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ECOLOGY OF *ALLOCASUARINA LITTORALIS* (SALISB.) L. JOHNSON AND *A. TORULOSA* (AIT.) L. JOHNSON IN NORTH QUEENSLAND

Thesis submitted
by Gabriel Mary CROWLEY, BSc Hons (Monash)
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ABSTRACT

Allocasuarina littoralis and *A. torulosa* occur in the woodlands of North Queensland in areas receiving between 1,000 and 2,000 mm annual rainfall. This thesis examines factors influencing their distributional patterns, and discusses the implications of their comparative ecology for life history modelling, tropical revegetation programs and re-construction of North Queensland's environmental history.

The life-cycle is divided into several stages: seed dispersal and losses, germination and early seedling recruitment, the first year juvenile stage, and established juvenile stage to reproduction. Factors limiting survival in each stage of the life-cycle and progression to subsequent stages are identified.

Seed-fall, post-dispersal seed losses, seedling germination and recruitment, growth rate and mortality of juvenile and adult plants, and reproductive output were measured in contiguous stands in Kirrama State Forest. Seed germination, population structure and recovery from fire were measured for other North Queensland sites. The effects of fire, light and moisture conditions on germination and seedling survivorship, growth and competition were examined in the laboratory.

A. littoralis is found to be adapted to low or intermittent moisture availability and high light levels. This is contributed to by erect cladodes, high root : shoot ratio, maintenance of a high transpiration rate relative to *A. torulosa* at all soil moisture levels, maintenance of seed viability through wetting and drying cycles and protracted germination.

Life history characteristics appear to be influenced by the environments suitable to growth. *A. littoralis*, typically found in more open vegetation than *A. torulosa*, has an earlier onset of reproductive maturity and greater reproductive effort, and consequently a shorter life span; in *A. torulosa*, reproduction does not generally occur until individuals reach sub-canopy height. Recruitment in *A. torulosa* is aided by larger seeds and lignotuber reserves.

A. littoralis produces more seed per individual, but, with greater seed-fall and smaller seeds, experiences a greater level of seed loss due to predation than does *A. torulosa*. This ultimately results in *A. littoralis* having lower seed viability and a smaller soil stored seed bank.

While lignotuber reserves may result in a greater ability of established *A. torulosa* than *A. littoralis* plants to recover after fire, before these reserves are developed, *A. littoralis* shows the greater recovery rates, possibly aided by a higher root : shoot ratio. *A. littoralis* seeds appear to be more sensitive to heating by fire than those of *A. torulosa*, and germination in the former species is delayed by ash, but in neither species is affected by charcoal. Post-dispersal seed losses of both species are substantially lower from charcoal and ash beds, than from bare ground. The observed effects of ash and charcoal on seed harvesting are likely to operate with other seed species and therefore have important implications for forestry.

Assessment of published models of life history characteristics are found to be inadequate to explain the data collected in this thesis.

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CHAPTER 1

INTRODUCTION

1.1 Introduction

Allocasuarina littoralis (Salisb.) L. Johnson and *A. torulosa* (Ait.) L. Johnson are among the more widespread members of the Casuarinaceae, being found throughout much of moist eastern Australia. While *A. littoralis* has been the subject of ecological studies in the southern part of its distribution (Withers and Ashton 1977; Withers 1978a,b, 1979a,b), no such studies have been undertaken in the tropics, nor have there been any ecological studies of *A. torulosa*.

In North Queensland, both species are associated with vegetation communities on the sclerophyll side of the rainforest-sclerophyll boundary (Tracey 1982). While rarely found interspersed, stands of *A. littoralis* and *A. torulosa* may be contiguous. *A. littoralis* is apparently favoured in extreme sites, such as on rocky pavements and poorly drained soils (Tracey 1982), but, in most habitats, factors determining the distributions of the two species are unclear and are the principal subject of this thesis.

Reconstructions of Australian vegetation history indicate that in North Queensland, and elsewhere on the continent, members of the Casuarinaceae were more important during the Tertiary and Pleistocene than they are at present, (Hekel 1972; Kershaw 1985; Kershaw *et al.* in press). In North Queensland, members of the Casuarinaceae were particularly abundant during the two most recent glacial maxima, apparently expanding their distributions relative to rainforests

(Kershaw 1985). Although little is known of the present day ecology of most members of the Casuarinaceae, changes in representation of the family in pollen sequences, both in North Queensland and elsewhere, have been attributed to a combination of changes in climate and fire frequency (Singh *et al.* 1981).

Because they occur near the rainforest-sclerophyll boundary, *A. littoralis* and *A. torulosa* are the species most likely to have been involved in the glacial replacement of North Queensland rainforests. Although pollen morphology in the Casuarinaceae is fairly uniform (Kershaw 1970), the size range of fossil grains suggests that *A. torulosa* was the most abundant species during the glacial periods (A.P. Kershaw pers. comm.). A study of the ecology of *A. littoralis* and *A. torulosa* should therefore assist interpretation of past vegetation patterns in North Queensland.

In recent years, there has been increasing interest in the potential of members of the Casuarinaceae for revegetation of marginal lands (Anon. 1984b). Many members of the family, including *A. littoralis* and *A. torulosa*, form symbiotic relationship with the nitrogen fixing actinomycete *Frankia* (Coyne 1983; Lawrie 1982), and may therefore improve soil nutrient status. As they also rapidly stabilize soils and provide a fast-growing source of timber, fuel and fodder, Casuarinaceae species are suitable for revegetation in tropical countries where population pressures have resulted in large areas being denuded of native vegetation with associated soil erosion and loss of livelihood (Anon. 1984; Midgely *et al.* 1983). However, the species most frequently employed, *Casuarina cunninghamiana*, *C. equisetifolia* and *C. glauca*, are not fire tolerant, although they will resprout after cutting in the absence of fire (Anon. 1984). As fire is a significant feature of the North Queensland environment, in which *A. littoralis* and *A. torulosa* are found (Luke and MacArthur 1978), these species may be more suitable in fire-prone habitats than those traditionally employed for revegetation programs.

1.2 Thesis Framework

To investigate the ecology of *A. littoralis* and *A. torulosa*, a comparative autecological study at the population level is undertaken. Such studies examine the changes in population which occur over time: with the addition of individuals through birth and immigration, and the loss of individuals through emigration and mortality (Kitching 1983). Emphasis has often been placed on birth rates, although different stages of development have been used to indicate natality (Harper 1977; Sarukhán and Harper 1973; Sharitz and McCormick 1972). However, as it is the transition through successive life-stages that determines the success of a population, rather than natality alone, this study examines population changes occurring in all stages of the plant's life-history.

After a review of the literature pertaining to Casuarinaceae ecology (Chapter 2) and a description of the North Queensland environment (Chapter 3), detailed studies are made of the factors affecting survival and development of *A. littoralis* and *A. torulosa*. The life-cycle of these species is divided into stages, each of which is examined in a separate chapter (Fig. 1.1): seed dispersal and losses (Chapter 4), germination (Chapter 5), first year seedlings (Chapter 6) and older juveniles to reproductively mature adults (Chapter 7). The effect of fire on each stage is also analysed (Chapter 8).

While each of these studies stands alone, each contributes to the understanding of the comparative ecology and life history characteristics of the two species. Predictions are therefore made regarding the comparative responses of *A. littoralis* and *A. torulosa* to varying environmental conditions, initially from the ecological information gathered in this thesis (Chapter 9). An examination of life history models proposed by Pianka (1970), Schaffer (1974a) and Grime (1974, 1977, 1979) is then undertaken to determine the capacity of such models to contribute to the understanding of the two species. Implications of this study for the issues in forestry and the reconstruction of Australian palaeoenvironments are also discussed (Chapter 9).

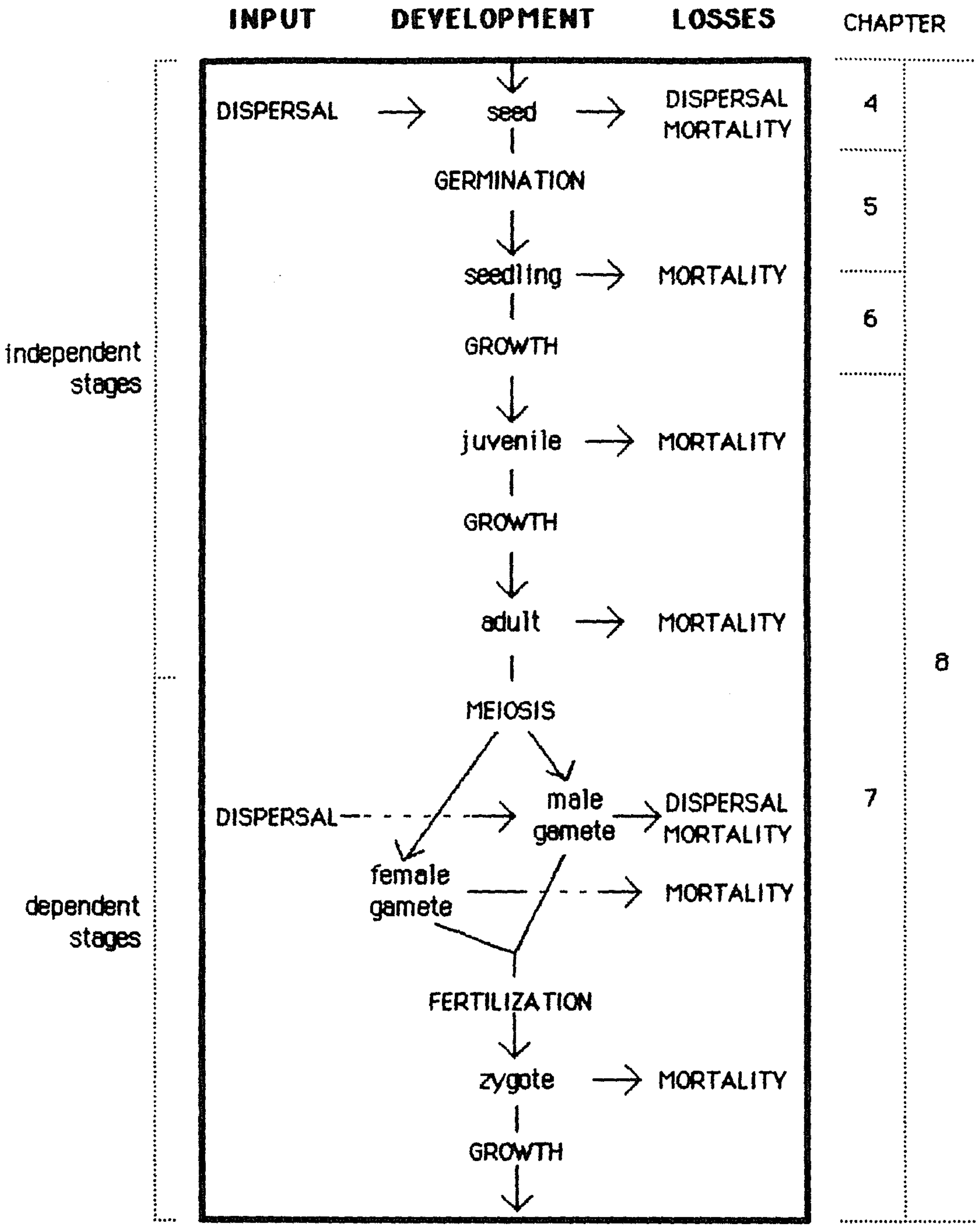


Fig. 1.1 **Idealized higher plant life-history.**

(After Harper 1977). Developmental stages are labelled in lower-case. Processes by which individuals may be added or lost to the population are labelled in upper-case. The chapters in which each process is examined are indicated.

CHAPTER 2

CASUARINACEAE ECOLOGY

2.1 Description of Species

The family Casuarinaceae contains about 70 species largely restricted to the Australasian region (Johnson and Wilson 1983). Until recent taxonomic revisions (Johnson 1980, 1982), the family consisted of a single genus, *Casuarina* Adans. Two further genera have now been added: *Gymnostoma* L. Johnson and *Allocasuarina* L. Johnson, and the description of a third extra-Australian genus has been foreshadowed (Johnson 1980, 1982). Most of the 46 *Allocasuarina* species occur in temperate Australia, with five extending into tropical and subtropical regions (Doran and Hall 1983; Johnson 1982). The term casuarina is now used as a common name referring to any member of the family (Barlow 1983).

A. littoralis has the broadest latitudinal range of any species in the family, occurring within 100 km of the coast in eastern Australia, from Torres Strait to southeastern Tasmania (Doran and Hall 1983). It grows to a small tree (2-12m), in woodland, and open- and tall open-forest, on a variety of soil types (Section 2.3), and in rocky areas where soil is absent (Doran and Hall 1983). *A. torulosa* is a taller tree (12-30m), with a more restricted and discontinuous distribution, extending from Cape York Peninsula to southern New South Wales (Boland *et al.* 1984; Doran and Hall 1983). It is generally found in moister environments (Doran and Hall 1983), where Ashton (1981) describes it as a significant understorey species, although it may also be a component of the canopy.

A. littoralis is thought to tolerate more acidic soils (Cambage 1911) and grow in areas receiving lower rainfall (Doran and Hall 1983). However, the distinction between the habitats of these two species is not clearly defined, and their similar appearance has led to their confusion in vegetation mapping (Chapter 3).

A. littoralis and *A. torulosa* do not appear to be closely related species, and hybrids are unknown. The closest relative to *A. torulosa* is *A. decussata*, a Western Australian species (Boland *et al.* 1984). *A. littoralis* belongs to the sub-generic "*distyla*" group, whose members have the haploid number of n = 11. Polyploids of *A. littoralis* are more widespread than diploids (Barlow 1959b). Diploid populations (2n=22) have a patchy distribution between Brisbane and Goulburn, while the majority of the populations south of Maryborough, Queensland are tetraploid (4n=44) (Barlow 1958). Initially faster growth rate of tetraploid *A. littoralis* seedlings led Barlow (1958) to suggest that the superior competitive ability of the derived tetraploid form may have resulted in the restricted distribution of the diploid. Chromosome determinations have not been undertaken for tropical populations, although these show morphological similarity to the tetraploid form (B.A. Barlow pers. comm.). *A. torulosa* has a basic haploid number of n = 24, and is not known to form polyploids (Barlow 1959a).

2.2 Phylogeny and Biogeography

The present distribution of the Casuarinaceae led to the assumption that the family had evolved in Australia (Barlow 1983). However, from fossil evidence, in conjunction with the theory of plate tectonics, it now appears that the family could have evolved anywhere in Gondwana, where it was widespread from at least the early Tertiary (Barlow 1983). *Allocasuarina* is believed to have evolved before Australia approached the Sunda Plate (Barlow 1983). An absence of suitable soils in the adjoining Malesian region is thought to have prevented its dispersal beyond Australia (Barlow 1983).

Macrofossil evidence suggests a shift in the dominant Australian casuarinas from *Gymnostoma* to *Casuarina* and/or *Allocasuarina* towards the end of the Tertiary (Christophel 1980). As pollen of Casuarinaceae species is morphologically similar (Kershaw 1970), palynological studies generally indicate the abundance of the family, rather than that of individual genera or species. Where there are few local species, pollen size has been used as a guide to species identity (Dodson 1974; Singh *et al.* 1981; Singh and Geissler 1985), but this approach is probably only valid in sequences deposited since the species attained their present distributional limits. Pollen sequences show that casuarina abundance fluctuated widely during the Quaternary. On the Atherton Tableland, in northeastern Queensland, casuarinas have gained prominence during glacial maxima (Singh *et al.* 1981). Although eucalypts were only a minor component during the previous interglacial, both casuarinas and eucalypts replaced Araucarian rainforests during the last interglacial period (Kershaw 1985). Casuarinas, along with rainforest taxa, are well represented during the interglacial periods between 350,000 and 128,000 years B.P., at Lake George, in the southern New South Wales tablelands (Singh 1982). From 128,000 years B.P. onwards, eucalypts appear to have largely replaced these taxa in interglacial periods (Singh 1982). These changes have been attributed to changing fire regimes brought about by Aboriginal burning practices (Singh *et al.* 1981).

Casuarina abundance has fluctuated in southeastern Australia through the Holocene (Crowley 1981; Dodson 1975, 1977, 1979; Dodson and Wilson 1975; Edney *et al.* in prep.; Head 1983; Hooley *et al.* 1980; Ladd 1978; Singh *et al.* 1981). The presence of casuarina pollen in the palynological record of coastal sites has sometimes been interpreted as indicating a wetter climate (Dodson 1975, 1977, 1979; Dodson and Wilson 1975; Edney *et al.* 1985). Recent reduction in casuarina populations appears to have been caused by the arrival of Europeans (Singh *et al.* 1981).

2.3 Soil and Topography

A. littoralis occurs on a wide range of substrates including sands, podzols, skeletal soils and rocky areas where soil is absent (Doran and Hall 1983). It is commonly found on well-drained hill and mountain slopes, but also occurs on lowland flats and mountain peaks, in rocky gorges, near swamp edges, on heathlands and on sandy lowlands behind sand dunes (Doran and Hall 1983). *A. torulosa* occurs on deep podzols, sandy alluvials and heavy clays, also in a range of sites, from undulating lowlands to steep slopes; parent materials range from basalts and granites to various sedimentary rocks (Doran and Hall 1983). In North Queensland, *A. littoralis* is recorded as growing on shallow leached or bleached sands overlying stony hill slopes, and *A. torulosa* on red or yellow massive earths, red acid leached structured earths, massive loamy earth and acid mottled, red, or yellow, bleached duplex soils (Isbell and Murtha 1972).

Limited plantation trials in Israel have shown good performance of *A. torulosa* on red sandy loam of the coastal plain, while growth rates and survival were poor on calcareous sandy loam of the Negev (Karschon 1962). *A. littoralis* had poor growth rates on histosols in humid regions of Hawaii (Anon. 1984b) but shows a strong ability to colonize disturbed sites, such as gravel road banks (Torrey 1983).

2.4 Nutrition

Nutritional studies of casuarinas have focused on nitrogen fixing by the symbiotic actinomycete *Frankia* spp. which has been recorded as between 41 and 58 kg N ha^{-1} yr^{-1} (Dommergues 1963). Nodulation has been reported for both *A. littoralis* and *A. torulosa* (Coyne 1983; Hannon 1956). The nitrogen content of the foliage of both *Allocasuarina littoralis* and *A. torulosa*, on the Hawkesbury Sandstone, New South Wales, is similar to that of local legumes (about 12,000 ppm), with the contribution to the soil of *A. littoralis* litter-fall amounting to 290 kg ha^{-1} yr^{-1} (Hannon 1956).

