus, using fire to promote germination in the conservation of acacias should be considered carefully.

Larger seed gives seedlings an initial growth advantage. In *A. fauntleroyi* (Chapter 6, 6.2.3.3), small seeds produce seedlings with slightly greater root: shoot ratio than seedlings from large seeds. Small seedlings must expend more energy to develop roots than do large seedlings. In *A. prainii* (Chapter 6, 6.3.3.4), small seedlings have a higher shoot ratio than do large seedlings. Small seedlings expend more energy to develop shoots. The different seedling allocation patterns between species may be related to differences in habitat-specific selection pressures that lead to successful seedling establishment.

Large seeds have better resources; enhanced nutrient reserves in large seeds and their translocation from cotyledons to seedling during early growth can reduce reliance of the seedlings on an external supply of nutrients. This trait would be an advantage on infertile soil (Stock *et al.* 1990). In some cases, seeds function as a selective store of particular nutrients so that the seed nutrient reserve complements the nutrients available in the soil (Vaughton & Ramsey 2001). Large seeds often produce large seedlings with lower relative growth rate than small seeds. An increase in the absolute size of the root system (or relative allocation to root) promotes access to soil nutrients, while lower growth rates reduce the requirement for nutrients by the seedling. Vaughton and Ramsey (2001) found that in *Banksia cunninghamii* (Proteaceae), large seeds have an advantage for seedling establishment in nutrient poor soil. Large seeds had more nutrients (N and

P). N and P are generally considered to be the main nutrients limiting plant growth in Australian sclerophyllous vegetation. For seedlings, P availability is considered especially important because of the insoluble nature of this nutrient and the inability of seedlings to obtain sufficient quantities with their small root systems.

REFERENCES

Abdulfatih, H. A. (1995). Seed germination in *Acacia* species and their relation to altitudinal gradient in south-western Arabia. *Journal of Arid Environments* **31**, 171-178.

Aiba, S. I. & Kitayama, K. (1999). Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology* **140**, 139-157.

Arachchi, D. H. M., Naylor, R. E. L. & Bingham, I. J. (1999). A thermal time analysis of ageing of Maize (*Zea mays* L.) seed can account for reduced germination in hot moist soil. *Field Crops Research* **63**, 159-167.

Atkins, O. K., Schortmeyer, M., McFarlane, N. & Evans, J. R. (1998). Variation in the components of relative growth rate in ten *Acacia* species from contrasting environments. *Plant, Cell and Environment* **21**, 1007-1017.

Auld, T. D. & O'Connell, M. A. (1991). Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. *Australian Journal of Ecology* **16**, 53-70.

Baker, H. G. (1972). Seed weight in relation to environmental condition in California. *Ecology* **53**, 997-1010.

Ballard, L. A. T. (1973). Physical barriers to germination. *Seed Science and Technology* **1**, 285-301.

Barnes, M. E. (2001). Effect of large herbivores and fire on the regeneration of *Acacia erioloba* woodland in Chobe National Park, Botswana. *African Journal of Ecology* **39**, 340-350.

Barrett, D. A. (1997). Ecology of *Acacia hemiteles* in relation to mine-site rehabilitation, in the Yilgarn. Honours Thesis. School of Environmental Biology, Curtin University, Perth.

Barrett, D. R. (1995). Review of the ecological characteristics of *A. acuminata* Benth. *Mulga Research Centre Journal* **12**, 31-38.

Baskin, C. C. & Baskin, J. M. (1988). Germination ecophysiology of herbaceous plants species in a temperate region. *American Journal of Botany* **75**, 286-305.

Baskin, C. C. & Baskin, J. M. (1998). **Seed: Ecology, Biogeography and Evolution of Dormancy and Germination**. Academic Press, San Diego.

Beadle, N. C. W. (1981). **The Vegetation of Australia**. Cambridge University Press. Cambridge.

Beard, J. S. (1981). Explanatory Notes to Sheet 7 Swan. **Vegetation Survey of Western Australia 1:1 000 000 Series**. University of Western Australia Press.

Bell, D. T., King, L. A. & Plummer, J. A. (1998). Ecophysiological effect of light quality and nitrate on seed germination in species from Western Australia. *Australian Journal of Ecology* **24**, 2-10.

BenDavid-Novak, H. & Schick, A. P. (1997). The response of *Acacia* tree population on small alluvial fans to changes in the hydrological regime: Southern Negev desert, Israel. *Catena* **29**, 341-351.

Bewley, J. D. & Black, M. (1994). **Seeds: Physiology of Development and Germination**. New York: Plenum Press.

Bhalla, P. L. & Slattery, H. D. (1984). Callose deposition makes clover seeds impermeable to water. *Annals of Botany* **53**, 125-128.

Black, J. N. (1955). The influence of seed size and depth of sowing on pre-emergence and early vegetative growth of subterranean clover (*Trifolium subterraneum* L.). *Australian Journal of Agricultural Research* **7**, 98-109.

Bond, J. W., Smythe, K. A. & Balfour, D. A. (2001). *Acacia* species turn over in space and time in an African savanna. *Journal of Biogeography* **28**, 117-128.

Bonfil, C. (1998). The effect of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugosa* and *Q. laurina* (Fagaceae). *American Journal of Botany* **85**, 79-87.

Brothers, T. (1992). Forest fragmentation and alien plant invasion of central Indiana old-growth forest. *Conservation Biology* **6**, 91-100.

Bureau of Meterology (2002). Climate data for the Perth Metropolitan Area.

Burgman, M. A. (1987). An analysis of the distribution of plants on granite outcrops in Southern Western Australia using mantle test. *Vegetatio* **71**, 79-86.

Cavanagh, A. K. (1980). A review of some aspects of the germination of acacias. *Proceedings Royal Society Victoria* **91** (1-2), 161-180.

Cavanagh, A. K. (1985). Germination of hard-seeded species (Order *Fabales*) *In* Langkamp, P. (ed.). **Germination of Australian Native Plant Seed**. The Australian Mineral Industries Research Association Ltd.

Cervantes, V., Carabias, J. & Vazquez-Yanes, C. (1996). Seed germination of woody legumes from deciduous tropical forest of southern Mexico. *Forest Ecology and Management* **82**, 171-184.

Clements, J., Jones, P. G. & Gilbert, N. H. (1977). Effect of seed treatments on germination in *Acacia*. *Australian Journal of Botany* **25**, 269-276.

Cox, J. R., Alba-Avila, A., Rice, R.W. & Cox, J. N. (1993). Biological and physical factors influencing *Acacia constricta* and *Prosopis volutina* establishment in the Sonoran Desert. *Journal Range Management* **46**, 43-48.

Cunningham, S. A. (1997). The effect of light environment, leaf area, and stored carbohydrates on inflorescence production by a rain forest understorey palm. *Ecologia* **111,** 36-44.

Cunningham, S. A. (2000). Depressed pollination in habitat fragments causes low fruit set. *Proceedings of the Royal Society of London-Biological Sciences* **267,** 1149-1152.

Danthu, P., Ndongo, M., Diaou, M., Thiam, O., Sarr, A., Dedhiou, B. & Vall, A. O. M. (2002). Impact of bush fire on germination of some West African acacias. *Forest Ecology and Management* (in press).

Davies, S. J. J. F. (1968). Aspects of a study of emus in semi-arid Western Australia. *Proceedings Ecological Society of Australia* **3,** 160-166.

Dell, B. (1980). Structure and function of the strophiolar plug in seeds of *Albizia lophantha. American Journal of Botany* **67,** 556-563.

Doran, J. C., Turnbull, J. W., Boland, D. J. & Gun, B. V. (1983). **Hand Book on Seeds of Dry-zone Acacias**. FAO. Rome.

Dunlop, J. R. & Barnett, J. P. (1983). Influence of seed size on germination and early development of loblolly pine (*Pinus taeda* L.) germination. *Canadian Journal of Forest Research* **13,** 40-44.

Egley, G. H. (1976). Germination of developing prickly sida seeds. *Weed Science* **24,** 239-243.

Egley, G. H. (1979). Seed coat impermeability and germination of showy crotalaria (*Crotalaria spectabilis*) seeds. *Weed Science* **27,** 355-361.

Egley, G. H. (1989). Water-impermeable seed covering as barrier to germination. *In* Taylorson, R. B. (Ed.). **Recent Advances in the Development and Germination of Seeds**. Plenum Press, New York.

Egley, G. H. & Paul, R. N. (1982). Development structure and function of sub-palisade cells in water impermeable *Sida spinosa* seeds. *American Journal of Botany* **69,** 1402-1409.

Elliot, W. R. & Jones, D. L. (1990). **Encyclopaedia of Australian Plants Suitable for Cultivation**. Lothian Publishing, Melbourne.

Eriksson, O. (1999). Seed size variation and its effect on germination and seedling performance in the clonal herb *Convallaria majalis. Acta Oecologiea* **20,** 61-66.

Erwin, J. E., Glomsrud, N., Vikor, T., Moe, R. & Etzel, P. (1997). Cutting position, leaf removal and time of year affects *Rosa* axillary shoot development. *Scientia Horticulturae* **68,** 157-170.

Fenner, M. (1985). **Seed Ecology**. London and New York. Chapman and Hall.

Fitter, A. H. & Hay, R. K. M. (1992). **Environmental Physiology of Plants**. Academic Press. New York.

Fox, J. E. D. (1997). Why is *Santalum spicatum* common near granite rocks? *Journal of the Royal Society of Western Australia* **80**, 209-220.

Fox, J. E. D., Keenan, C. & Shepherd, D. P. (1993). Some stand characteristics of remnant vegetation in the eastern wheatbelt of Western Australia. *Santalum* **14**, 35-47.