Occurrence of nodulation may be patchy, and factors controlling nodulation in the field are poorly understood (Lawrie 1982). Nodulation appears to be inhibited by dry conditions (Lawrie 1982), and by extreme soil pH values (Coyne 1973). Nitrogen production in casuarinas by *Frankia* depends on trace elements such as molybdenum and cobalt, and nodulated plants grown in the absence of these elements exhibit symptoms of nitrogen deficiency (Hewitt and Bond 1961; Bond and Hewitt 1962). Conversely, nodule formation is inhibited when adequate supplies of nitrogen are available to the plant (Coyne 1973).

Casuarinas also have endomycorrhizal and ectomycorrhizal associations, which improve the roots' ability to absorb nutrients, such as phosphorus and micronutrients, including zinc and copper, which enhance their nitrogen fixing capacity, and allow plants to thrive in nutrient deficient soils (Gauthier *et al.* 1984). Casuarinas also have proteoid roots, which are believed to assist assimilation of phosphorus (Diem *et al.* 1981). Conservation of phosphorus reserves in *A. pusilla* is achieved by the retention of green foliage and conversion of trichloracetic acid-insoluble phosphorus to orthophosphate, which can be recirculated to actively growing roots and shoots (Specht and Groves 1966). Fraser (1948) found evidence for the remobilization of nutrients, other than calcium, from the foliage of *A. littoralis* before litter-fall.

When supplies of nitrogen are not limiting, optimum root growth of *Casuarina* spp. occurs in the pH range 4 to 6 (Coyne 1973). The effect on shoot growth is unclear, although maximum total biomass production occurs between pH values of 6 to 7 in *C. glauca* and *C. cristata*, at 5 in *C. cunninghamiana* (Coyne 1973), and between 4 and 6 in *C. equisetifolia* (Kitamura *et al.* 1965). Specht (1963) found that germination in *A. pusilla* was not affected by the addition of fertilizers although seedlings responded positively to low levels of added nitrogen and phosphorus. *A. pusilla* seedlings are sensitive to phosphorus toxicity, which results in apical necrosis of shoots or seedling death (Specht and Groves 1966).

Some members of the Casuarinaceae are known to be salt tolerant (El-lakany and Luard 1982; Roa 1972). However, *A. littoralis* and *A. torulosa* are among the least salt-tolerant members of the family, maintaining constant growth rates up to a salinity of 250 mmol l^{-1} Na Cl, but dying at higher salinities (El-lakany and Luard 1982), and neither species is recorded as growing in saline environments.

2.5 Seeds

The seed of casuarinas is enclosed in a samara, an indehiscent fruit with a single wing (Johnson 1982). In this thesis, the term seed is used collectively to refer to the seed and its enclosing samara.

2.5.1 Seed Production and Losses

Seed-fall has been documented in three species in southern Australia. *A. verticillata* seed-fall reaches a maximum of 300 seed m^{-2} yr^{-1} at about 50 years, with heaviest falls in mid to late summer, following long periods of high temperature and low humidity (Hueneke 1976). *A. paradoxa* seed-fall is also heaviest in summer months (Andersen 1985b), while that of *C. cunninghamiana* reaches a maximum in winter (Woolfrey 1985). Although winged, most seed falls beneath the canopy of potential maternal parents (Hueneke 1976; Woolfrey 1985). Seed release from the infructescence, or "cone", may be stimulated by fire (Gill 1981b).

Insects reduce the number of viable seed in cones of *A. paradoxa* (Andersen 1985b). Casuarina seed is also eaten in the canopy by a number of parrots, finches and doves (Blakers *et al.* 1984; Clifford and Drake 1981). Seedling recruitment of *A. littoralis* and *A. paradoxa* in Victoria is affected by removal of seeds from the soil surface by ants (Andersen 1985b; Withers 1978a).

2.5.2 Germination

In *Allocasuarina*, the dark brown body of the samara produces a mucilaginous gel on wetting, which is thought to improve moisture retention, seed-soil contact and root penetration (Turnbull and Martenz 1982). Viability of *Casuarina* seed appears to decline on storage at a faster rate than that of *Allocasuarina* spp. (Barlow 1983; Turnbull and Martenz 1982). Samples of *A. verticillata* seed retained viability in dry grassland for up to 4 months (Hueneke 1976).

Germination characteristics of casuarinas vary, according to species, with light and temperature conditions. Most species germinate in the absence of light, with a 12 hour photoperiod increasing germination rate (Turnbull and Martenz 1982; El-Lakany and Shepherd 1983).

Germination characteristics of casuarinas have also been shown to vary between provenances. For non-tropical populations of *C. cunninghamiana*, there is a quadratic relationship between percent germination at 30°C and latitude, with germination rate reaching a maximum of about 65% at 35°S and declining further to the north and south (El-Lakany and Shepherd 1983). However, reduction in seed viability appears to be a function of insect attack (Andersen 1985b).

Studies of seed germination in *A. littoralis* and *A. torulosa* have investigated the effects of storage, light and temperature. Under room conditions, the viability of *A. torulosa* seed was reduced from 45% to 39% over an eighteen month period (Turnbull and Martenz 1982). The seeds of both *A. littoralis* and *A. torulosa* germinate through the temperature range of 10° to 40° C (Turnbull and Martenz 1982). Under a 12 hour photo-period, maximum germination rates have been recorded within the 28° to 36° C temperature range for both *A. littoralis* and *A. torulosa* (Turnbull and Martenz 1982). In the absence of light, germination was delayed slightly and minimum optimum temperatures for germination were reduced by 4 to 5 degrees, in both species, while maximum optimum temperature was similarly reduced only in *A. littoralis*. In each of these studies, the seed of only one, non-tropical, provenance was used.

2.5.3 Allelopathy and Litter Effects

Casuarinas have been reported both to produce allelopathic substances inhibitory to other plants and to be adversely affected by the production of such substances by other plants. Green cladodes and freshly fallen litter of *A. littoralis* delayed *Eucalyptus ovata* germination for up to 55 days (Withers 1978a). However, powdered foliage of all of the four major species in the community, *A. littoralis*, *A. verticillata*, *E. ovata* and *E. leucoxylon*, delayed seed germination in each of the other species. While *C. cunninghamiana* foliage-litter leachates causes deformation of seedling roots in the same species, addition of litter was found to enhance germination success (Woolfrey 1985). Thus, it appears that concentrations of leachates used in these experiments were higher than those produced by natural rates of release, and there is no indication that residues of inhibitory substances occur in the soil (Withers 1978a). Inhibition of *Juncus* species by litter of *C. glauca* has been found to be caused by shading, rather than allelopathic substances (Clarke and Hannon 1971). In contrast, both leaf leachates and topsoil extracts from below *E. baxteri* suppress the growth of *A. pusilla*, indicating that the absence of *A. pusilla* from beneath *E. baxteri* may be the result of allelopathy (del Moral *et al.* 1978).

The litter produced by casuarinas may prevent establishment of seedlings of all species by intercepting rainfall and reducing light penetration (Withers 1978a), or may improve the availability of immobile nutrients to the plant roots, e.g. water soluble substances in the leachates of casuarina litter assist the downward mobilization of manganese (Hadimani *et al.* 1974).

2.6 Seedlings

2.6.1 Establishment

Seedlings establishing in most habitats in Australia must cope with nutrient deficient soils, and thus rely on seed-stored nutrients for their initial growth (Bowen 1981). The nutrient content of *A. littoralis* seeds has been described for provenances from Ocean Grove, Victoria, and Wallum heaths, southeastern Queensland (Table 2.1). These nutrient stores are greater per seed than those of co-existing *Eucalyptus* spp. in Victoria, although nutrient concentrations are lower (Withers 1978a).

A. littoralis seedlings avoid drought stress by efficient cooling through a large cladode surface area to volume ratio, and reduction of transpiration rates before their water content has declined to any great extent (Withers 1978b).

Table 2.1. Nutrient content of *A. littoralis* seed.

ercentages calculated from figures of ^{a} Grundon (1972) and ^{b} Withers (1978a). N/R - not recorded.

Locality	Seed Weight (mg)	N %	P %	Ca %	K %	Mg %	Na %	Fe %
Queensland ^{a}	2.6	4.3	.28	1.63	.20	N/R	N/R	N/R
Victoria ^{b}	3.4	4.5	.32	1.79	.36	.24	.10	.039

Seedling establishment in *C. cunninghamiana* and *A. verticillata* is related to substrate. In *C. cunninghamiana*, a streamside tree, successful establishment is associated with substrates of large particle size, which provide adequate aeration, below the level of 500 year floods (Woolfrey 1985). Establishment of *A. verticillata* depends on reliable and effective rainfall at the time of seed fall, a roughened soil surface, protection from ant removal of seed and a reduction of competing grasses and herbs (Hueneke 1976).

2.6.2 Growth Rates

Seedling growth rates in the Casuarinaceae are affected by competition, provenance and chromosome variation. Reduction of competition from *Themeda australis* by burning at Ocean Grove, Victoria, resulted in improved growth rates in *A. littoralis* seedlings (Withers 1978a). Seedling growth of tetraploid *A. littoralis* is faster than that of diploids (Barlow 1958). In *C. cunninghamiana*, the relationship between plant height at one year and latitude shows a similar pattern to that of percent germination (Section 2.5.2), with plants collected from 36° S showing maximum growth rates (El-Lakany and Shepherd 1983). A relationship between biomass of *C. glauca* at one year and latitude has also been demonstrated, with minimum values for populations at about 31° S, with the most vigorous forms occurring at latitudinal extremes of the species' distribution (El-Lakany and Shepherd 1983).

A. littoralis seedlings are relatively shade-tolerant, surviving a nine month period of 4% sunlight (Withers 1979a), but casuarinas do not regenerate under a well-developed or slightly disturbed rainforest canopy (Webb and Tracey 1981). Reduction of natural sunlight by 75% reduces *C. equisetifolia* biomass production, but not height increment (Shafiq *et al*. 1974), while growth rates of *C. glauca* are reduced by shading (Clarke and Hannon 1971).

2.7 Adults

2.7.1 Growth Rates

A. littoralis and *A. torulosa* are reported to grow tup to 12 and 30 metres respectively (Boland *et al.* 1984; Doran and Hall 1983). In Israeli plantation trials, *A. torulosa* was found to be of variable form and vigour, being relatively successful on red sandy loams of the coastal plains, where it reached a height of 5.7 to 8.5 m in six years and a diameter at breast height (DBH) of 12 to 18 cm (Karschon 1962). Trees of the same species planted a year later ranged between 6.2 and 8.0 m in height, with a mean DBH of 9 cm (Karschon 1962). In contrast, *A. torulosa* trees grown in the Negev reached only 0.6 - 2.2 m in five years, with a DBH of no more than 2 cm (Karschon 1962). No information on the provenances used in these trials was provided.

2.7.2 Phenology and Breeding Systems

A. littoralis and *A. torulosa* are anemophilous, with separate male and female flowers, on mostly dioecious plants. Both male and female flowers are considered to be either simple or reduced (Lam 1948; Meeuse 1975). Male flowers are borne in catkin-like spikes, and female inflorescences develop into woody infructescences or "cones", which, at maturity, release seeds on desiccation (Johnson and Wilson 1983). Seasonality of flowering has not been described.

There have been no direct measurements of shoot growth in the Casuarinaceae. However, shedding of cladodes appears to coincide with the growth of new foliage, and can therefore be used as an indicator of growth (Hannon 1958). Maximum litter-fall of *A. verticillata* is in January (Hueneke 1976), and of *A. littoralis* is between September and January (Hannon 1958).

2.8 Diseases and Pests

Many of the insect pests of *Allocasuarina* spp. have been described by Jones and Elliot (1986). Casuarinas may be defoliated by locusts *Aulaches miliaris* (Anon. 1957), and crickets *Gymnogryllus humeralis* (Chatterjee 1955), casuarina caterpillar *Perna exposita* or brown stick insect *Ctenomorphodes tessulatus* (Jones and Elliot 1986) or ring-barked by twig girdling longicorn *Platyomopsis humeralis* (Jones and Elliot 1986). The wood may be attacked by boring insects, such as *Apate monachus*, *Phassus malabaricus* and *Arbela tetronis* (Anon. 1984) and root borers (Curculionidae) (Jones and Elliot 1986). Psyllids penetrate the joints between stems and stomatal groves to suck phloem sap

(A.L. Yen pers. comm.). Fruit predators of *Allocasuarina* spp. include species of the Lepidoptera (Cosmopterigidae) and Hymenoptera (*Eurytoma*, *Bootanelleus* and *Megastigmus*) (Andersen 1985b).

Other pests include casuarina gall insects *Cylindrococcus* spp., casuarina scale *Frenchia casuarinae*, nigra scale *Parasaissetia nigra*, cuckoo spit *Bathylus albicinctus*, *Philagra parva*, froghoppers *Machaerota finitima*, thrips *Thaumatothrips*, and jewel beetles (Buprestidae) (Jones and Elliot 1986).

A wide range of fungal diseases are known to affect casuarinas (Titze and van der Pennen 1983). Both *A. littoralis* and *A. torulosa* are adversely affected by *Phytophthora cinnamomi*, while *Fomes robustus* attacks *A. torulosa* (Titze and van der Pennen 1983). Studies of the effect of *Phytophthora cinnamomi* on *A. pusilla* show that plants in well-drained locations are less likely to be significantly affected than those subjected to prolonged waterlogging or drought (Weste 1981). The shoot deformation, witches broom, is caused by fungi or mycoplasma-like organisms (Jones and Elliot 1986).

2.9 Fire

Casuarinas have been labelled as fire sensitive due to the replacement of dominant *Eucalyptus* species in woodland which has not been burnt in over 90 years by *A. littoralis* (Withers and Ashton 1977), the association of casuarinas with mesic genera in the pollen flora of Lake George (Walker and Singh 1981), and regardless of their association with the pyric genus *Eucalyptus* in the pollen sequences of Lynch's Crater (cf. Section 2.2; Singh *et al.* 1981). However, the response to fire varies within the family, with most fire-tolerant species belonging to *Allocasuarina* (Crowley in press). *A. pusilla* has been shown to be dependent on a fire interval of less than 30 years (Specht *et al.* 1958). Both *A. littoralis* and *A. torulosa* are recorded as resprouting after fire damage (Anon. 1984b), and *A. torulosa* seedlings develop a starch-rich lignotuber (Boland *et al.* 1984).

Fire-stimulated seed release from the cones of casuarinas (Gill 1981b) may result in mass establishment of seedlings in the following year (Specht *et al.* 1958). However, this does not occur after stands of *C. cristata* have been killed by fire (Johnson and Purdie 1981).

CHAPTER 3

ENVIRONMENTAL SETTING

3.1 The North Queensland Environment

3.1.1 Location of the Study Region

The selected study area lies in northeastern Queensland, Australia, between 15° and 20°S, and between 145°E and the coast (Fig. 3.1). This area includes the majority of *A. littoralis* and *A. torulosa* populations found north of the Tropic of Capricorn. It excludes isolated populations of both species in the Clarke Range, about 170 km to the southwest, the only known northern outlier of *A. torulosa*, which is in the McIlwraith Range, approximately 200 km to the north, and scattered populations of *A. littoralis* between the study region and the McIlwraith Range, and on Torres Strait islands.

3.1.2 Geomorphology and Geology

The region lies in the northern section of the Eastern Uplands of Australia (Mabbutt 1970). A narrow coastal plain rises rapidly to the mountains of the Great Dividing Range, of which the highest peaks are Mt Bartle Frere at 1622 m and Mt Bellenden Ker at 1593 m, which are inland from Innisfail. The remainder of the range rarely rises above 1000 m and there is a gentle slope to the inland, reaching about 500 m on the western boundary of the study area.

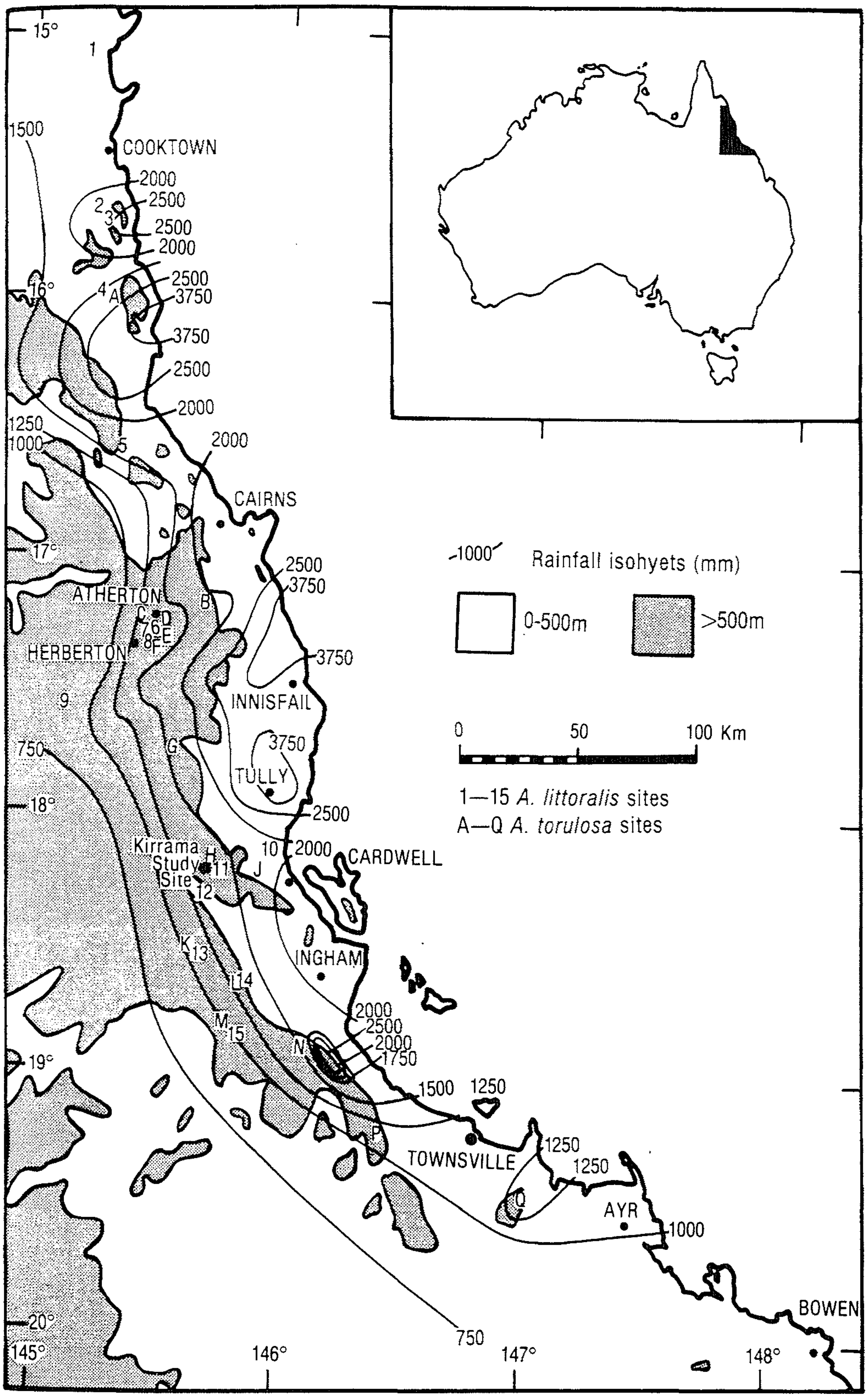


Fig 3.1 **Location of the study region and study sites**

For site descriptions see Table 3.1

Rainfall data from the Australian Bureau of Meteorology

Surface rocks are dominated by quartz-rich sediments, which were deposited with volcanic basalts in a Silurian to Devonian basin, and bisected by the Palmerville Fault, which runs northwest from about Ingham (Arnold and Fawlkener 1980). The highest parts of the present mountainous areas were formed from intrusion of Upper Palaeozoic granites and adamellites (Tracey 1982). The region experienced major volcanic activity in the Tertiary, giving rise to the broad laval plain of the Atherton Tableland, of 700 to 800 m elevation, and two smaller centres of activity in the vicinity of the Herbert River Falls and the most recent eruption cone at Mt Fox (Stephenson *et al.* 1980). Plio-Pleistocene upwarping of the Great Dividing Range initiated the deposition of the coastal plain sediments (Coventry *et al.* 1980). Coastal deposition has continued to the present, and is largely controlled by sea-level changes and climatic fluctuations (Coventry *et al.* 1980). In places where the older deposits have been exposed, they have been lateritized and silicified (Grimes 1980).