Fry, G. & Main, A. R. (1993). Restoring seemingly natural communities on agricultural land. *In* Saunders, D. A., Hobbs, R. J. & Ehrlich, R. R. (ed.). **Nature Conservation: Reconstruction on Fragmented Ecosystems**. Surrey Beatty & Sons. Chipping-Norton. pp. 225-241.

Gathe, J. (1971). Host range and symptoms in Western Australia of the gall rust, *Uromycladium tepperianum*. *Journal of the Royal Society of Western Australia* **54**, 114-118.

Gibson, N., Keighery, G. & Keighery, B. (2000). Threatened plant communities of Western Australia. 1. The ironstone communities of the Swan and Scott Coastal Plains. *Journal of the Royal Society of Western Australia* **83**, 1-11.

Gill, A. M. (1975). Fire and the Australian flora: A Review. *Australian Forestry* **38**, 4-25.

Gill, A. M. (1984). *Acacia cyclops* and *Hakea sericea* at home and abroad. *Proceedings 4th International Conference Mediterranean Ecosystem*, Perth, 57-58.

Glossop, B. L. (1980). Germination responses of thirteen legume species to boiling. *Alcoa of Australia Limited Environmental Research Bulletin*. No. **5**, 1-8.

Goverde, M., Schweizer, K., Baur, B. & Erhardt, A. (2002). Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands. *Biological Conservation* **104**, 293-299.

Gow, D. A. (1997). The natural regeneration of sandalwood, *Santalum spicatum* at Sandford Rock Nature Reserve. Honours Thesis. School of Environmental Biology, Curtin University, Perth.

Green, J. W. (1985). **Census of the Vascular Plants of Western Australia**. Second Edition. Western Australian Herbarium. Department of Agriculture, Perth. Pp.312.

Griffin, A. R. (1972). The effect of seed size, germination time and growing density on seedling development in radiata pine. *Australian Forest Research* **5**, 25-60.

Gross, K. L. & Soule, J. D. (1981). Differences in biomass allocation to reproductive and vegetative structures of male and female plants of dioecious, perennial herb, *Silene alba* (Miller) Krause. *American Journal of Botany* **68**, 801-807.

Hagon, M. W. & Groves, R. H. (1977). Some factors affecting the establishment of four native grasses. *Australian Journal of Experimental Agriculture and Animal Husbandry* **17**, 90-96.

Halevy, G. & Orshan, G. (1973). Ecological studies on *Acacia* species in the Negev and Sinai. I. Distribution of *Acacia raddiata*, *A. tortilis* and *A. gerrardi* spp. Negevensis as related to environmental factors. *Israel Journal of Botany* **21**, 197-208.

Hard, J. S. (1963). Frost damage to red pine conelets. United States Forest Service Research Note LS-5, United State Forest Experiment Station, St. Paul, Minnesota, USA.

Harding, J. F. (1940). *Acacia* germination trial. *Australian Forestry* **5**, 53-56.

Harper, J. L. (1977). **The Population Biology of Plants**. Academic Press. New York. USA.

Harper, J. L., Lovell, K. G. & Moore, P. H. (1970). The shape and sizes of seeds. *Annual Review of Ecology and Systematics* **1**, 327-356.

Harper, J. L. & White, J. (1974). The demography of plants. *Annual Review of Ecology and Systematics* **5**, 419-463.

Herranz, J. M., Ferrandis, P. & Martinez-Sanchez, J. J. (1998). Influence of heat on seed germination of seven Mediterranean Leguminosae species. *Plant Ecology* **136**, 95-103.

Hobbs, R. J. (1987). Disturbance regimes in remnants of natural vegetation. *In* Saunders, D. A., Arnold, G. W., Burbidge, A. A. & Hopkins, A. J. M. 1987. **Nature Conservation: The Role of Remnants of Native Vegetation**. Surrey Beatty & Sons, Chipping-Norton. pp. 233-240.

Hobbs, R. J. & Atkins, L. (1988). Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian Wheatbelt. *Australian Journal of Ecology* **13**, 171-179.

Hocking, P. J. & Pate, J. S. (1977). Mobilisation of minerals to developing seeds of legumes. *Annals of Botany* **41**, 1259-1278.

Hopper, S. J., Brown, A. P. & Marchant, N. G. (1997). Plants of Western Australia granite outcrops. *Journal of the Royal Society of Western Australia* **80**, 141-158.

Howe, H. F. & Richter, W. M. (1982). Effect of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. *Ecologia* **53**, 347-351.

Howell, N. (1981). The effect of seed size and relative emergence time on fitness in natural population of *Inpatients capensis* Meerb. (Balsaminaceae). *American Midland Naturalist* **105**, 312-320.

Hulme, P. E. (1996). Natural regeneration of yew (*Taxus baccata* L.): microcyte, seed or herbivore limited? *Journal of Ecology* **84**, 853-863.

Hunt, R. (1982). **Plant Growth Curves**. The Functional Approach to Growth Analysis. Edward Arnold, London.

Inouye, D. W. (2000). The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters* **3**, 457-463.

Janzen, D. H. (1976). Effect of defoliation on fruit-bearing branches of the Kentucky coffee tree, *Gymnocladus dioicus* (Leguminosae). *American Midland Naturalist* **95**, 474-478.

Jones, B. & Gliddon, C. (1999). Reproductive biology and genetic structure in *Lloydia serotina*. *Plant Ecology* **141**, 151-161.

Jurado, E. & Westoby, M. (1992). Germination biology of selected central Australia plant. *Australian Journal of Ecology* **17**, 341-348.

Kang, H., Jascheck, G. & Bawa, K. S. (1992). Variation in seed and seedling traits in *Pithecellobium pedicellare*, a tropical rainforest tree. *Oecologia* **91**, 239-244.

Keenan, C. (1993). A description of relatively undisturbed salmon gum woodland in the eastern Wheatbelt. Honours Thesis. School of Environmental Biology, Curtin University, Perth.

Kent, M. & Coker, P. (1992). **Vegetation Description and Analysis a Practical Approach**. Belhaven Press. London.

Kitchener, D. J., Chapman, A., Dell, J. & Muir, B. G. (1980). Lizard assemblage and reserve size in the Western Australia Wheatbelt - some implications for conservation. *Biological Conservation* **17**, 25-62.

Kozlowski, T. T. (1971). **Growth and Development of Trees**. Vol. 2. Academic Press, New York. Pp.514.

Lamarque, A. L., Fortunato, R. H., Maestri, D. M. & Guzman, C. A. (2000). Seed components and taxonomy of some *Acacia* species. *Biological Systematics and Ecology* **28**, 53-60.

Lamont, B. (1985). Gradient and zonal analysis of understorey suppression by *Eucalyptus wandoo*. *Vegetatio* **63**, 46-66.

Lange, R. T. (1960). Rainfall and soil control of tree species distribution around Narrogin, Western Australia. *Journal of the Royal Society of Western Australia* **43**, 104–110.

Larsen, E. (1964). Germination response of *Acacia* seeds to boiling. *Australian Forestry Research* **1**, 51-53.

Law, B., Mackowski, C., Schoer, L. & Tweedie, T. (2000). Flowering phenology of Myrtaceous trees and their relation to climatic, environmental and disturbance variables in northern New South Wales. *Austral Ecology* **25,** 160-178.

Lechowicz, M. J. (1984). The effect of individual variation in physiological and morphological traits on the reproductive capacity of the common cocklebурr, *Xanthium strumarium* L. *Evolution* **38,** 833-844.

Lefroy, E. C., Hobbs, R. J. & Atkins, L. S. (1991). Revegetation quide to the central wheatbelt. *Department of Agriculture Western Australia Bulletin* **4231**.

Leopold, A. C. & Scott, F. I. (1952). Physiological factors in tomato fruit-set. *American Journal of Botany* **39**, 310-317.

Letnic, M., Dickman, C.R. & McNaught, G. (2000). Bet-hedging and germination in the Australian arid zone shrub *Acacia ligulata*. *Austral Ecology* **25**, 368-374.

Lloyd, D. C. (1979). Parental strategies of angiosperms. *New Zealand Journal of Botany* **17**, 595-606.

Lodder, M. S., Groves, R. H. & Muller, W. J. (1994). Early seedling growth of three species of *Danthonia* as affected by depth of sowing and nutrient supply. *Australian Journal of Botany* **42**, 543-554.

Manning, J. C. & Staden, J. V. (1987). The role of the lens in seed imbibition and seedling vigour of *Sesbania punicea* (Cav.) Benth. (Leguminosae: Papilionoideae). *Annals of Botany* **59**, 705-713.

Marbach, I. & Mayer, A. M. (1974). Permeability of seed coat to water as related to drying conditions and metabolism of phenolic. *Plant Physiology* **54**, 817-820.

Marchant, N., Wheeler, J., Rye, B., Bennett, E., Lander, N. & Macfarlane, T. (1987). **Flora of the Perth Region**: Part 2. WA Herbarium, Department of Agriculture, Western Australia.

McArthur, W. M. (1991). **Reference Soils of South-western Australia**. Department of Agriculture, Western Australia, Pp. 265.

Menzel, A. & Fabian, P. (1999). Growing season extended in Europe. *Nature*, 397, 659.

Mitchell, A. A. & Wilcox, D. G. (1994). **Arid Shrubland Plant of Western Australia**. University of Western Australia. Nedlands.

Moegenburg, S. M. (1996). Sabal palmetto seed size: causes of variation, choice of predators, and consequences for seedling. *Ecologia* **106**, 539-543.

Moffett, A. A. (1952). Differential germination in the black wattle (*Acacia mellisima* Wild) caused by seed treatment. *Wattle Research Institute Report*. 39-50.

Mooney, H. A. (1972). The carbon balance of plants. *Annual Review of Ecology and Systematic* **3**, 315-346.