3.1.3 Climate

The study area encompasses the humid tropics of North Queensland (Tracey 1982), including the region of Australia's highest rainfall in the coastal strip between Cardwell and Cooktown (Anon. 1971; Fig. 3.1). The climate of the study area is controlled by the subtropical high pressure belt and the intertropical convergence zone (Gentilli 1971). A southward shift of the intertropical convergence and the associated perturbation belt brings high rainfall to the region between November and April (Nix and Kalma 1972). Tropical cyclones may develop from this belt, with approximately 1.1 cyclones crossing the coast between Cooktown and Townsville each year (Coleman 1971). Although they can produce intense rainfall, they are usually responsible for only a small proportion of the total annual rainfall (Bonnell *et al.* in press; Nix and Kalma 1972).

On the eastern faces of the ranges, uplifted, moisture-laden, southeasterly winds across the Coral Sea produce high rainfall in the cooler part of the year, from April to November (Bonnell *et al.* in press; Nix and Kalma 1972), with mean rainfall of the driest month exceeding 60 mm (Dick 1975). However, the southeasterly winds bring little rain to the remainder of the region, where most rain falling between April and November is due to the occasional southward shift of the upper trough (Bonnell *et al.* in press). Thus away from the high mountains, rainfall is strongly seasonal, with between 75 and 90% of the annual rainfall occurring from November to April (Anon. 1971), with a prolonged and intense dry period in the cooler part of the year and substantial rainfall in the warmer part of the year (Dick 1975).

The timing of the southward shift in the intertropical convergence, and thus onset and duration of the wet season, is highly variable (Ridpath 1985). Hence, droughts of 2 - 3 years duration occur in the region on a regular basis, with eight such droughts occurring in the 50 years from 1899 to 1949 (Anon. 1971). Floods occur in the region in about seven out of every 10 years (Anon. 1971). Hail occurs rarely, the greatest frequency (in 2 years out of 10) being recorded at Cairns (Anon. 1971).

Mean annual temperature in the region varies from about 20° - 25°C in the lowlands, and 15° - 20°C in the uplands (Nix 1981). Solar radiation, and hence temperature maxima, reflects cloud cover, with mean daily solar radiation ranging from about 16 to 20 MJ m^{-2} d^{-1} (Nix 1981). Highest mean monthly temperature maxima occur from November to January and vary from 15° to 23°C; lowest mean monthly minima occur in June or July and vary from 8° to 19°C (Anon. 1971). Mean annual range varies from 15° to 23°C with the lowest temperature range being experienced at the coast near Tully, where mean temperature of the coldest month is greater than 18°C (Dick 1975). Away from the coastal plain, an average of 0 - 2 heavy frosts (< 0°C) may occur between May and September, with an average of 0 - 4 lighter frosts (0° - 2°C) occurring between April and October year (Anon. 1971).

Although annual rainfall is equivalent to or greater than evaporation through most of the region, the length of the growing season is limited by seasonality of moisture availability rather than temperature, and varies from 4.5 months in the north, through 7.5 months at Herberton, to 12 months in the Cairns region (Anon. 1971).

3.1.4 Soils

The soils of the region have been described by Gunn (1970), Hubble and Isbell (1983), Murtha (1982) and Stace *et al.* (1968), whose descriptions are summarized below. Soil differentiation has been primarily determined by parent material, with further differentiation due to water regime, drainage and period of exposure.

Red earths dominate on the acid volcanics and granites of the ranges and upper piedmont slopes and the alluvial fans derived from them. On the lower parts of the fans, yellow earths (xanthosems and yellow podzolic soils) have formed. Shallow sandy lithosols occur to the west of the Great Dividing Range. Deep soils have developed on basalts in the high rainfall zone, with krasnozems occurring in the uplands and friable loams of high fertility in the lowlands. Under lower rainfall, on the basalts, and derived alluvium, are black earths and grey cracking clays, in which there may be some calcium carbonate nodule formation.

On the Townsville plain, solodized solonetz and solodic soils of hard neutral to alkaline, yellow bleached duplex soils have formed. Where tidal inundation occurs more than four times a year, solonchaks, salty duplex soils, or deep, dark brown mangrove muds are found. On the coastal plain sediments derived from granite and acid volcanic alluvium, soils range from humic gleys and gleyed podzols to yellowish friable loam, as drainage improves. Profile development on the beach ridges increases with age, from younger siliceous and calcareous uniform textured sands to giant and humic podzols. Acid peats have developed in the sites of poorest drainage.

3.1.5 Vegetation

3.1.5.1 General Vegetation Communities

The region contains a diverse range of terrestrial vegetation communities, which have been described by Story (1970), Isbell and Murtha (1972), Tracey (1982) and Tracey and Webb (1975). Their descriptions are summarized below.

Mangrove communities line the tidal mudflats along the coast and rivers. Where the coast is more sandy, mangroves are replaced by

Casuarina equisetifolia above high water level. Beach strand vegetation, in which *Eucalyptus tessellaris*, *E. pellita*, *Scaevola sericea* and *Argusia argentea* and *Casuarina equisetifolia* are major components, occurs on the higher coastal sands. Extensive dune and swale systems in the coastal hinterlands are covered by *Melaleuca* woodland.

Rainforests occur in the higher rainfall zones of the region. Rainforest species composition is related to climate, parent rock, soil type, drainage and disturbance (Tracey 1969, 1982; Webb 1969). Variation in these factors has resulted in a diversity of rainforest communities, which have been described structurally (Webb 1959; 1968) and floristically (Webb *et al.* 1984). Although no single genus or family dominates the rainforest flora, common families include Proteaceae, Lauraceae and Myrtaceae. The distributions of several monospecific genera are entirely contained within the rainforests of the region (Tracey 1982).

On the western edge of the fragmented rainforest massif, there is a gradation from tall open-forest dominated by *E. grandis*, through open-forest dominated by *E. resinifera*, *E. intermedia* and *E. tereticornis*, to drier ironbark communities. In the north, ironbark woodland is dominated by *E. cullenii*, which is replaced by *E. leptophleba* in the country west of Cooktown to Atherton. *E. crebra* woodlands occur on the western slopes of the Cardwell and Seaview Ranges. Further south, these are replaced by *E. drepanophylla* - *E. alba* open-woodland. There is a general absence of shrubs in the ironbark communities; *Imperata cylindrica*, *Themeda australis* and *Heteropogon contortus* dominate the ground layer vegetation. Woodlands dominated by *E. dichromophloia*, *E. tetrodonta* and *E. phoenicea* occur in the northern extremity of the region.

Little has been written regarding the impact of Aboriginal culture on the North Queensland environment, although their burning practices may have increased the area of sclerophyll vegetation at the expense of rainforests (Kershaw 1986; Singh *et al.* 1981; Stocker 1980). Mining, grazing, logging and clearance of vegetation for agriculture and urban development has resulted in major environmental alteration since colonization of the area by Europeans in the 1870s, particularly on the coastal lowlands and the Atherton Tableland (Fitzgerald 1982; Frawley in press; Leeper 1970).

3.1.5.2 North Queensland Populations of *A. littoralis* and *A. torulosa*

A. littoralis and *A. torulosa* are found in non-rainforest communities in the higher rainfall regions. *A. torulosa* is restricted to areas receiving between 1,000 and 2,000 mm average annual rainfall (Fig. 3.1). The rainfall range of *A. littoralis* is slightly broader: from about 900 mm to a maximum of 2,500 mm on rocky escarpments. However, the majority of the populations of this species also occur within an annual rainfall range of 1,000 to 2,000 mm (Fig. 3.1).

A. littoralis is found most commonly in low to medium open-forest and medium woodland, where it is found beneath canopies of *E. intermedia*, *E. tereticornis*, *E. tessellaris*, *E. acmenioides*, *E. citriodora* and *Syncarpia glomulifera* (Tracey 1982). These communities are typically found on the fringes of tall open-forest and tall woodland on the western slopes of the ranges, and on the dry uplands west of the rainforest massif (Tracey 1982). In the high rainfall zone between Ingham and Tully, *A. littoralis* occurs as a dominant species in closed scrub on well-drained mountain rock pavements, and as a locally common element on texture-contrast soils with impeded drainage of the coastal plains (Tracey 1982).

A. torulosa is described as occurring on deep soils over granites and acid volcanics in tall open-forest and tall woodland dominated by *Eucalyptus grandis*, *E. intermedia*, *E. resinifera* and *E. tereticornis* on the western edge of the rainforest massif, and in medium to low woodland dominated by *E. intermedia*, *E. acmenioides* and *E. tereticornis* (Isbell and Murtha 1972; Tracey 1982).

Where the western side of the ranges has a gradual slope and gentle rainfall gradient, *A. torulosa* occurs in extensive stands, in which it may be the dominant species (Tracey 1982). However, where the soils are well drained, it is often replaced by *A. littoralis* (per. obs.). Changes in topography thus result in a mosaic, with stands of *A. littoralis* and *A. torulosa* alternating across the landscape. In the vicinity of Oak Hills (e.g. Sites K,13; Fig 3.1), such a vegetation mosaic has been erroneously mapped as extensive stands of *A. torulosa* (Isbell and Murtha 1972; Tracey and Webb 1975).

A. torulosa is also frequently found on rocky mountain pavements, particularly on the eastern face of steep slopes, where rapid drainage is compensated for by high rainfall and interception of moisture laden air masses (pers. obs.). In such places, e.g. on the eastern escarpments of the Atherton Tableland (Site B) and on the ranges inland from Cardwell (18° 12' S 145° 50' E 400 m), this species has been incorrectly mapped as *A. littoralis* (Tracey and Webb 1975). A further vegetation type not characteristic of those described by Isbell and Murtha (1972) or Tracey (1982) is a tall stand of *A. littoralis* in open-forest in association with the moist forest species *E. pellita* and *Dillenia alata* (Site 3).

Thus, while the differentiation between habitats of *A. littoralis* and *A. torulosa* has previously appeared clear cut, with *A. torulosa* growing on gentler topography and deeper soils than *A. littoralis*, which in turn has been thought to predominate on sites with excessive or impeded drainage, it is apparent that there are many exceptions to these general habitat descriptions.

Where stands of *A. littoralis* and *A. torulosa* are found in the same area, such as at Kirrama Forest (Sites H, 11), Oak Hills (Sites K, 14) and Wallaman Falls (Sites L, 14), they are frequently contiguous, but rarely mixed (pers. obs.). Occasional plants of one species may penetrate stands of the other species for about 5 m beyond an otherwise distinct interspecific boundary. There is rarely any perceptible change in surface soil characteristics, or in the frequency of other species associated with this boundary. However, there may be a gradual increase in the density of understorey species, from the *A. littoralis* side to the *A. torulosa* side of the boundary.

3.2 Study Sites

3.2.1 North Queensland

Several North Queensland sites were selected for the study of *A. littoralis* and *A. torulosa* in this thesis (Table 3.1, Fig 3.1). These sites were subjectively selected by reconaissance, using the vegetation maps of Isbell and Murtha (1972) and Tracey and Webb (1975) as a guide to the distribution of the species, and with the aim of sampling a broad latitudinal and altitudinal range, and including a diversity of vegetation communities.

Sites were selected where populations were of sufficient size to estimate population structure and sex ratio (Chapter 7), for seed collection (Chapter 5), or where recent burning allowed an assessment of response to fire (Chapter 8).

3.2.2 Kirrama

3.2.2.1 Site Description

Contiguous stands of *A. littoralis* and *A. torulosa* at the Kirrama study site (Fig. 3.1; Sites H, 11)., were chosen for detailed examination of processes affecting seed availability, germination, recruitment and plant growth and reproduction, in existing stands under similar conditions. The factors producing the current distribution patterns were not examined, as these are historical and may no longer be in operation (Harper 1977). Except where stated, all observations and experiments described in this thesis were undertaken at this site.

Table 3.1 Description of the sites studied in this thesis.

Site no. refers to numbers in Fig. 3.1. Vegetation descriptions follow Specht (1970): open-forest (of), low open-forest (lof), woodland (w), low woodland (lw), open-woodland (ow).

Species	Site no.	Site name	Vegetation	Lat. (S)	Long. (E)	Alt. (m)
A. littoralis	1	Isabella	ow	15°08'18"	145°00'57"	800
A. littoralis	2	Wallaby	of	15°43'18"	145°14'48"	210
A. littoralis	3	Home Rule	of	15°45'08"	145°17'12"	150
A. littoralis	4	Boolbun 1	w	15°59'44"	145°13'13"	750
A. littoralis	5	Julatten	lw	16°37'22"	145°19'24"	460
A. littoralis	6	Atherton 1	lw	17°15'28"	145°25'34"	1080
A. littoralis	7	Atherton 2	w	17°16'10"	145°26'58"	800
A. littoralis	8	Holdcroft	w	17°20'16"	145°24'45"	1040
A. littoralis	9	Coolgara	lw	17°32'10"	145°13'14"	1000
A. littoralis	10	Bilyana	lw	18°07'00"	145°54'29"	30
A. littoralis	11	Kirrama	of	18°11'02"	145°44'19"	620
A. littoralis	12	Sullivan	w	18°14'12"	145°02'16"	40
A. littoralis	13	Oak Hills 1	lw	18°33'32"	145°40'07"	640
A. littoralis	14	Wallaman	lof	18°35'36"	145°47'23"	800
A. littoralis	15	Fox 1	lw	18°49'27"	145°49'19"	680
A. torulosa	A	Boolbun 2	w	15°59'37"	145°13'27"	800
A. torulosa	B	Gillies	of	17°12'21"	145°41'51"	560
A. torulosa	C	Atherton 3	w	17°15'34"	145°25'41"	1020
A. torulosa	D	Wongabel 1	of	17°27'07"	145°28'18"	795
A. torulosa	E	Wongabel 2	w	17°19'40"	145°27'00"	800
A. torulosa	F	Wild River	of	17°22'05"	145°25'41"	1040
A. torulosa	G	Cardstone	lof	17°45'11"	145°36'59"	200
A. torulosa	H	Kirrama	of	18°11'02"	145°44'19"	620
A. torulosa	J	Kennedy	of	18°12'07"	145°52'47"	100
A. torulosa	K	Oak Hills 2	w	18°32'31"	145°37'22"	660
A. torulosa	L	Wallaman	lof	18°35'36"	145°47'23"	800
A. torulosa	M	Fox 2	w	18°50'26"	145°48'31"	680
A. torulosa	N_1	Paluma 1	of	18°52'32"	146°06'06"	360
A. torulosa	N_2	Paluma 2	of	19°00'05"	146°15'35"	600
A. torulosa	N_3	Paluma 3	of	19°01'30"	146°08'30"	900
A. torulosa	P	Bluewater	of	19°13'52"	146°24'17"	610
A. torulosa	Q	Elliot	of	19°28'47"	146°59'09"	400

The stand of *Allocasuarina* spp. occurred on a ridge top between two rainforested gullies. At the study site, the stand was about 150 m wide. The western 20 m of the *Allocasuarina* stand was dominated by *A. littoralis*. A sharp north-south oriented boundary delineated this *A. littoralis* stand from a stand of *A. torulosa*, which extended to the west of the study site for approximately 1 km. The soils of Kirrama study site are yellow-red sandy clay loam overlying granite.

The road giving access to Kirrama State Forest, constructed for log extraction, was completed in 1941, and rainforest logging has remained the major land use of the area (Jones 1961). Remnants of corrugated iron shanties and *in situ* stumps in the vicinity of the study site suggested that the limited disturbance associated with logging had not occurred within the previous ten years. Where the grass understorey would carry fire, communities with *Allocasurina* spp. were burnt by the Queensland Department of Forestry every three to five years, with the aim of preventing intense fires penetrating into the nearby rainforest (J. Snell pers. comm.). The vegetation to the east of the study site was burnt in the 1983 dry season. In sclerophyll vegetation to the west of the study site, cattle grazing occurs on leasehold land. Cattle occasionally wandered into the study site during prolonged dry weather.

3.2.2.2 Climate

The Kirrama State Forest site is located in the climatic province with strongly seasonal contrasts between a rainy warm season and a dry cooler season (Dick 1975). Daily variation in temperature and rainfall at the site were recorded for approximately two and a half years during this study.

Nearest climate stations were located at Cardwell, 30 km to the east, and Herberton, 60 km to the north (Fig. 3.1). Rainfall statistics were available for a number of closer locations including Kirrama Station, 20 km to the west. As the topography results in a marked rainfall gradient across this region, it was desirable to produce more accurate estimates of climate.

Climate statistics were predicted for the study site by the Bioclimate Prediction System (BIOCLIM) (H.A. Nix pers. comm.). The operation of this system has been described in detail by Busby (1986). In summary, algorithms are used to predict site-specific climate estimates from mathematical surfaces fitted to data from stations where climate statistics are available (Busby 1986). Mean monthly minimum temperatures and maximum temperatures predicted by BIOCLIM corresponded closely to those measured at the study site (Fig. 3.2). Therefore the BIOCLIM predictions were accepted as a fair representation of temperature variation at the Kirrama study site. BIOCLIM predictions estimated mean annual temperature as 21.4°C, maximum temperature of the hottest month as 31.0°C, mean minimum of the coldest month as 9.8°C and mean annual range as 21.2°C.

Actual annual rainfall totals measured from September to August were found to exceed those predicted by BIOCLIM (Fig. 3.3), despite the region's rainfall being below average through this period (Anon. 1982, 1983, 1984a). Therefore BIOCLIM estimates were not accepted as representing rainfall at Kirrama State Forest. Monthly rainfall records were obtained from the Bureau of Meteorology for rainfall stations at Kirrama Station and Cardwell Post Office for the period from September

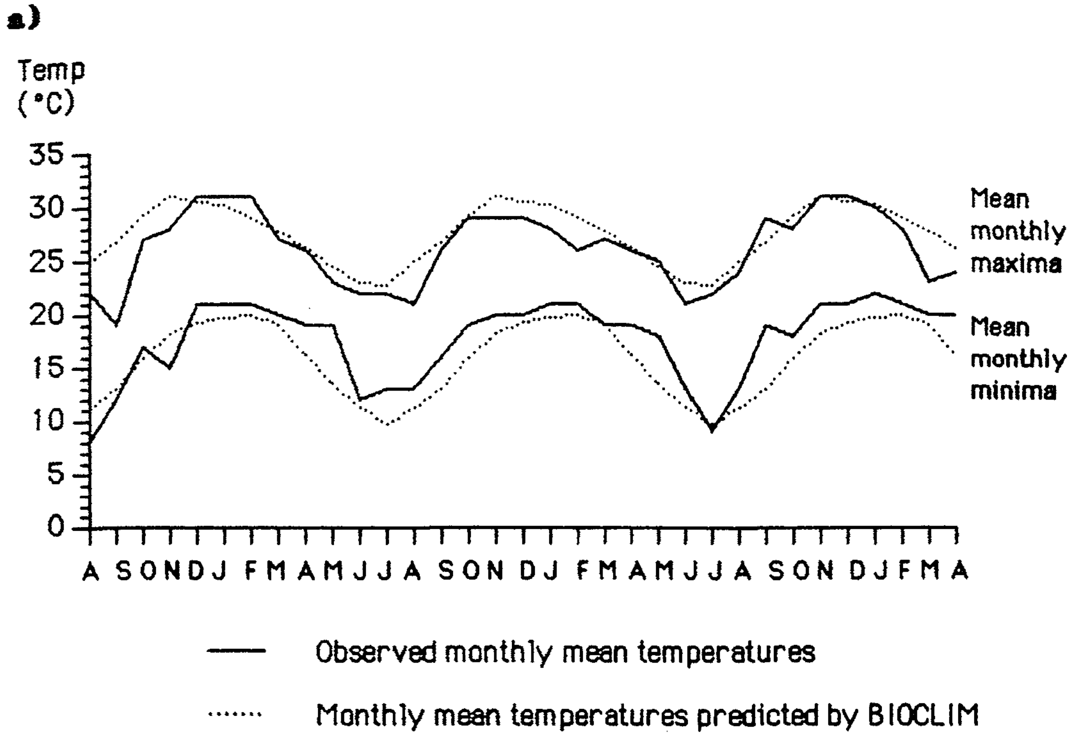


Fig. 3.2 **Temperature statistics for Kirrama State Forest.**
August 1982 to April 1985

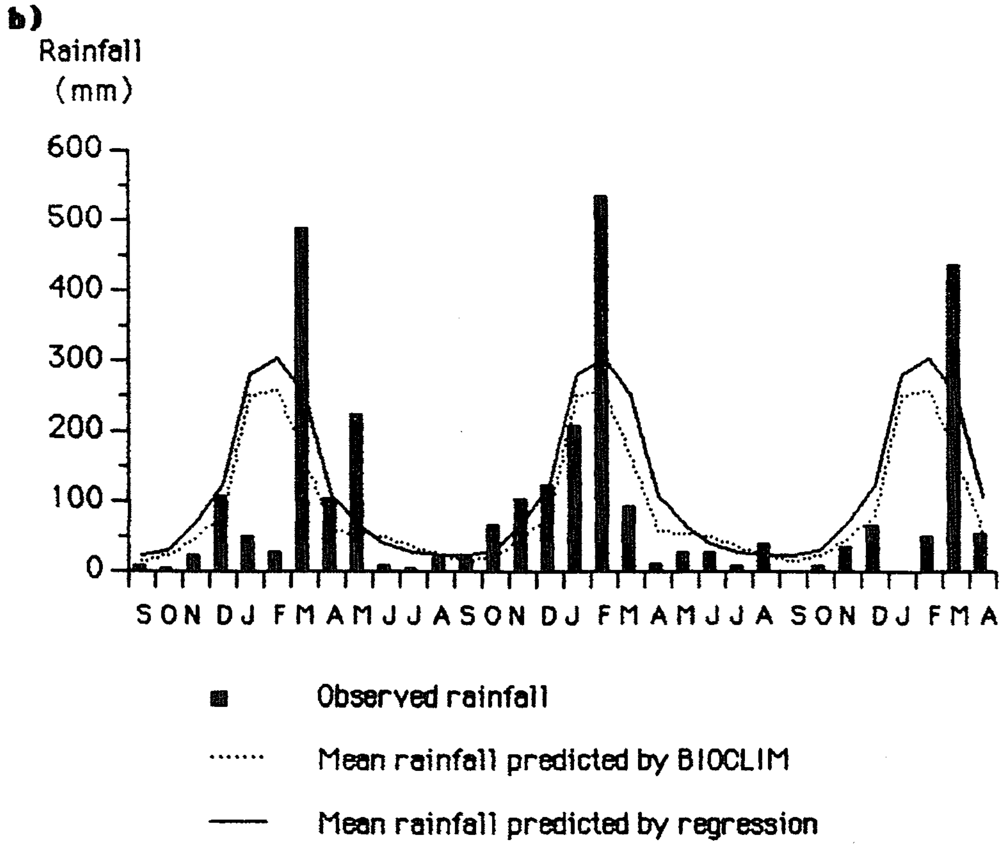


Fig. 3.3 **Rainfall statistics for the Kirrama study site.**
September 1982 to April 1985

1982 to April 1985. Multiple regression (Steel and Torrie 1960 p 281) was used to derive a relationship for rainfall at Kirrama State Forest. The following equation was found to describe the rainfall at Kirrama State Forest:

$$Y = (0.6736 \times A) + (0.2746 \times B) - 1.6937,$$

$$(F_S = 56.51,\ d.f. = 2,29,\ P < 0.001),$$

where Y = monthly rainfall at Kirrama State Forest (mm),

A = monthly rainfall at Kirrama Station (mm),

and B = monthly rainfall at Cardwell Post Office (mm),

from September 1982 to April 1985.

This equation was used to predict the average monthly rainfall at Kirrama State Forest (Fig 3.3). Predicted average annual rainfall for the site was 1338 mm, with 79% of annual rainfall occurring in the five months from December to April, slightly more than the mean annual recorded in the first two years of the experimental period (1163 mm). Rainfall totals in the three months from March to May 1983, and the four months from November 1983 to February 1984 both accounted for 77% of the actual annual rain falling from September to August in the respective 12 month period. Hence, observed rainfall was more strongly seasonal during the experimental period than the average monthly rainfall predictions suggest. While rainfall in March to May 1983, February 1984 and March 1985 greatly exceeded predicted mean rainfall, the six months from September 1982 to February 1983 and twelve months from March 1984 to February 1985 were notably drier than predicted. These data also highlight the variability of the timing and duration of moisture availability in the area.

3.2.2.3 Vegetation

The study site was situated on an interfluve between two rainforested gullies. The rainforests to the north of the study site were mapped by Tracey and Webb (1975) as mesophyll vine forest, and those to the south, as complex notophyll vine forest. *Eucalyptus intermedia* - *E. tereticornis* woodland dominated the interfluve. To the west of the study site, there was a dense sub-canopy of *Allocasuarina*, but there was no marked sub-canopy to the east.

A 100 x 40 m grid was located on the southern side of the ridge top, across the boundary between the *A. littoralis* and *A. torulosa* stands. The grid was subdivided into 40 10 x 10 m quadrats. Species lists were compiled for each quadrat (App. 1). The main vegetation features are summarized below.

The vegetation within the grid was open-forest, in which the main canopy species (≈ 20m) were *Eucalyptus tereticornis* and *E. intermedia*. Although both species occurred throughout the grid, the abundance of *E. tereticornis* increased to the western half of the grid. One individual of *E. grandis* dominated the southwestern corner of the grid.

A. littoralis was the dominant sub-canopy (≈ 10 m) species in the eastern half of the grid, and *A. torulosa* was the dominant sub-canopy (≈ 15 m) species in the western half of the grid. The density of *A. torulosa* was higher than that of *A. littoralis*, and the density of both species declined from north to south of the grid. Other sub-canopy species which were common throughout the grid were

Timonius timon, *Guioa acutifolia*, *Banksia integrifolia*, *Glochidion* spp., *Acacia aulacocarpa*, *Euroshinus falcata* and *Eucalyptus torelliana*. While some sub-canopy species were more common in one part of the grid, most occurred in both the eastern and western halves.

The shrub layer (< 3 m) included many juvenile individuals of sub-canopy species. The more common shrub species were *Callicarpa pedunculata*, *Rhodomyrtus trineura* and *Ficus* spp. Several other species occurred less frequently, and with a patchy distribution. The few vine or scrambler species had a limited occurrence, and *Maesa dependens*, the most frequent, was restricted to below a dense sub-canopy of *A. torulosa*.

Where there was a dense sub-canopy of *Allocasuarina* spp., a build-up of cladodes on the soil surface and low light penetration was associated with an sparse ground layer vegetation. Grasses were the dominant ground layer species, with *Themeda australis*, *Imperata cylindrica* and *Sorghum laxiflorum* being the most prevalent species throughout the grid. Species diversity (number of species per quadrat) of all vegetation strata was slightly higher for quadrats in the western half of the grid.

CHAPTER 4

SEED DISPERSAL AND LOSSES

4.1 Introduction

Casuarina seed is dispersed by wind, after the dehiscence of the cones. Seed release appears to occur annually in most species (Andersen 1985b; Hueneke 1976; Woolfrey 1985), although some species are thought to retain seed until fire-induced stem death (Gill 1981a). No species have been found to form soil-stored seed banks (Andersen 1985b; A. House pers. comm.; Hueneke 1976). Therefore, for seedling recruitment to occur, seed-fall would be expected to coincide with climatically favourable periods. However, in all species studied so far, seed-fall occurs throughout the year, with broad peaks varying in season between species and habitats (Andersen 1985b; Hueneke 1976; Woolfrey 1985), and appears to be related to the drying out of cones (A.N. Andersen pers. comm.), rather than coinciding with periods favourable for germination and recruitment (Hueneke 1976; Woolfrey 1985). Such a seed-fall pattern would optimize dispersal (Frankie *et al.* 1974), but may limit regeneration success.

Dispersal of seed away from the maternal parent is believed to enhance escape from density dependent competition and mortality, and to enable colonization of newly available habitat (Howe and Smallwood 1982). Nevertheless, despite bearing a wing, most casuarina seeds fall beneath the canopy of the maternal parent (Hueneke 1976; Woolfrey 1985), although secondary dispersal via water may result in greater dispersal distances being achieved (Woolfrey 1985).

Pre-dispersal seed losses may be caused by birds (Cleland and Sims 1968; Clifford and Drake 1981), or by insects, which have been reported to reduce seed-set in *Allocasuarina* spp. by as much as 77% (Andersen 1985b). Seed reaching the soil surface may be destroyed by seed-eating ants (Andersen and Ashton 1985; Woolfrey 1985), which have been observed removing seeds of *A. littoralis* and *A. torulosa* (Withers 1978a; Majer 1985). Minor post-dispersal seed predation by Lygaeid bugs (Andersen 1985a) and grasshoppers (Majer 1985) has been recorded elsewhere.

In this chapter, the factors affecting the availability of *A. littoralis* and *A. torulosa* seeds for germination are investigated, particularly patterns of seed release from the canopy and loss of seed to predators.

4.2 Methods

4.2.1 Seed Dispersal

A study grid of 100 x 40 m was established at Kirrama, across the boundary between contiguous stands of *A. littoralis* and *A. torulosa* (Chapter 3). The grid was sub-divided into 40 10 x 10m plots, with a circular trap for collection of seed-fall randomly located in each. The traps consisted of a hoop (diameter 0.762 m) supported by three 1.2 m wooden legs, and from which a terylene bag was suspended. A strip of Rentokil "Bird Repellent" was applied to each leg, and maintained, to prevent ants from entering the traps and removing seeds. The traps were emptied at periods of between three and eight weeks from August 1982 to July 1984. All seed and cones of *A. littoralis* and *A. torulosa* from each trap were counted.

Seed-fall data were converted to daily seed-fall m^{-2}. Data were then transformed by natural logarithms before analysis (Sokal and Rohlf 1969 p 382). All data sets to be compared were tested for homogeneity of variance using Bartlett's chi-square test (Sokal and Rohlf 1969 p370) and found to be homoscedastic. The effects of species, month and year (first 12 months against second 12 months) on seed-fall were tested using a three-way analysis of variance without replication, assuming no significant three-way interaction (Sokal and Rohlf 1969 p 346). Daily seed-fall levels were compared with monthly rainfall statistics.

Mean daily seed-fall m^{-2} was calculated in relation to distance to the canopy of the nearest potential maternal parent. The number of cones per trap for each collection period was tested for correlation with the number of seeds (Sokal and Rohlf 1969 p 509). Regression equations were calculated to describe the relationship between seed-fall and cone-fall, for all traps in which seed of each species had at any time been recorded (Sokal and Rohlf 1969 p 430).

A total of 30 cones from a minimum of six trees of each species were collected and air dried to release seeds. Seeds were counted, and average seeds per cone calculated. Mean weight of *A. littoralis* and *A. torulosa* seed from Kirrama was calculated by weighing two samples of 500 seed per species. Surface area was calculated by tracing onto paper the outline of a subsample of 30 seed per species, and comparing the weights with that of a known area of paper.

4.2.2 Seed Losses

Seed predation of *A. littoralis* and *A. torulosa* was observed at Kirrama 11 times over the 12 month period from September 1983 to December 1984, by monitoring the fate of seed baits placed on the ground. The experiment was designed to produce minimum interference with natural seed availability, and to mimic natural seed-fall patterns (Andersen and Ashton 1985). Single seeds were placed on a 9 x 9 m grid of one hundred seed stations at one metre intervals, adding approximately one seed m^{-2} to the natural seed-fall. Each station was marked with a labelled peg and the immediate area cleared of vegetation (10 cm diam.). At the commencement of each trial, each station was randomly assigned a seed of either species, until 50 seed of each species had been allocated. The seed was placed in the centre of the cleared station between 1800 and 1900 hrs. Predation of the seed by destruction *in situ*, or removal, was recorded at 12 hour intervals for 72 hrs. One grid was located beneath a dense sub-canopy of *A. littoralis*, another beneath a dense sub-canopy of *A. torulosa*. The term "seed-loss" is used to refer to all seed that was removed or eaten *in situ*. Seed-loss per month was calculated as a proportion of total seed and compared for each seed species within sub-canopy species. Seed-loss per station was also calculated as a proportion of seed placed at the station over the 11 trials. As an index of change in seed loss rates over the observation period, the ratio between seed-loss in 24 and 72 hrs was calculated.

Angular transformations were performed on proportion data before analysis (Sokal and Rohlf 1969 p 386). All data sets to be compared were tested for homogeneity of variance using Bartlett's chi- test (Sokal and Rohlf 1969 p370) and found to be homoscedastic. The effects of seed species, sub-canopy species and month on seed-loss over the 11 trials, and on the ratio between seed-loss in 24 and 72 hrs were tested using three-way analysis of variance without replication, assuming no significant three-way interactions (Sokal and Rohlf 1969 p346).

Heterogeneity of seed-loss was examined by calculating mean, minimum and maximum seed-loss per station for each sub-canopy species. The effects of seed species, sub-canopy species and month on seed destroyed *in situ*, as a proportion of seed-loss, were tested using a three-way analysis of variance without replication (Sokal and Rohlf 1969 p 346).

Seed-loss in each 12 hr period, of seed present on the grid at the commencement of that period (p), was calculated as follows:

$$P = r/c$$

where r = no. seeds removed in the 12 hr period,
c = no. seeds on the grid at the start of the 12 hr period.

Relative seed-loss at night (N) was then derived. Such that:

$$N = n/(n + d)$$

where n = mean p, for the three night-time 12hr periods
and d = mean p, for the three day-time 12hr periods.

Monthly seed-loss and relative seed-loss at night were tested for correlation with mean maximum and mean minimum temperature for the three days of each monitoring session (Sokal and Rohlf 1969 p 509).

A collection of the ants from the study site was made by S.T. Garnett, and ant identifications were made by A.N. Andersen and S.T. Garnett.

Ants occurring at each grid are listed in Appendix 2. Opportunistic observations were made of ants collecting and eating *Allocasuarina* seed. Mammal trapping at the site and identification was undertaken by A. Taplin.