Moran, G. F. & Hopper, S. D. (1987). Conservation of genetic resources of rare and widespread eucalypts in remnant vegetation. *In* Saunders, D. A., Arnold, G. W., Burbidge, A. A. & Hopkins, A. J. M. (ed.). **Nature Conservation: The Role of Remnants of Native Vegetation.** Surrey Beatty & Sons. Chipping-Norton. Pp. 151-162.

Morgan, J.W. (1998). Comparative germination responses of 28 temperate grassland species. *Australian Journal of Botany* **46**, 209-219.

Mott, J. J. (1972). Germination studies on some annual species from an arid region of Western Australia. *Journal of Ecology* **60**, 293-304.

Mott, J. J. (1973). Temporal and spatial distribution of an annual flora in an arid region of Western Australia. *Tropical Grasslands* **7**, 89-97.

Mott, J. J. (1974a). Mechanisms controlling dormancy in the arid zone grass *Aristida contorta*. I. Physiology and mechanisms of dormancy. *Australian Journal of Botany* **22**, 635-645.

Mott, J. J. (1974b). Factors affecting seed germination in three annual species from an arid region of Western Australia. *Journal of Ecology* **62**, 699-709.

Mott, J. J. & Tynan, P. W. (1974). Mechanisms controlling dormancy in the arid zone grass *Aristida contorta*. II. Anatomy of the hull. *Australian Journal of Botany* **22**, 647-653.

Mueller-Dombois, D. & Ellenberg, H. (1974). **Aim and Methods of Vegetation Ecology**. Jon Wiley & Sons, New York.

Muir, B. G. (1979). Some nature reserves of the WA. Wheatbelt. ***Part 14 Westonia Shire***. Unpubl. Department of Fisheries and Wildlife, Perth, Pp.55.

Murray, B. R. (1998). Density-dependent germination and the role of seed leachate. *Australian Journal of Ecology* **23**, 411-418.

Mwanamwenge, J., Loss, S. P., Siddique, K. H. M. & Cocks, P. S. (1999). Effect of water stress during floral initiation, flowering and podding on the growth and yield of faba bean (*Vicia faba* L.). *European Journal of Agronomy* **11**, 1-11.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Dafonseca, G. A. B. & Kent, J. (2002). Biodiversity hotspots for conservation priorities. *Nature* **403**, 853-858.

Norton, D. A. & Kelly, D. (1988). Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: The importance of the economies of scale. *Functional Ecology* **2**, 399-408.

Orchard, A. E. & Wilson, A. J. G. (2001a). (Editors) **Flora of Australia** Volume 11A, Mimosaceae, *Acacia* part 1. Melbourne : ABRS/CSIRO Publishing. pp. 673.

Orchard, A. E. & Wilson, A. J. G. (2001b). (Editors) **Flora of Australia** Volume 11B, Mimosaceae, *Acacia* part 2. Melbourne : ABRS/CSIRO Publishing. pp. 536.

Ott, R. L. (1993). **An Introduction to Statistical Methods and Data Analysis**. Ed. 4. Duxbury Press. California. pp.1051.

Pellew, R. A. P. (1983). The impact of elephant, giraffe and fire upon the *Acacia tortilis* woodland at the Serengeti. *African Journal of Ecology* **21**, 41-71.

Peterson, J. (1985). Seed testing procedures for native Australian plants. pp. 149-179. *In* Langkamp, P. J. (ed.). **Germination of Australian Native Plant Seed**. The Australian Mineral Industries Research Association Limited.

Pook, E. W., Gill, A. M. & Moore, P. H. R. (1997). Long-term variation of litterfall canopy leaf area and flowering in a *Eucalyptus maculata* forest on the south coast of New South Wales. *Australian Journal of Botany* **45,** 737-755.

Porter, J. W. (1978). Relationship between flowering and honey production of red ironbark, *Eucalyptus sideroxylon* (A. Cunn.) Benth. and climate in the Bendigo district of Victoria. *Australian Journal of Agricultural Research* **29,** 815-829.

Preece, P. B. (1971a). Contributions to the biology of Mulga. I. Flowering. *Australian Journal of Botany* **19,** 21-38.

Preece, P. B. (1971b). Contributions to the biology of Mulga. II. Germination. *Australian Journal of Botany* **19,** 39-49.

Preston, K. A. (1999). Can plasticity compensate for architectural constraints on reproduction? Pattern of seed production and carbohydrate translocation in *Perilla frutescens*. *Journal of Ecology* **87,** 697-712.

Prins, H. H. T. & Van der Jeugd, H. P. (1993). Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* **81,** 305-314.

Pukittayacamee, P. & Hellum, A. K. (1988). Seed germination in *Acacia auriculiformis:* Developmental aspects. *Canadian Journal of Botany* **66,** 388-393.

Quinlivan, B. J. (1971). Seed coat impermeability in legumes. *The Journal of the Australian Institute of Agricultural Science* **37,** 283-295.