It is sometimes possible to determine the animal which has eaten a seed by characteristic feeding marks on the remains (Begg and Dunlop 1980). Towards the end of the monitoring period, rodents were observed eating seeds of *A. littoralis* and *A. torulosa in situ,* with the remains of the samara bearing a characteristic longitudinal slit. Therefore, for the last five periods, experimental seed which appeared to have been eaten by rodents was separately recorded. Initial analyses of seed-loss included seed eaten by rodents. When analyses were repeated for the five months when separate data was available for rodent and non-rodent predation, there were no changes from the significance levels found in the initial analyses. Therefore, analyses in this chapter relate to total seed-loss.

To test for the presence of a soil-stored seed bank, twenty soil samples were collected from beneath the closed sub-canopy of each *A. littoralis* and *A. torulosa,* in late October 1983. Each sample was 15 x 15 cm, and taken to a depth of 2 cm. The samples were sieved, and components greater than 2 mm searched for seed. Mean number of seed m^{-2} was calculated for each species. Differences between species were tested using a Mann-Whitney U test (Siegel 1956 p 116). An approximation of seed-longevity in the soil was calculated by dividing the seed-bank size by October seed-fall.

Opportunistic records were made of bird species seen eating seed of *A. littoralis* and *A. torulosa* from the canopy, but no attempts were made to assess the extent of the damage caused by pre-dispersal seed-predators, including birds and insects.

4.2.3 Loss of Seed Falling within Unopened Cones

To test the fate of seed falling within unopened cones, 25 freshly picked cones of each species were placed under the parent sub-canopy. The cones were tethered by a 10 cm string to pegs on a 4 x 4 m grid, at 1 m intervals, on 29 October 1984. A clearing of 10 cm diam. was made in the litter and the cone placed in the centre. The cones, with the top 5 mm of surface soil and any accumulated litter, were collected four weeks later, placed in a paper bag and dried at 60°C before sorting. The number of intact remaining seeds was recorded. These were dissected to determine viability. The number of samara from which the embryo had been eaten, and indication of whether the embryo were eaten by rodents, was recorded. Bracteolate valves which had been chewed open and opened naturally were counted. The number of seed which had not been released from the valves was also recorded. An angular transformation was performed on proportion data before analysis (Sokal and Rohlf 1969 p 386). All data sets to be compared were tested for homogeneity of variance using Bartlett's chi-square test (Sokal and Rohlf 1969 p370) and found to be homoscedastic. Differences between the species were tested using a t-test (Sokal and Rohlf 1969 p222), or a Mann-Whitney U test (Siegel 1956 p 116).

4.3 Results

4.3.1 Seed Dispersal

Monitored seed-fall was consistently higher in *A. littoralis* than in *A. torulosa* (4.23 vs 0.513 seed m^{-2} d^{-1}, Table 4.1), but its seasonal distribution was similar in both species (Fig. 4.1). Seed fell throughout the year with highest levels from March to July. Mean seed-fall m^{-2} d^{-1} for March to July was 10.16 in *A. littoralis* compared to 2.26 for August to February, and in *A. torulosa* was 1.18 compared to 0.28. More seed fell during the second year of monitoring, and, although seed-fall was significantly affected by species, month and year, there were no significant interactions (Table 4.1). Seed-fall did not appear to respond to rainfall, although higher levels in the second year followed higher wet season rainfall than in the previous year (Figs 4.1, 4.2) as well as a heavy flowering season (Chapter 7).

Table 4.1 Effect of species, month and year on daily seed-fall.

Source of Variation	Sum of Squares	d.f.	Mean Square	F_s	P
Main Effects					
Species	53.3600	1	53.3600	104.496	<0.001
Month	36.7897	11	3.3445	6.549	<0.01
Year	11.3544	1	11.3544	22.236	<0.001
Interactions					
Species x Month	5.1584	11	0.4689	0.918	n.s.
Species x Year	0.2288	1	0.2288	0.4481	n.s.
Month x Year	11.1064	10	1.0097	1.977	n.s.
Residual	5.6171	11	0.5106		
Total	123.6147	47			

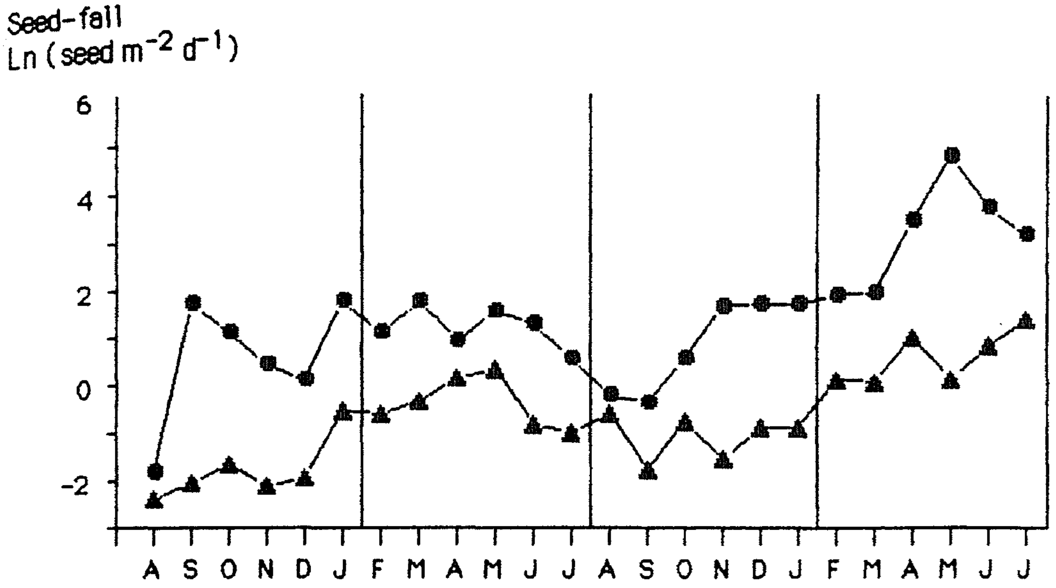


Fig. 4.1 **Monthly *Allocasuarina* seed-fall at Kirrama.**

(August 1982 to July 1984).

Seed species: *A. littoralis* ●

A. torulosa ▲

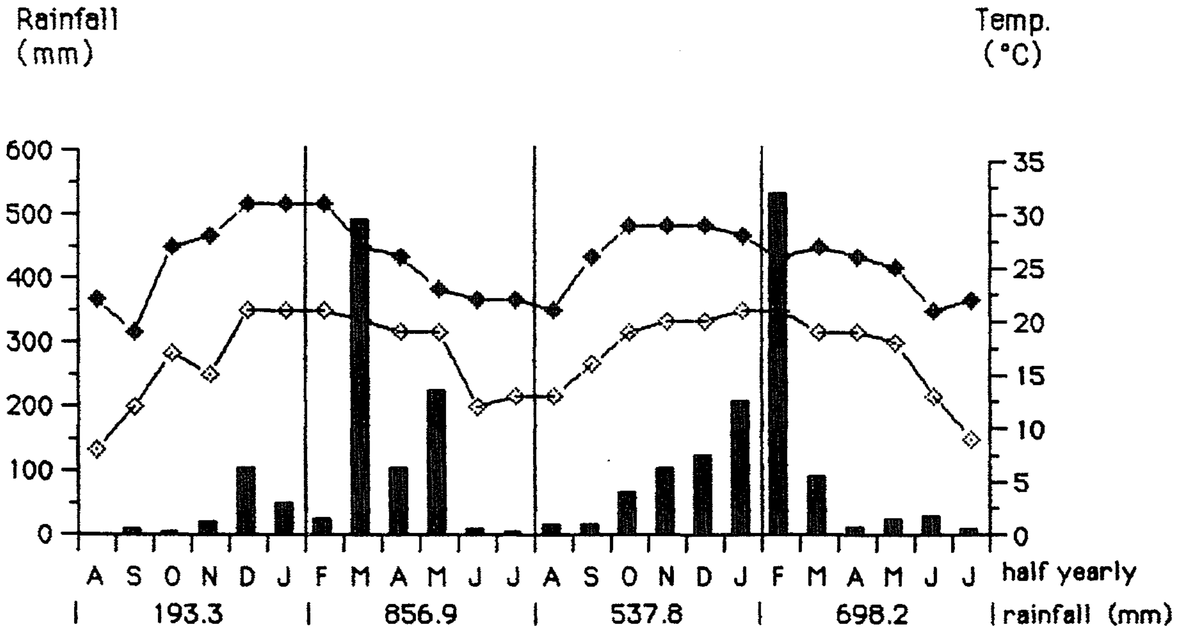


Fig. 4.2 **Weather statistics at Kirrama.**

(August 1982 to July 1984).

Temperature: Mean maximum◆, Mean minimum ◇.

Rainfall ■.

The number of seeds falling into individual traps each month was positively correlated with that of cones in both *A. littoralis* ($r = 0.9282$, $t_s = 49.773$, d.f. 398, $P < 0.001$) and *A. torulosa* ($r = 0.9512$, $t_s = 59.5014$, d.f. 373, $P < 0.001$) (Fig. 4.3). The relationships between seed-fall (S) and cone-fall (C) are described by the following regression equations:

$S = 2.11 + 20.70\ C$ ($F_s = 2477.334$, d.f. 1, 398 $P < 0.001$)
for *A. littoralis*,

and $S = 7.53 + 23.55\ C$ ($F_s = 3540.415$, d.f. 1, 373 $P < 0.001$)
for *A. torulosa*.

Seeds frequently had to be removed from cones to be counted. However, it was not possible to obtain an accurate estimate of the proportion of seed falling within unopened cones. The high correlations may result from cones falling with the seed enclosed, or soon after the seeds are released and having similar patterns of dispersal as the seeds. Average number of seeds per mature cone was 39.32 in *A. littoralis* and 38.37 in *A. torulosa*. Thus, about one-third of seed-fall of both species was not associated with cone-fall. While seeds falling into the traps varied in colour from white to dark brown, seeds that had to be removed from cones were frequently pale, and therefore likely to be immature (Chapter 5).

Density of seed-fall declined with distance from potential maternal parents in both species (Fig. 4.4). A higher proportion of seed-fall was recorded below the canopy of a mature female in *A. littoralis*, than in *A. torulosa*. However, while a small proportion of *A. littoralis* seed-fall was recorded landing beyond three metres from the canopy of a

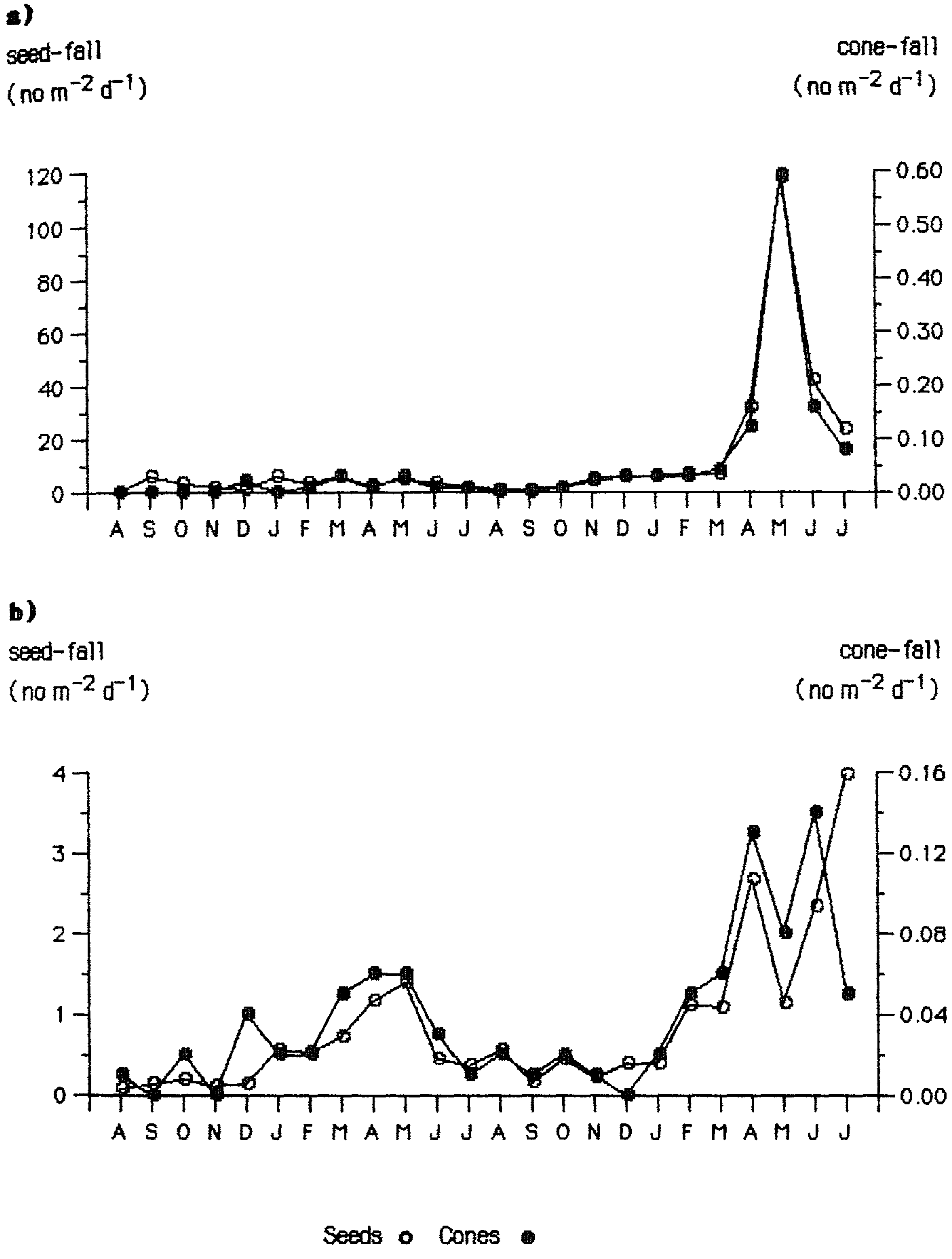


Fig. 4.3 **Seed-fall and cone-fall at Kirrama.**

August 1982 to July 1984.

a) *A. littoralis*, **b)** *A. torulosa*.

mature female (0.05 seed m^{-2} d^{-1}), no seeds of *A. torulosa* were recorded beyond three metres from a mature female tree.

Both weight and surface area were greater in *A. torulosa* seed than in *A. littoralis* seed (Table 4.2). However, surface area to weight ratio was higher in *A. littoralis*.

Table 4.2 Size of *A. littoralis* and *A. torulosa* seed from Kirrama.

Species	Seed Weight Mean ± s.d. (mg)	Surface Area Mean ± s.d. ($x 10^{-4}$ mm^2)	Surface to Weight Ratio ($x 10^{-4} mm^2$ mg^{-1})
A. littoralis	1.73 ± 0.006	9.07 ± 1.97	5.24
A. torulosa	2.79 ± 0.074	13.17 ± 2.25	4.72

4.3.3 Seed Losses from the Soil Surface

Seed-loss in 72 hrs was greater from beneath the *A. littoralis* (*A. littoralis* seed: 72.3, *A. torulosa* seed: 71.0) sub-canopy than from beneath the *A. torulosa* sub-canopy (*A. littoralis*: 64.9, *A. torulosa*: 52.5; Fig. 4.5a, Table 4.3). Seed-loss of *A. littoralis* was greater than for *A. torulosa* from beneath both sub-canopies, and although this difference was slight under *A. littoralis*, three-way analysis of variance showed it to be significant (Table 4.3). Seed-loss was generally between 50 and 90% (Fig. 4.5a), and variation between months was significantly different between sub-canopies (Table 4.3).

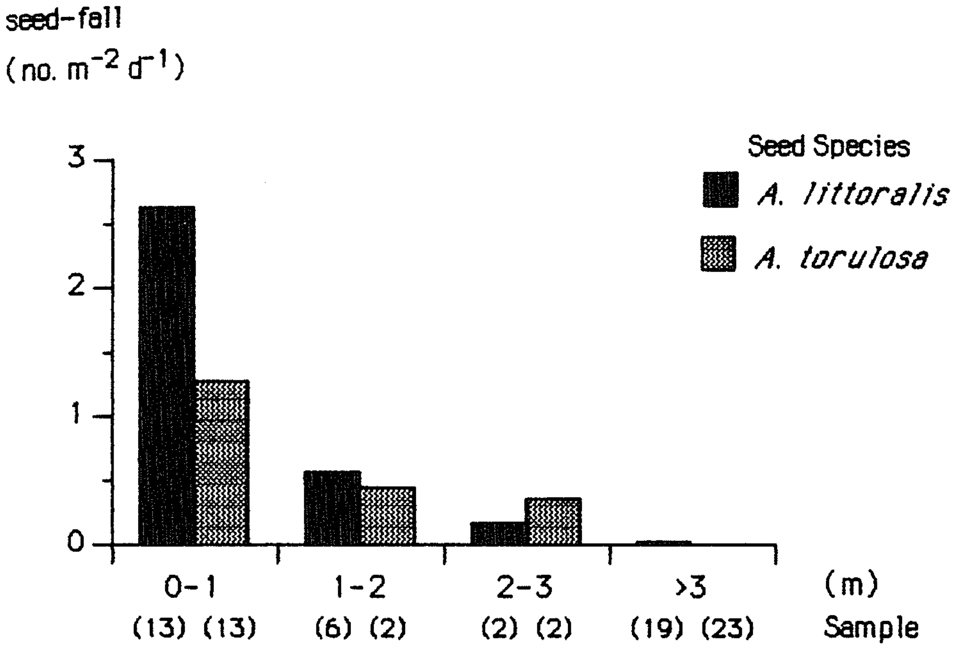


Fig. 4.4 Mean daily seed-fall in relation to distance from canopy of the nearest potential maternal parent.

Under *A. littoralis*, most seed-loss occurred at night, except in June, when the mean minimum temperature approached freezing point (Fig. 4.5b,c). Seed-loss was positively correlated with minimum temperature ($r = 0.6138, t_s = 2.332$, d.f. 9, $P < 0.05$). Relative seed-loss at night was also positively correlated with minimum temperature ($r = 0.6498$, $t_s = 2.564$, d.f. 9, $P < 0.05$). However, when the June data were excluded, neither variable was significantly correlated with temperature (d.f. 8, $P > 0.05$). Both seed-loss and relative seed-loss at night were independent of seed-fall (d.f. 8, $P > 0.05$).

Table 4.3 Effect of sub-canopy species, seed species and month on seed-loss within 72 hours.