Rochner, C. & Ward, D. (1999). Large mammalian herbivores and the conservation of Arid *Acacia* stands in the Middle East. *Conservation Biology* **13,** 1162-1171.

Saharjo, B. H. & Watanabe, H. (1997). The effect of fire on the germination of *Acacia magium* in a plantation in South Sumatera, Indonesia. *Commonwealth Forestry Review* **76,** 128-131.

Sakai, A., Paton, D. & Wardle, P. (1981). Freezing resistance of trees of the south temperate zone, especially sub-alpine species of Australia. *Ecology* **62,** 563-570.

Salisbury, E. J. (1974). Seed size and mass in relation to environment. *Proceedings of the Royal Society,* London B, **186,** 83-88.

Saunders, D. A., Arnold, G. W., Burbidge, A. A. & Hopkins, A. J. M. (1987). **Nature Conservation: The Role of Remnants of Native Vegetation**. Surrey Beatty & Sons. Chipping-Norton.

Saunders, D. A., Hobbs, R. J. & Margules, C. R. (1991). Biological conservation of ecosystem fragmentation: A review. *Conservation Biology* **5,** 18-32.

Schaal, B. A. (1980). Reproductive capacity and seed size in *Lupinus texensis*. *American Journal of Botany* **67,** 703-709.

Sedgley, M. (1985). Some effects of temperature and lights on floral initiation and development in *Acacia pycnantha*. *Australian Journal of Plant Physiology* **12,** 109-118.

Seiwa, K. (2000). Effects of seed size and emergence time on tree seedling establishment: importance of development constraints. *Oecologia* **123**, 208-215.

Shea, S. R., McCormick, J. & Portlock, C. C. (1979). The effect of fires on regeneration of leguminous species in the Northern Jarrah (*Eucalyptus marginata* Sm.) forest of Western Australia. *Australian Journal of Ecology* **4**, 195-205.

Simons, A. M. & Johnston, M. O. (2000). Variation in seed traits of *Lobelia inflata* (*Campanulaceae*): Sources and fitness consequences. *American Journal of Botany* **87**, 124-132.

Smith, M. A., Bell, D. T. & Loneragan, W. A. (1999). Comparative seed germination ecology of *Austrostipa compressa* and *Ehrharta calycina* (Poaceae) in a Western Australia *Banksia* woodland. *Australian Journal of Ecology* **24**, 35-42.

Smith, T. H & Goodman, P. S. (1986). The effect of competition on the structure and dynamic of *Acacia* savanna in Southern Africa. *Journal of Ecology* **74**, 1031-1044.

Sork, V. L. & Bramble, J. (1993). Ecology of mast fruiting in three species of North American Deciduous Oaks. *Ecology* **74**, 528-541.

Specht, R. L. (1972). **The Vegetation of South Australia**. A. B. James, Adelaide, South Australia.

Stephenson, A. G. (1979). Evolutionary examination of the floral display of *Catalpa speciosa* (Bignoniaceae). *Evolution* **33,** 1200-1209.

Stephenson, A. G. (1980). Fruit set, herbivory, fruit reduction and the fruiting strategy of *Catalpa speciosa* (Bignoniaceae). *Ecology* **61,** 57-64.

Stephenson, A. G. (1981). Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* **12,** 253-279.

Stephenson, A. G., Devlin, B. & Horton, J. B. (1988). The effect of seed number and fruit dominance on the pattern of fruit production in Cucurbita pepo (*Zucchina squash*). *Annals of Botany* **26,** 653-661.

Stock, W. D., Pate, J. S. & Delfs, J. (1990). Influence of seed size and quality on seedling development under low nutrient condition in five Australian and South African member of the Proteaceae. *Journal of Ecology* **78,** 1005-1020.

Stoneman, T. C. (1992). An introduction to the soils of the Merredin advisory district-description, illustration and notes on nine common soils. *Western Australian Department of Agriculture Bulletin* 4235.

Susko, D. J. & Lavett-Doust, L. L. (2000). Pattern of seed mass variation and their effects on seedling traits in *Alliaria petiolata* (Brassicaceae). *The American Journal of Botany* **87**, 56-66.

Taketay, D. (1998). Germination of *Acacia origena, A. pilispina* and *Pterolobium stellatum* in response to different pre-sowing seed treatments, temperature and light. *Journal of Arid Environments* **38,** 551-560.

Tran, V. N. & Cavanagh, A. K. (1980). Taxonomic implication of fracture load and deformation histograms and the effects of treatment on the impermeable seed coat of *Acacia* species. *Australian Journal of Botany* **28,** 39-51.

Tran, V. N. & Cavanagh, A. K. (1984). Structural Aspects of Dormancy. *In* Murray, D. R. (ed.). **Seed Physiology**. Academic Press, Sydney.

Tripathi, R. S. & Khan, M. C. (1990). Effect of seed weight and microcyte characteristics on germination and seedling fitness in two species of *Quercus* in subtropical wet hill forest. *Oikos* **57,** 289-296.

Turnbull, L. A., Rees, M. & Crawley, M. J. (1999). Seed mass and the competition/ colonisation trade-off: a sowing experiment. *Journal of Ecology* **87,** 899-912.

Van den Berg, M. A. (1978). Natural enemies of certain acacias in Australia. *Proceedings Second National Weeds Conference.* South Africa, Stellenbosch. Pp.75-82.

Vaughton, G. & Ramsey, M. (1998). Sources and consequence of seed mass variation in *Banksia marginata* (Proteaceae). *Journal of Ecology* **86,** 563-573.

Vaughton, G. & Ramsey, M. (2001). Relationship between seed mass, seed nutrients, and seedling growth in *Banksia cunninghamii* (Proteaceae). *International Journal of Plant Science* **162,** 599-606.

Wallace, K. J. & Morre, S. A. (1987). Management of remnant bushland for nature conservation in agriculture areas of Southern Western Australia - Operational and planning perspective. *In* Saunders, D. A., Arnold, G. W., Burbidge, A. A. & Hopkins, A. J. M. (Ed.). **Nature Conservation**: The Role of Remnants of Native Vegetation. Surrey Beatty & Sons. Chipping-Norton. Pp. 259-268.

Wardlaw, I. F. (1990). The control of carbon partitioning in plants. *New Phytologist* **116,** 341-381.

Watson, M. A. & Casper, B. B. (1984). Morphological constraints on patterns of carbon distribution in plants. *Annual Review of Ecology and Systematics* **15,** 233-258.

Weller, S. G. (1985). Establishment of *Lithospermum caroliniensis* on sand dunes: The role of nutlets mass. *Ecology* **66,** 1893-1901.

Werker, E., Marbach, J. & Mayer, A. M. (1979). Relation between the anatomy of the testa, water permeability and the presence of phenolics in the genus *Pisum. Annals of Botany* **43,** 765-771.

Westoby, M. (1981). How diversified seed germination behaviour is selected. *American Naturalist* **118,** 882-885.

Westoby, M., Jurado, E. & Leisman, M. (1992). Comparative evolutionary ecology of seed size. *Trends in Ecology and Evolution* **7,** 368-372.

Westoby, M., Leisman, M. & Lord, J. (1996). Comparative ecology of seed size and dispersal. *Phil. Trans. R. Soc. Lond.* B351, 1309-1318.

Whalley, R. D. B. (1987). Germination in the Poaceae (Gramineae). *In* Langkamp P. J. (ed.). **Germination of Australian Native Plant Seed**. Ikata Press, Melbourne for the Australian Mineral Industries Research Association. pp. 236.

Willson, M. F. (1972). The evolutionary ecology of plants. A review. *Biologist* **54,** 140-147.

Willson, M. E. & Price, P. W. (1980). Resource limitation of fruit and seed production in some *Asclepias* species. *Canadian Journal of Botany* **58,** 2229-2233.

Wilson, T. B. & Witkowski, E. T. F. (1998). Water requirements for germination and early seedling establishment in four African savanna woody plant species. *Journal of Arid Environment* **38,** 541-550.

Witkowski, E. T. F. & Garner, R. D. (2000). Spatial distribution of soil seed banks of three African savanna woody species at two contrasting sites. *Plant Ecology* **149,** 91-106.

Wulff, R. D. (1986). Seed size variation in *Desmodium paniculatum* 1. Factors affecting seed size. *Journal of Ecology* **74,** 87-91.

Xia, M. Z. (1994). Effect of soil drought during the generative development phase of faba bean *(Vicia faba)* on photosynthetic character and biomass production. *Journal of Agricultural Science* **122,** 67-72.

Xia, M. Z. (1997). Effect of soil drought during the generative development phase on seed yield and nutrient uptake of faba bean (*Vicia faba*). *Australian Journal of Agricultural Research* **48,** 447-451.

Yates, C. J. & Broadhurst, L. M. (2002). Assessing limitations on population growth in two critically endangered *Acacia* taxa. *Biological Conservation* (in press)

Zimmerman, J. K. & Weis, I. M. (1983). Fruit size variation and its effects on germination and seedling growth in *Xanthium strumarium. Canadian Journal of Botany* **61,** 2309-2315.