Source of Variation	Sum of Squares	d.f.	Mean Square	F_s	P
Main Effects					
Sub-canopy	0.2026	1	0.2026	20.813	< 0.01
Seed	0.0545	1	0.0545	5.603	< 0.05
Month	0.5831	10	0.0583	5.989	< 0.01
Interactions					
Sub-canopy x Seed	0.0336	1	0.0336	3.452	n.s.
Sub-canopy x Month	0.3630	10	0.0363	3.727	< 0.05
Seed x Month	0.1532	10	0.0153	1.574	n.s.
Residual	0.0974	10	0.0097		
Total	1.4874	43			

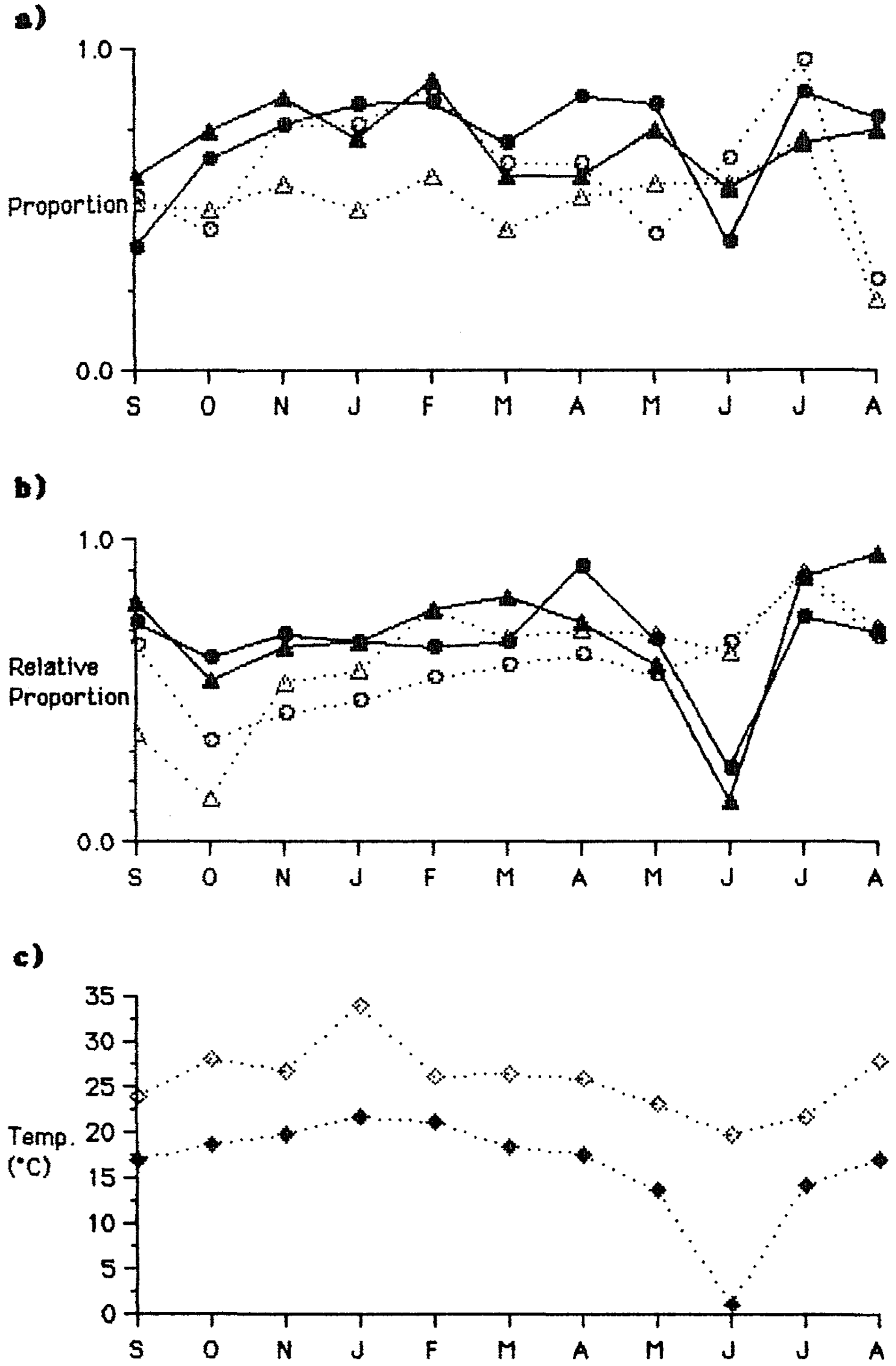


Fig. 4.5 Seasonal patterns of seed-loss and temperature. September 1983 to August 1984. **a)** Seed-loss in 72 hours, **b)** Relative seed-loss at night, **c)** Temperature during monitorings.

Sub-canopy:		*A. littoralis*	*A. torulosa*.
Seed:	*A. littoralis*	—●—	··○··
	A. torulosa	—▲—	··△··

Mean Daily: Minimum ··◆·· Maximum ··◇··

Under *A. torulosa*, there was a gradual increase in relative seed-loss at night through the 11 month periods. Seed-loss and relative seed-loss at night were not found to respond to temperature (d.f. 9, $P > 0.05$). Only relative seed-loss at night was positively correlated with seed-fall ($r = 0.8153$, $t_s = 3.983$, d.f. 8, $P < 0.01$).

There seemed to be no clear response between seed-loss and rainfall patterns in either species. However, *Pheidole* spp. were frequently observed chewing through the seed coat and consuming the embryo of seeds of both species which had become imbibed due to heavy rainfall.

Pheidole spp. and *Rhytidoponera* spp. were frequently seen removing seeds of both species, and *Pheidole* spp. were seen eating seeds *in situ*. The rodent, Fawn-footed Melomys (*Melomys cervinipes*), trapped at the study site, ate seeds of both species in captivity (A. Taplin pers. comm.). Seed-loss attributable to rodents was low (3.13%), and while it was not significantly affected by seed or sub-canopy species, higher values under *A. torulosa* in June resulted in a significant interaction between month and sub-canopy species ($F_S = 9.890$, d.f. 4,4, $P < 0.05$).

Seed-loss was heterogeneous within sub-canopy plots (Fig. 4.6). Seed-loss occurred from every station under both sub-canopies no fewer than three times out of eleven. Mean seed-loss per station was significantly higher under *A. littoralis* than under *A. torulosa* (73.1% vs 57.7%; $t_s = 6.368$, d.f. 198, $P < 0.001$). There appears to be a higher level of seed-loss in the north-eastern half of the grid under *A. littoralis*.

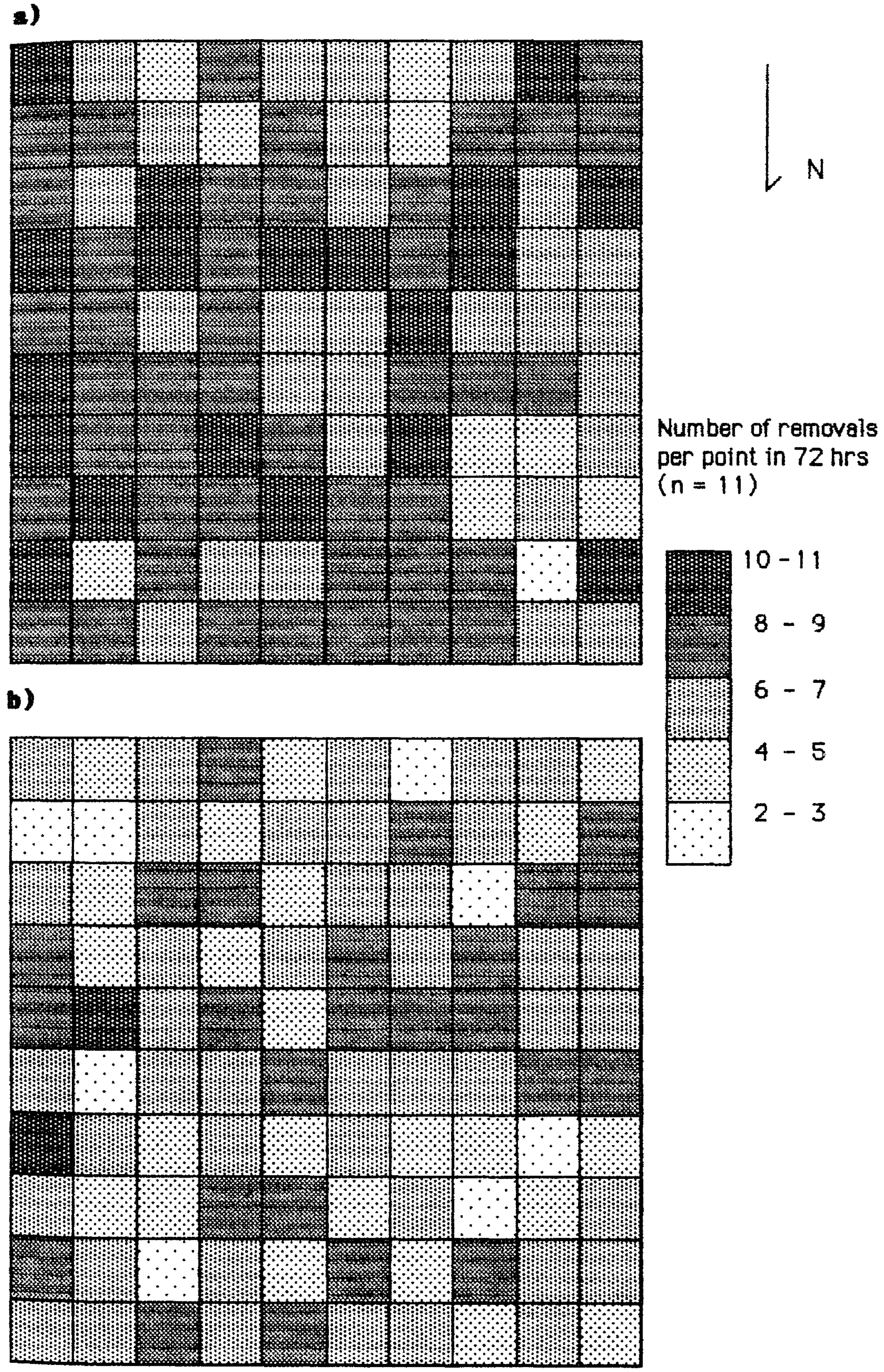


Fig. 4.6 **Seed-loss within 72 hrs per station.**

Sub-canopy species: **a)** *A. littoralis* **b)** *A. torulosa*

The ratio between seed-loss in 24 and 72 hrs was higher under *A. littoralis* than under *A. torulosa* (75.4 vs 61.9%). The ratio was not influenced by seed species, but variation between months differed significantly between the two sub-canopies (Table 4.4). Although no attempt was made to make an accurate estimate of the number of seeds surviving on the ground for one month, seed of the species used in the trial was present at 0 - 3% of the monitoring stations, when the grids were prepared for subsequent trials.

Table 4.4 Effect of sub-canopy species, seed species and month on the ratio between seed-loss in 24 and 72 hrs.

Source of Variation	Sum of Squares	d.f.	Mean Square	F_S	P
Main Effects					
Sub-canopy	0.2359	1	0.2359	22.815	<0.001
Seed	0.0049	1	0.0049	0.471	n.s.
Month	1.0256	10	0.1026	9.920	<0.001
Interactions					
Sub-canopy x Seed	0.0000	1	0.0000	0.0000	n.s.
Sub-canopy x Month	0.3307	10	0.0331	3.199	<0.05
Seed x Month	0.1191	10	0.0119	1.152	n.s.
Residual	0.1034	10	0.0103		
Total	1.8196	43			

In October 1983, topsoil from beneath the closed *A. littoralis* stand contained 4.44 *A. littoralis* seeds m^{-2}, and from beneath closed *A. torulosa* stand contained 17.76 *A. torulosa* seeds m^{-2}. The difference between soil seed content was significant ($U = 168$, $n_1 = 20$,

$n_2 = 20$, $P < 0.001$). The seed bank of *A. littoralis* represented 2.57 days' seed-fall, and that of *A. torulosa* represented 38.61 days' seed-fall.

Several bird species were observed eating seed from the canopy of *A. littoralis* and *A. torulosa*. Red-tailed Black-Cockatoos (*Calyptorhynchus magnificus*) frequently congregated in flocks in single trees of *A. torulosa*, destroying hundreds of cones. Crimson Rosellas (*Platycerus elegans*) were observed eating seed from immature *A. littoralis* cones in a similar manner in the ranges inland from Cardwell. Birds seen removing seeds protruding from open bracteoles of *A. littoralis* cones were Rainbow Lorikeet (*Trichoglossus haematodus*), Scaly-breasted Lorikeet (*Trichoglossus chlorolepidotus*), Little Lorikeet (*Glossopsitta pusilla*) and Red-browed Firetail (*Emblema temporalis*). Birds were more frequently seen in the more fecund females of both species. No birds were seen taking seed of either *A. littoralis* or *A. torulosa* from the ground, and Red-browed Firetails, feeding on grass seeds on the ground, did not respond to seed baits of either species.

4.3.3 Loss of Seed from Cones

While a small proportion of the *A. littoralis* cones placed on the ground were chewed, all those of *A. torulosa* remained intact (Table 4.5). A small proportion of seed of both species was not released from the bracteolar valves. Most of the seed that was released from the cones was removed. In *A. torulosa*, a large proportion of this seed was eaten *in situ* by rats. Less than 0.5% of either species remained at the site in a viable condition.

Table 4.5 Fate after one month of cones and seeds placed on the ground.

Chewed cones tested using the Mann-Whitney U test ($n_1 = 25$, $n_2 = 24$). All other variables tested using a t-test (d.f. 47).

Variable	*A. littoralis* Mean (%)	*A. torulosa* Mean (%)	t_s	P
Bracteolar Valves				
-Opened Naturally:	0.9962	0.9984	-0.798	n.s.
-Chewed Open:	0.0130	0.0000	(U = 216)	< 0.01
Released Seed				
-Eaten by Rats:	0.0091	0.2770	-10.086	< 0.001
-Eaten by Ants:	0.0127	0.0200	-0.832	n.s.
-Removed:	0.9281	0.6478	7.009	< 0.001
Total seed-loss	0.9713	0.9795	0.519	n.s.
Seed remaining				
-and viable:	0.00013	0.00003	0.6525	n.s.
-and non-viable:	0.0274	0.0201	0.6053	n.s.

4.4 Discussion

4.4.1 Seed Dispersal

Although the winged seeds of *A. littoralis* and *A. torulosa* could be expected to be widely dispersed, restricted dispersal appears to be characteristic of these and other Casuarinaceae species (Hueneke 1976; Woolfrey 1985). This contrasts with wider seed-dispersal in other species with single-winged seeds (Lamont 1985; Norberg 1973; Yocum 1968). In the species studied here, restricted dispersal appears to be due to a tendency for cones to be shed before dehiscence. Although this tendency has been observed in other North Queensland populations of

A. torulosa (A. House pers. comm.), it was not noted in other studies of seed-fall in *Allocasuarina* spp. (Hueneke 1976; Woolfrey 1985), and did not occur in a study of *A. paradoxa* seed-fall, in which dispersal distances were not measured (A.N. Andersen pers. comm.).

As *A. littoralis* seed is lighter and has a greater surface area to weight ratio, singly dispersed seeds of this species would be expected to be more widely dispersed than those of *A. torulosa*, as was indicated by the small amounts of seed falling beyond 3 m from mature female trees. That the proportion of seeds of *A. torulosa* falling at intermediate distances (2 to 3 m from mature females) was greater than that of *A. littoralis*, can probably be attributed to the taller stature of *A. torulosa* females at the Kirrama study site.

That *A. littoralis* had higher seed-fall than did *A. torulosa* does not necessarily mean that more seed are available for recruitment. The rates of seed-fall measured here are only an indication of the likely relative trends of the two species, as seed-fall is likely to be both spacially and temporally variable. Their main importance is in the calculation of loss to predators and other causes, which is discussed in the following sections. Ultimately, whether seed-dispersal is effective also depends on the distribution of sites suitable for germination and recruitment (Chapter 5).

4.4.2 Predator Escape

This study shows that for seeds of *A. littoralis* and *A. torulosa* to be available for germination, they must escape both pre-dispersal predation by birds, and post-dispersal predation by ants and rodents.

Other insect groups may cause major pre-dispersal seed losses (Andersen 1985b) and minor post-dispersal seed losses (Andersen 1985b; Majer 1985).

Dispersal characteristics which protect seeds from some predators may increase exposure to others. Retention of seed in the canopy may reduce post-dispersal seed predation (Cowling and Lamont 1985), but large canopy-stored seed crops may be more attractive to pre-dispersal predators (Shaw 1968), as was suggested by the congregation of large flocks of seed-eating birds in the more fecund *A. littoralis* and *A. torulosa*. Shedding of cones before dehiscence may reduce losses to the smaller birds unable to bite into the cones to remove seeds, but may increase losses to rodents. However, premature shedding of cones appears to be a function of resource availability (Chapter 7), rather than predator pressure, as the probability of seeds surviving one month on the soil surface appeared to be similar for seed dispersed singly or within cones.

The relative predation rate of seeds distributed on the soil surface in clumps or singly appears to be related to the foraging habits of the predators involved. Where the solitary-foraging ant *Rhytidoponera* sp. was the main agent of seed-loss, survival rate was higher for clumped seeds (Andersen and Ashton 1985). However, rodents and recruit-foraging ants of *Pheidole* spp., which were present at the Kirrama study site along with *Rhytidoponera* spp., may be more effective at depleting clumps of seeds. Rodents may stay at one site and consume all seed. As rodents can chew into the cones, seeds are accessible to them before the dehiscence of fallen cones. Rodents may also be less likely to detect single seed (Beattie and Lyons 1975).

While other studies have identified "safe sites" (Andersen and Ashton 1985; Wellington and Noble 1985b), from which no seed-losses were observed, such sites were not detected at Kirrama. Elsewhere heterogeneity has been related to proximity to nest entrances (Ashton 1979). Seed falling on undisturbed litter may be more likely to escape predation by rodents than seed lying exposed on bare soil, such that measures of seed predation by rodents here may be over-estimates of natural predation rates. However, estimates of seed-loss to the more important seed predators, ants, are less likely to be inflated, since ant predation is relatively unaffected by the presence of litter (Andersen and Ashton 1985).

While variation in seed predation is sometimes related to seed availability (Andersen 1982; Brown *et al.* 1979b; O'Dowd and Gill 1984), overall levels of seed predation were insensitive to availability, indicating that the numbers of seeds escaping predation will be highest during periods of high seed-fall. However, the correlation between relative seed-loss at night and seed-fall under *A. torulosa* suggests that some seed predators at the site may respond to greater seed availability.

Reduction of total seed predation and the proportion of seed-loss occurring at night under *A. littoralis* during the cold weather in June, is consistent with ant predation patterns reported elsewhere, of seed predation being lowest during periods of extreme temperature (Andersen 1982; Andersen and Ashton 1985; O'Dowd and Gill 1984), and there being a shift in seed predation from night to day during winter (Andersen 1982; Wellington and Noble 1985b). Although no such relationship was observed under *A. torulosa*, reduced ant activity appeared to be obscured by counteracting high predation by rodents.

Greater rodent activity under *A. torulosa* was also suggested by the greater loss of seeds to rodents from cones. Thus, any reduction in importance of ants as seed predators may result in a greater proportion of seeds being destroyed by rodents. Such competition between ants and rodents has been observed elsewhere, both in myrmecochorous species (Beattie and Lyons 1975; Culver and Beattie 1978; Heithaus 1981; O'Dowd and Hay 1980) and non-myrmecochorous species of seed (Abramsky 1983; Brown and Davidson 1977; Brown *et al.* 1979a).

Seed is vulnerable to predation at least until radicle emergence, which usually does not occur in less than four days after imbibition commences (Chapter 5). Loss rates within the first 72 hours, therefore represent a minimum impact on the seed pool. However, the decline in seed-loss rates, with the majority of recorded seed-loss occurring within the first 24 hrs, indicates that the probability of predator escape increases with time on the soil surface. Such a decline has been observed in other studies (Andersen and Ashton 1985; Ashton 1979; Drake 1981; Majer and Lamont 1985), and suggests reduction in seed attractiveness over time, or difference in attractiveness among the original seed. However, the low viability after one month of seed that escaped predation suggests viability of seed on the soil surface is rapidly lost, possibly due to pathogenic attack. Although the probability of later destruction of seed by pathogenic attack is unknown, it can be assumed that it will increase with time. Thus the longer the period between seed fall and germination, the lower is the likelihood of the seed surviving to germination.

Most seeds removed from the grid were likely to have been taken to ant nests, where some might have escaped destruction (Andersen and

Ashton 1985). Seed was found in nests of *Rhytidoponera* spp. at Kirrama and ants of *Pheidole* sp. were seen to leave piles of seed near the entrance to the nest (S.T. Garnett pers. comm.). Some of this seed may escape destruction and germinate successfully. Successful germination from within nests will depend on the depth from which seedlings can emerge, and the rate at which seed is destroyed. However, germinants observed at Kirrama did not appear to be associated with ant nests.

Although ants distinguish between the seed and chaff of *Eucalyptus* spp. (Ashton 1979), and non-viable seeds of *Allocasuarina* frequently contain no more than shrivelled embryos of little nutritional value, seed-loss often exceeded seed viability in this study, as was also the case with *A. paradoxa* (Andersen 1985b). It therefore appears that seed predators cannot distinguish between viable and non-viable seed of *Allocasuarina* spp. Hence the probability of viable seed escaping predation may be no less than that of non-viable seed.

Factors which may influence the attractiveness of seeds to predators include chemical attractants, toxins, nutritional value, seed coat thickness and seed size (Andersen and Ashton 1985; Janzen 1971; Russell *et al.* 1967). While nutritional information is available for *A. littoralis* seed (Grundon 1972; Withers 1978a), there is none available for *A. torulosa* to enable comparison of their relative value to predators. There are no data available on other biochemical factors which might influence seed predation. Observations here of *Pheidole* spp. chewing through moistened seed coats suggests that any obstacle presented by the seed coat is overcome by wetting. Thus, seeds may be more prone to predation by ants when wet, due to a softening of the samara. Although Andersen and Ashton (1985) report that rain reduces ant activity, *Pheidole* spp. may at this time eat seed left close to the nest entrance. Higher losses of seed of *A. littoralis* than of *A. torulosa* may be due to differences in seed size, as *A. torulosa* seed is the heavier, and may be more difficult to transport. However Majer (1985) found no relationship between seed size and predation rates, and no significant difference between ant predation of *A. littoralis* and *A. torulosa* on North Stradbroke Island.

The differences in seed-loss between stands of *A. littoralis* and *A. torulosa*, and the variation within grids are likely to be caused by differences in the ant faunas responsible for predation (App. 2), the location of ant nests and the relative importance of rats. They do not necessarily indicate that seed-losses under *A. littoralis* stands will be higher than from under all *A. torulosa* stands. Similar studies at other sites would be required to determine the extent of such trends.

The smaller size of the seed bank detected under *A. littoralis* than under *A. torulosa* during the period of low seed-fall reflected the greater vulnerability of seed of the former species to predation. While the *A. torulosa* seed bank was four times the size of the *A. littoralis* seed bank, mean daily seed-fall levels, after correction for mean predation rates, predict that the number of *A. littoralis* seeds entering the seed bank will far exceed that of *A. torulosa* (1.17 vs 0.24 seed m^{-2} d^{-1}, persisting for more than three days). This discrepancy was probably caused by the sampling area selected: seed-fall was sampled for the entire population, whereas the seed bank and seed predation rates were sampled under dense sub-canopies in which there were reproductively active female trees. The measure of the seed bank in such a situation will over-estimate that of the entire population, and as reproductively active female trees were far less common in *A. torulosa* than in *A. littoralis* (Chapter 7), the discrepancy will be far greater for the former species.

4.4.3 Effect of Seed-fall and Post-dispersal Predation on Seed Availability for Germination and Seedling Recruitment

Because of the large proportion of seed removed by predators and the rapid loss of viability in seeds remaining on the soil surface, the sooner germination-stimulating rainfall occurs after seed-fall, the higher will be the probability of seeds surviving to germination. Furthermore, as levels of seed-loss to predation were fairly constant through the year (except during extreme low temperatures), and did not correspond to seed-fall levels, the probability of seed surviving to germination will be a function of seed-fall.

From the concurrence of high rainfall and high seed-fall overlap from March to May, it is predicted that most germination will occur during this period, from seed recently released from the canopy. As low temperatures occur during the middle of the dry season, several months before the likely onset of heavy rains, seeds which escape predation due to depressed temperatures will be less likely to survive to germination.

While predation of seed may be inconsequential to the species during periods which are unfavourable for recruitment (Ashton 1979), seed-losses at other times will be important as they may alter the distribution patterns of seedlings (Janzen 1970), reduce the level of recruitment (Louda 1982b) and will result in the natural selection of traits which enhance predator escape (Janzen 1969).

As conditions favourable for recruitment appear to be confined to periods of high rainfall (Chapter 5), and seed does not appear to accumulate in the soil, seed predation through most of the year may not affect seedling recruitment in *A. littoralis* and *A. torulosa*. However, seed landing in sites protected from predators, such as charcoal beds, may be recruited after unseasonal rains (Chapter 8). While heavy seed-fall in the late wet season, may act as a form of predator satiation, such as that which occurs after fire (Ashton 1979; O'Dowd and Gill 1984), there was no evidence of depressed seed predation during this period. Seeded plots which had been protected from predators had a greater number of seedlings surviving at the end of 12 months, than those which were unprotected (Chapter 5). Thus it appears that seed (or seedling) predation does have a real impact on recruitment in the first year. Whether this eventually affects population size will depend on the effects of increased recruitment on the probability of year-old plants surviving to reproductive maturity, which will be affected by both intraspecific and interspecific interference. Even though it may be possible for population size to be unaffected by seed predation, the effect of predation on the genetic makeup of a population will affect the long term fitness of the species (Janzen 1969).

4.5 Summary

Seed-fall in *A. littoralis* and *A. torulosa* occurs throughout the year, with highest levels between March and July. Seed-fall per unit area is greater in *A. littoralis* than in *A. torulosa*. Most seed, especially that falling within cones, is poorly dispersed, falling within three metres of the canopy of female trees, but seed released from the cones in the canopy may be dispersed some distance by wind. Seed of *A. torulosa* is better dispersed locally, because of the higher average tree height, but lower weight and higher surface area to mass ratio in *A. littoralis* results in more seed of this species being dispersed beyond three metres from the maternal parent.

Causes of seed losses in *A. littoralis* and *A. torulosa* seed banks observed here include pre-dispersal predation by birds and post-dispersal predation by ants and rodents. Ants were the major cause of post-dispersal seed predation, removing between 30 and 80% of single seeds within 3 days. Seed predation levels did not respond to seed-fall levels and were insensitive to changes in temperature within the range generally experienced at Kirrama. However, during exceptionally cold weather, both seed predation and predator activity at night were depressed under *A. littoralis*. Reduced predation by ants at this time was partially compensated for by increased predation by rodents, which otherwise removed about 2% of the seed.

A. littoralis seed, possibly because of its smaller size, is more vulnerable to predation than that of *A. torulosa*. Predators did not appear to distinguish between viable and non-viable seeds. Wet seed may be more likely to be eaten by ants *in situ*, although this may be offset by reduced foraging activity during wet weather. No sites safe from seed predation were identified in this study. Singly dispersed seeds and seeds released from cones after cone-fall have similar probability of predation. While mixed seed dispersal patterns may prevent the total depletion of seed reserves, seed falling within closed cones may be more likely to be removed by rats, which can chew into the cones. Seeds remaining on the soil surface for as long as one month had a low level of viability.

Lack of seasonality in predation levels will result in more seed surviving when seed-fall levels are highest. As seed banks of these appear to be small, the shorter the time interval between seed-fall and the onset of germination conditions, the higher will be the chance of survival until successful germination. Thus, most germination should occur between March and May, when both seed-fall and rainfall are high, from seed which has recently been released from the canopy. While it could not be confirmed that seed predation affected population growth, the likely effects on the gene pool and therefore the fitness of *A. littoralis* and *A. torulosa* should not be disregarded.

CHAPTER 5

GERMINATION AND EARLY SEEDLING SURVIVORSHIP

5.1 Introduction

Seed germination marks the end of the dispersal and dormancy phase of the plant's life history (Harper 1977), and is inhibited or triggered by a combination of internal and external factors (Mayer and Poljakoff-Mayber 1982). Innate dormancy is the result of internal factors, while induced and enforced dormancy are the result of external factors (Harper 1957).

Although some members of the Casuarinaceae may require an after-ripening period of up to three months, there appears to be no innate dormancy in the seed of either *A. littoralis* or *A. torulosa* (Turnbull and Martenz 1982). Therefore, at the advent of favourable conditions, seed that has dispersed and escaped predation and pathogenic attack should be available for germination. However, much of the seed-fall of *A. littoralis* and *A. torulosa* is of pale, but apparently fully-developed, seed, an unknown proportion of which is available for germination (Chapter 4). Such seed is frequently produced by the premature shedding of cones. It is not known whether such seed is viable, or requires after-ripening.

Enforced dormancy occurs when germination is prevented by an environmental restraint (Harper 1977). The most common external factors limiting germination are moisture availability, temperature, light and atmospheric gases (Mayer and Poljakoff-Mayber 1982). As neither *A. littoralis* nor *A. torulosa* is found in permanently water-logged habitats, and viable seed is rarely buried to any depth, oxygen levels should be favourable to germination (Mayer and Poljakoff-Mayber 1982). No data have been published regarding the effect of moisture regime on germination in the Casuarinaceae. However, in some plant species, imbibition of seed may be arrested before radicle emergence should moisture availability fall below required levels (Watt 1978). Germination may also be inhibited by water-logging (Beadle 1952; Harty and McDonald 1972).

Germination responses to temperature and light have been described for a non-tropical population of each of *A. littoralis* and *A. torulosa* (Turnbull and Martenz 1982). When moisture availabilty is not limiting and temperatures are between 15 and 40°C, germination of *A. littoralis* and *A. torulosa* commences within four to five days (Turnbull and Martenz 1982). Rapid germination is aided by the presence of a mucilage seed coating (Mott and Groves 1981; Turnbull and Martenz 1982) which increases the seed substrate contact and the zone of water flow making the seed less sensitive to variations in water supply (Harper and Benton 1966).

When conditions favourable to germination do not occur immediately after seed fall, seed will generally remain on the soil surface and be exposed to predation, and fungal and bacterial attack (Chapter 4). If seed survives these pressures, inherent seed longevity assumes importance. *A. littoralis* (Wither 1978a) and *A. torulosa* (Turnbull and Martenz 1982) seed has been stored under room conditions, with little loss of viability, for up to 3 and 18 years respectively. However, tropical conditions have been reported to reduce seed longevity in the Casuarinaceae, although the reason for this has not been explained (Turnbull and Martenz 1982).

Toxic substances have been reported to induce dormancy in both *A. littoralis* and *A. torulosa*, germination being practically eliminated at 200 mM Na Cl, with the result that neither species is found on saline soils (Clemens *et al.* 1983), and although *A. littoralis* is found in coastal environments, it does not appear to occur within the influence of saltwater (pers. obs.). Germination of *A. littoralis* seed has been shown to be delayed in the laboratory by foliage leachates from both *A. littoralis* and *A. verticillata* although there appears to be no accumulation of the responsible toxin in the soil (Withers 1978a).

Germination also exposes the individual to different hazards, with desiccation and grazing replacing seed predation. Frequently, moisture levels required for seed germination are higher than those necessary for seedling establishment (Edgar 1977; Hegarthy and Ross 1980/81; Watt 1982). However, elevated moisture levels may not always be sustained to ensure seedling survivorship.

In this chapter, the stage of maturity at which seed of *A. littoralis* and *A. torulosa* becomes viable, and whether after-ripening occurs in immature seed, is ascertained. Influence of moisture regime on germination is investigated. Provenance trials are undertaken to determine the germination response of tropical populations of *A. littoralis* and *A. torulosa* to different temperature and light regimes. The effect of storage temperature and humidity on seed viability is also investigated.

As laboratory testing of allelopathy does not reflect processes occurring in the field (Stowe 1979), the effect of different canopy and litter characteristics on germination in *A. littoralis* and *A. torulosa* were investigated only under field conditions. Mortality of the field germinants was monitored, and factors causing mortality investigated.

5.2 Methods

The following experimental method was adopted in all germination trials, except where specified. All seed was collected from Kirrama State Forest (Sites H,11). A total of 30 cones, sufficiently mature to release seeds, was collected from a minimum of four trees per population, and placed in a paper bag in a warm dry place. After one week, the samples were sieved and sufficient firm fat seed selected for germination trials, which were commenced within two months of seed collection. Once the pattern of changing viability with seed development was established (Section 5.2.1.), seed was selected in the colour range which produced maximum germination for subsequent germination trials.

For each factor tested, four replicates of 20 seed were placed on Whatman No. 1 filter paper, over vermiculite which was kept saturated with distilled water, in a covered petri dish, in a constant temperature room. For treatments requiring light, illumination was provided by fluorescent tube at 5 μMol m^{-2} s^{-1}. In all experiments, control conditions were at a constant temperature of 25°C with a 14 hour day length. Germination was recorded at emergence of the radicle (Turnbull and Martenz 1982). Germinants were counted and removed daily. Monitoring was continued for a minimum of 21 days, or until germination approached zero over seven days.

Two parameters were chosen to represent germination characteristics. These were percent germination and median germination time. The methods by which these parameters were obtained are outlined below.

a) Percent Germination

Some of the treatments used here were likely to affect seed viability and/or the probability of seed germinating within a specified time. While percent viability is affected by insect predation (Andersen 1985b), that of sub-samples from a well-mixed seedlot should be constant. Therefore, to compare treatments, percent germination was calculated as the percentage of seed used in each treatment which had germinated by the end of the experiment. In preliminary trials, it was found that percent germination after 14 days under control conditions was equivalent to the viability of seedlot, as determined by dissection.

b) Median Germination Time

Time to 50% germination has been adopted by many authors for characterization of the germination response of a seedlot to a temperature continuum (Sonia and Heslehurst 1978; Thompson 1970a, 1970b; Turnbull and Martenz 1983). Thompson (1970a, 1970b) and Turnbull and Martenz (1982) have calculated percent germination as a percentage of the total seed used under each set of conditions, apparently without adjustment for variations in the viability of different seedlots. Therefore, while shape of germination response curves constructed from this parameter may be compared, the parameter is not statistically comparable between different seedlots.

Viability varies considerably in North Queensland seedlots of *A. littoralis* and *A. torulosa*, and in some seedlots was found to be less than 50% by dissection, even when only apparently viable seed is selected (pers. obs.). While a lesser percentage could be used (Turnbull and Martenz 1982), this would not solve the problem of comparison between seedlots of different viability. Sonia and Heslehurst (1978) have used 50% potential germination which is calculated from the maximum germination recorded for each seedlot. This would be suitable where treatments were not expected to affect viability. Experimental treatments undertaken in this thesis may affect seed viability. Gramshaw (1976) calculated 50% in relation to only the seed which germinated within the monitoring period. This measure, adopted here, is referred to as median germination to distinguish it from the previously mentioned measures. Median germination time is a measure which is statistically comparable between different conditions, seedlots and species.

Median germination time was interpolated as follows:

$$t_{1/2} = \frac{(G/2 - g_1) \times d_2 - (G/2 - g_2) \times d_1}{g_2 - g_1},$$

where G = 100% germination = number of germinants in each replicate at the conclusion of the experiment,

d_1 = day prior to cumulative germination reaching $G/2$,

d_2 = $d_1 + 1$,

g_1 = cumulative germination at d_1,

and g_2 = cumulative germination at d_2.

Before analysis of data, the appropriate transformations were performed. These were an angular transformation on percent germination data (Sokal and Rohlf 1969 p386), and a square root transformation on median germination time (Sokal and Rohlf 1969 p384). Data sets to be compared were then tested with Bartlett's chi-square test to confirm homogeneity of variance (Sokal and Rohlf 1969 p370). Analyses undertaken are outlined in each section.

5.2.1 Seed Maturation

A. littoralis and *A. torulosa* cones were collected at a range of developmental stages in August and November 1982. Seed stages were graded according to the colour of the samara, by comparison with the 10YR colour range of the Munsell Soil Colour Chart (1954).

Germination trials were carried out under control conditions in December 1982 and monitored every second day for 21 days. Lack of daily germination data prevented calculation of median germination time. The significance of differences in percent germination between seedlots and colour stages were examined using t-tests (Sokal and Rohlf 1969 p 220).