APPENDICES

Appendix 1. List of woody perennial species at SRNR (from 379 sampling points)

Family	No.	Species
1. Mimosaceae	1	*Acacia hemiteles*
	2	*Acacia acuminata*
	3	*Acacia erinaceae*
	4	*Acacia stereophylla*
	5	*Acacia neurophylla*
	6	*Acacia nyssophylla*
	7	*Acacia steedmanii*
	8	*Acacia jennerae*
	9	*Acacia prainii*
	10	*Acacia saligna*
	11	*Acacia colletioides*
	12	*Acacia coolgardiensis*
	13	*Acacia eremophila*
	14	*Acacia jibberdingensis*
	15	*Acacia lasiocalyx*
	16	*Acacia fauntleroyi*
	17	*Acacia sessilispica*
2. Myrtaceae	18	*Melaleuca macronychia*
	19	*Melaleuca acuminata*
	20	*Melaleuca uncinata*
	21	*Melaleuca pauperiflora*
	22	*Melaleuca eleuterostachya*
	23	*Melaleuca laxiflora*
	24	*Melaleuca lateriflora*
	25	*Melaleuca hamulosa*
	26	*Eucalyptus capillosa*
	27	*Eucalyptus subangusta*
	28	*Eucalyptus buracoppinensis*
	29	*Eucalyptus leptopoda*
	30	*Eucalyptus sheathiana*
	31	*Eucalyptus salubris*
	32	*Eucalyptus salmonophloia*
	33	*Eucalyptus loxophleba*
	34	*Eucalyptus myriadena*
	35	*Eucalyptus yilgarnensis*
	36	*Eucalyptus celastroides*
	37	*Baeckea behrii*
	38	*Baeckea elderiana*
	39	*Baeckea crispiflora*
	40	*Baeckea maidenii*
	41	*Calothamnus gilesii*
	42	*Micromyrtus racemosa*
	43	*Verticordia chrysantha*
	44	*Malleostemon roseus*
	45	*Kunzea pulchella*
	46	*Leptospermum erubescens*
	47	*Calothamnus asper*
3. Proteaceae	48	*Grevillea paniculata*
	49	*Grevillea paradoxa*
	50	*Grevillea didymobotrya*
	51	*Grevillea yorkrakinensis*
	52	*Hakea invaginata*
	53	*Hakea recurva*
	54	*Hakea coriaceae*
	55	*Hakea falcata*
	56	*Persoonia striata*
4. Rutaceae	57	*Phebalium tuberculosum*
	58	*Boronia ternata*
	59	*Eriostemon tomentellus*
	60	*Diplolaena sp*
5. Casuarinaceae	61	*Allocasuarina huegeliana*
	62	*Allocasuarina acutivalvis*
6. Sapindaceae	63	*Dodonaea caespitosa*
	64	*Dodonaea inaequifolia*
	65	*Dodonaea viscosa*
	66	*Dodonaea stenozyga*
7. Asteraceae	67	*Olearia muelleri*
	68	*Olearia revoluta*
8. Santalaceae	69	*Exocarpus aphyllus*
	70	*Santalum acuminatum*
	71	*Santalum spicatum*
9. Apocynaceae	72	*Alyxia buxifolia*
10. Dilleniaceae	73	*Hibbertia exasperata*
	74	*Hibbertia glomerosa*
	75	*Hibbertia verrucosa*
11.Caesalpiniaceae	76	*Cassia nemophila*
12. Epacridaceae	77	*Astroloma serratifolium*
13. Boraginaceae	78	*Halgania viscosa*
14. Sterculiaceae	79	*Keraudrenia integrifolia*
15. Lamiaceae	80	*Prostanthera baxteri*
16. Thymelaeaceae	81	*Pimelea angustifolia*
17. Haloragaceae	82	*Glischrocaryon aureum*
18. Myoporaceae	83	*Eremophila scoparia*
19. Chenopodiaceae	84	*Atriplex nummularia*
20. Solanaceae	85	*Solanum nummularium*

Appendix 2. Key for field determination of soil texture

Using a handful of moistened soil

A. Squeeze the soil

1. If soil does not hold together	**SAND***
2. If soil holds together	**B.**

B. Roll the soil with your fingers

1. If the soil breaks	**C.**
2. If the soil rolls out	**D.**

C. Rub the soil between thumb and finger

1. If it fells gritty	**SANDY LOAM**
2. If grains scarcely felt	**FINE SANDY LOAM**
3. If it fells smooth	**LOAM**

D. Roll the soil into a "worm" 6-7 mm in diameter

1. If the "worm" does not bend but breaks	**E.**
2. If the "worm" bends	**F.**

E. Rub the soil between thumb and finger

1. If the soil feels very gritty	**SANDY CLAY LOAM**
2. If the soil is not (or only slightly) gritty	**CLAY LOAM**

F. Bend the "worm" to form a circle

1. If it breaks	**SANDY CLAY**
2. If it bends easily to form a circle	**CLAY**

*Distinguish between **SAND** and **LOAMY SAND** as follows : both do not stick together or to the fingers. The **LOAMY SAND** leaves a dirty mark on the fingers, **SAND** does not.

Appendix 3. Publication

1. Gaol, M. L. & Fox, J. E. D (2002). Reproductive potential of *Acacia* species at Sandford Rock Nature Reserve (SRNR): Variation between years. *CALMScience* (in press).

2. Gaol, M. L. & Fox, J. E. D. The effect of seed size on germination and seedling characteristics of *Acacia fauntleroyi*, a species of remnant native vegetation in Western Australia. Prepared for Journal of *Biological Conservation.*