5.2.2 Storage Conditions

Mature seed was divided into nine subsamples per species and stored at four temperatures (0,18,24,30°C) by three relative humidities (25,50,75%). Relative humidity was controlled by altering sulphuric acid concentration in the base of air tight jars, above which seed was suspended in envelopes (Gleadow 1982; Wilson 1921). Germination trials were undertaken, after six months storage, under control conditions. Due to contamination with sulphuric acid of the seed envelopes in the 18°C, 50% R.H. storage jar, this treatment was excluded from the analysis. Two-way analysis of variance (Sokal and Rohlf 1969 p 310) was undertaken separately on each species, to investigate the influence of storage humidity and temperature on the variables percent germination and median germination time. Due to the exclusion of the 18°C, 50% R.H. storage treatment, two separate analyses of variance had to be undertaken for each variable. Initially, all storage treatments at 18°C were excluded, then all those at 50% R.H. were excluded.

5.2.3 Moisture Availability

Germination trials were performed under control conditions, at one temperature (25°C) by two day lengths (0, 14 hrs) by six treatments. After two days, seed of all experimental treatments was transferred to uncovered petri dishes in which the vermiculite and filter paper had not been moistened. Seed was thus left to dehydrate for 0,1,2,4,7 or 14 days, after which the vermiculite was saturated, and the cover placed on the petri dish. Monitoring was continued for 42 days.

The influence of number of days dry on percent germination and median germination time was tested by regression (Sokal and Rohlf 1969 p 430). Barlett's chi-square test for homogeneity of variances indicated that an angular tranformation was not required on median germination time data before analysis. Regression lines were tested against each other for equality of slope (Sokal and Rohlf 1969 p 450).

A second germination trial was undertaken under control conditions. In the experimental treatment, vermiculite and filter paper were replaced by 5 mm of distilled water. The experiment was monitored for 30 days. Two way analysis of variance (Sokal and Rohlf 1969 p 310) was used to test the significance of differences in germination parameters attributable to species and treatment.

5.2.4 Seed Source

Seed of *A. littoralis* was collected from ten North Queensland sites, and of *A. torulosa* from eight. Germination trials were undertaken at three temperatures (15,25,35°C) and two day lengths (0,14 hrs). In some provenances, shortage of seed meant that replicates of less than 20 seed were necessary. Where a factor did not contribute significantly, the data were pooled for further analysis. Two way analysis of variance (Sokal and Rohlf 1969 p 310) was used to test the effects of light and temperature treatments on germination parameters. Seed weight was calculated from bulk weighing of samples of at least 500 seeds. A t-test (Sokal and Rohlf 1969 p 220) was used to test the significance of differences in seed weight between species.

5.2.5 Field Germination and Early Seedling Survivorship

Monthly searches for *Allocasuarina* seedlings bearing cotyledons were made of 1 ha stands of each of *A. littoralis* and *A. torulosa*, from July 1982 to July 1984. All seedlings were marked with a numbered peg. Distance to the trunk of the nearest potential maternal parent was recorded; differences between the two species were tested for significance using the Mann-Whitney U test (Siegel 1956 p 16).

Whether each seedling occurred in a canopy gap or beneath a canopy, and, if so, whether the canopy was of the same species and of a potential maternal parent was also recorded. Survivorship to April 1985 was calculated for seedlings in each environment.

To examine the effect of site characteristics on germination, an experiment was set up during a period of high natural seed germination at the Kirrama study site. Thirty-two plots were established, comprising the following combinations:

2 *Allocasuarina* sub-canopy species (*A. littoralis, A .torulosa*)
x 2 *Allocasuarina* sub-canopy densities (open, closed)
x 2 ground covers (natural, cleared)
x 2 seed species (*A. littoralis, A. torulosa*)
x 2 exposures to animals (protected, exposed).

One plot of each possible combination was established. The plots were grouped at four locations as determined by the sub-canopy: open *A. littoralis*, open *A. torulosa*, closed *A. littoralis* and closed *A. torulosa*. Sites were chosen so that only one species of *Allocasuarina* contributed to the litter layer, although litter from other plant genera was present.

Closed sub-canopies were those in which the crowns of *Allocasuarina* sp. were continuous, and open sub-canopies those in which the gaps between the crowns were larger than the crown area. Closed sub-canopy sites were located towards the ridge top, while open sub-canopy sites were on the mid-slope, as was typical of *Allocasuarina* stands in the area. Within each sub-canopy type, sites were selected with representative ground cover. In the closed sites, this was a litter layer consisting of a thick mat of *Allocasuarina* cladodes, 2 to 4 cm deep. In the open sites, it was a grass sward with sparse litter, mostly dead grass, *Eucalyptus* leaves and *Allocasuarina* cladodes. Natural ground cover was removed from half the plots.

Under each canopy type, to exclude animals, four 0.5 x 0.5 m plots were located within a 2 x 2 m exclosure of 1cm mesh wire netting, 20 cm high. Each of these plots was sprayed with 100 ml of Chlordane at the recommended concentration. Four exposed, unsprayed plots were established nearby. All plots were seeded with 100 fully developed, mature seed of one of the two species.

The experiment was set up on 4 April 1984 and monitored at approximately monthly intervals for 12 months. New germinants were marked with a labelled peg. Number of shoots and plant height were measured from 6 August 1984. A Biomass Index (B.I.) was calculated as a product of number of shoots and plant height (Chapter 7). Survivorship of seedlings was compared with Biomass Index at August 1984 Significance of differences in survivorship were tested using chi-squared test for independent samples (Siegel 1956 p175) on raw data. Percentage survivorship per month was calculated for each treatment.

Rainfall between each monitoring period was recorded at the weather station 500m away. To determine litter and soil moisture content in the zone influencing seedling growth, five litter and surface soil samples (10 x 10 x 2 cm) were collected from each of the four canopy types. These were weighed, dried to constant weight at 60°C and reweighed. Significance of canopy species and density to percent moisture of litter and soil were tested each month using analysis of variance with replication (Sokal and Rohlf 1969 p 302).

5.3 Results

5.3.1 Seed Development

Seven developmental stages were recognized in *A. littoralis*, and four in *A. torulosa* (Table 5.1). Although in both species seed appeared to darken with age, developmental stages were not directly comparable between species. Not all stages were represented in seedlots from each collection period. In *A. littoralis*, stage 1 was present only in the August seedlot, and an extra stage (6) was present in the November seedlot. In *A. torulosa*, more immature stages were present in the November seedlot. This was due to the seed being retained in least mature cones from the August collection. For both species, shortage of seed in some stages meant that fewer or smaller replicates were used for these stages (Table 5.1). In most replicates, germination commenced on day four or five, exceeded 50% on day six and was complete by day eight.

In *A. littoralis*, all seeds in the two palest seed stages collected in August were non-viable, while in the November seedlot, Stage 2 showed some viability (11.8%). Seed viability then increased in both seedlots with colour until Stage 5, and declined slightly in the later stages (Fig. 5.1). Changes in viability were significantly different between stages and month of collection up to Stage 4 (Table 5.2). A significant decline in viability was observed between the stage of maximum viability and the seed of darkest colour in November (5 vs 7; $t_s = 3.560$, d.f. 6, $P < 0.05$), but not in August (Table 5.2).

Table 5.1 Seed maturity classes present in *A. littoralis* and *A. torulosa* seed collected in August and November 1982. [a]Munsell Soil Colour Chart (1954).

			Collection Date			
			August (Seed Age 4 Months)		November (Seed Age 1 Month)	
Species	Seed Stage	Seed Colour[a]	No. of Replicates	Replicate Size	No. of Replicates	Replicate Size
A. littoralis	1	6/3	4	20	-	-
	2	5/6	4	10	2	8,9
	3	5/4	4	20	4	20
	4	4/4	4	20	4	20
	5	3/3	4	20	4	20
	6	3/2	-	-	4	20
	7	2.5/2	4	20	4	20
A. torulosa	1	5/6	-	-	2	10,11
	2	4/6	-	-	3	10,11,11
	3	3/4	4	20	4	20
	4	3/2	4	20	4	20

In *A. torulosa*, there was extremely low germination in the palest seed stage (Fig. 5.1). In the November seedlot, viability increased significantly as the seed darkened (Table 5.2). While there were no significant differences between the viability of the third colour stage of the August and November seedlots, the viability of the darkest seed stage collected in August was significantly lower than both that of the same stage in the November seedlot (Table 5.2), and that of the third stage of the August seedlot ($t_s = 4.235$, d.f. 6, $P < 0.01$).

Table 5.2 Significance of differences in seed viability between consecutive seed stages in *A. littoralis* and *A. torulosa*.

Species	Month	Stages	d.f.	t_s	P
A. littoralis	Aug.	4,5	6	3.189	<0.05
		5,7	6	1.691	n.s.
	Nov.	2,3	4	3.484	<0.05
		3,4	6	5.064	<0.01
		4,5	6	0.797	n.s.
		5,6	6	0.699	n.s
		6,7	6	1.980	n.s.
A. torulosa	Aug.	3,4	6	3.033	<0.05
	Nov.	1,2	3	1.625	n.s.
		2,3	5	5.870	<0.01
		3,4	6	3.643	<0.05

5.3.2 Storage Conditions

The seed of both *A. littoralis* and *A. torulosa* was little affected by the experimental storage conditions. Percent germination was not significantly affected by either storage temperature or storage humidity (Table 5.3). Mean percent germination of *A. littoralis* was 67.8%, and that of *A. torulosa* 82.5%. Median time to germination was significantly affected by both storage temperature and storage humidity, but the magnitudes of the differences were small, with no trends being evident (Table 5.4). The variation may have occurred because seed in each envelope had been slightly but uniformly affected by sulphuric acid contamination. Mean median time to germination of *A. littoralis* was 6.1 days, and that of *A. torulosa* 5.2 days. These statistics compare favourably with those of fresh seed germinated under control conditions as described in the preceding experiments.

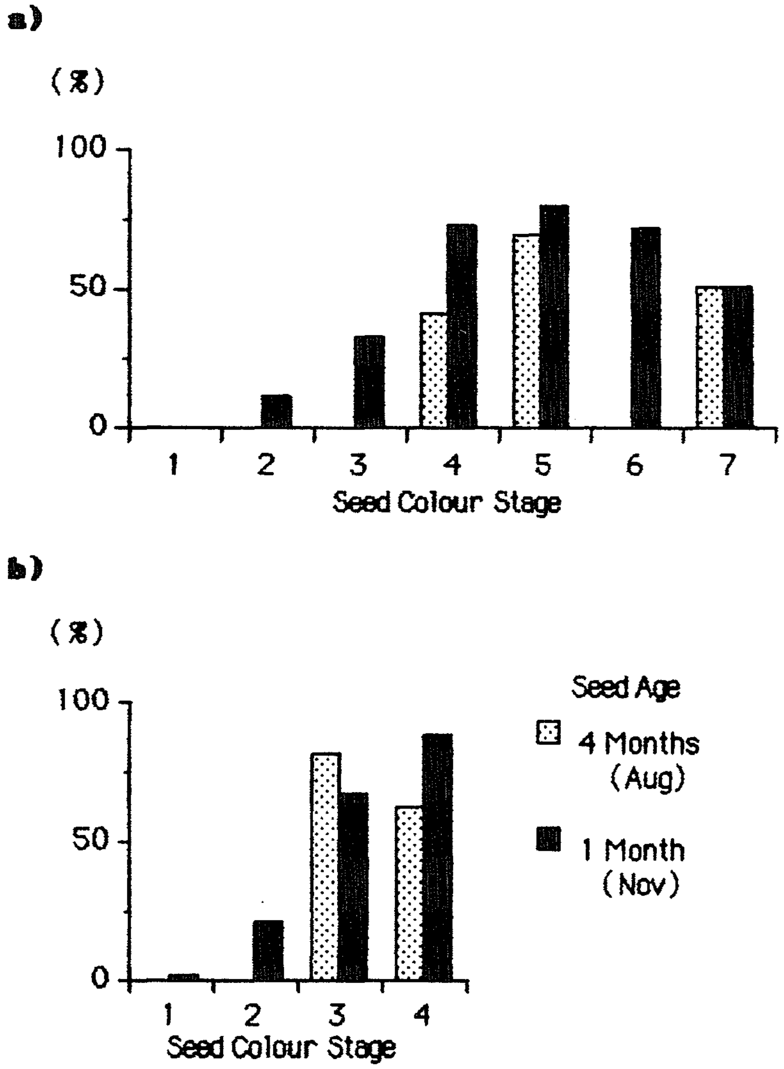


Fig. 5.1 **Percent viability of *A. littoralis* and *A. torulosa* seed in relation to seed colour.**

a) *A. littoralis*, **b)** *A. torulosa*.
For significance of differences, refer to Table 5.2.

Table 5.3 **Percent germination after storage of seed under different temperatures (Temp.) and relative humidities (R.H.).**

[1] All 50% R.H. treatments excluded from analysis.

[2] All 18°C treatments excluded from analysis.

n.s. $P > 0.05$.

Species		*A. littoralis*				Temp.	
Temp. (°C)	0	18	24	30		^1F_s	^2F_s
R.H. (%)					(d.f.	2,27	1,24)
25	71.9	68.0	76.4	85.9		0.044	0.015
50	69.0	-	69.0	73.0		n.s.	n.s.
75	69.1	61.4	67.9	75.5			
R.H.						Interactions	
					(d.f.	4,27	3,24)
^1F_s (d.f. 2,27)		0.172	n.s			0.872 n.s	
^2F_s (d.f. 3,24)		0.525	n.s.				1.138 n.s.

Species		*A. torulosa*				Temp.	
Temp. (°C)	0	18	24	30		^1F_s	^2F_s
R.H. (%)					(d.f.	2,27	1,24)
25	78.9	78.0	74.6	81.3		0.656	0.980
50	74.4	-	81.8	77.1		n.s.	n.s.
75	73.8	76.9	66.3	79.6			
R.H.						Interactions	
					(d.f.	4,27	3,24)
^1F_s (d.f. 2,27)		0.583	n.s			0.729 n.s	
^2F_s (d.f. 3,24)		1.057	n.s.				0.146 n.s.

Table 5.4 **Median germination time (days) after storage of seed under different temperatures and relative humidities.**

For explanation of superscripts see Table 5.3.

n.s. $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	*A. littoralis*					Temp.	
Temp. (°C)	0	18	24	30		^1F_s	^2F_s
R.H. (%)					(d.f.	2,27	1,24)
25	6.6	6.8	5.9	6.4		30.257	13.217
50	5.7	-	7.0	5.9		***	**
75	4.6	7.4	5.7	5.5			
R.H.						Interactions	
					(d.f.	4,27	3,24)
^1F_s (d.f. 2,27)		6.953	**			9.552 ***	
^2F_s (d.f. 3,24)		13.972	***				9.870 ***

Species	*A. torulosa*					Temp.	
Temp. (°C)	0	18	24	30		^1F_s	^2F_s
R.H. (%)					(d.f.	2,27	1,24)
25	5.1	5.6	5.0	5.5		4.008	1.306
50	4.6	-	5.0	4.9		*	n.s.
75	5.1	6.1	4.9	5.7			
R.H.						Interactions	
					(d.f.	4,27	3,24)
^1F_s (d.f. 2,27)		3.728	*			1.476 n.s	
^2F_s (d.f. 3,24)		8.034	***				0.799 n.s.

5.3.3 Moisture Availability

No relationship was found between number of days dry and percent germination in *A. littoralis* for either the dark treatment (F_s = 1.894, d.f. 1,18, $P > 0.05$), the light treatment (F_s = 1.355, d.f. 1,18, $P > 0.05$) or when results from the two treatments were combined (F_s = 2.8094, d.f. 1,42, $P > 0.05$). When percent germination in *A. torulosa* was compared with number of days dry, for each light condition separately, a significant relationship was not found (Table 5.5). However, when data from the two light treatments were combined, a significant regression was found which indicated percent germination was reduced by dehydration (Table 5.5).

Table 5.5 Relationship between number of days dry and percent germination in *A. torulosa*.

G - percent germination, d - number of days dry.

Light (hrs)	Regression	d.f.	F_s	P
0	$\mathrm{asin}\sqrt{G} = 1.2358 - 0.0171\,d$,	1,4	5.747	n.s
14	$\mathrm{asin}\sqrt{G} = 1.1692 - 0.0092\,d$,	1,4	7.062	n.s.
combined	$\mathrm{asin}\sqrt{G} = 1.2025 - 0.0132\,d$,	1,4	8.359	< 0.05

Linear relationships were found between number of days dry and median germination time for both species and light conditions (Table 5.6). There was no difference between species or light condition in the reduction caused by dehydration (F_s - 1.3035 d.f. 3,16 $P > 0.05$). Median germination was delayed by approximately one day for every dry day.

Table 5.6 Relationship between number of days dry and median germination time.

t = median germination time, d = number of days dry.

Species	Light (hrs)	Regression	d.f.	F_s	P
A. littoralis	0	t = 6.1586 + 1.0517 d	1,4	782.208	< 0.001
	14	t = 7.4565 + 0.9120 d	1,4	34.542	< 0.01
A. torulosa	0	t = 5.1797 + 1.0070 d	1,4	2737.699	< 0.001
	14	t = 5.4388 + 1.1381 d	1,4	978.337	< 0.001

Seeds of both *A. littoralis* and *A. torulosa* floated on the free water used in the second moisture availability experiment, and germination progressed normally. In *A. littoralis*, percent germination in the control was 61.7% and that in the wet treatment 61.4%, and median germination time was 4.6 days and 4.7 days respectively. In *A. torulosa*, percent germination in the control was 79.3% and that in the wet treatment 75.3%, and median germination time was 4.1 days and 3.5 days respectively. Although the differences between species were significant for both percent germination (F_s = 7.293, d.f. 1,12, $P < 0.05$) and median germination time (F_s = 13.868, d.f. 1,12, $P < 0.01$), differences between treatments were not significant for either variable (percent germination: F_s = 0.160, d.f. 1,12, $P > 0.05$; median germination time: F_s = 0.917, d.f. 1,12, $P > 0.05$).

5.3.4 Seed Source

Mean seed weight in *A. torulosa* was approximately twice that in *A. littoralis* (Table 5.7; t_s = 7.749, d.f. 17, $P < 0.001$). Percent germination was extremely variable between provenances, ranging from 11.4% to 73.5% in *A. littoralis*, and from 54.3% to 78.7% in *A. torulosa* (Table 5.7, Fig. 5.2). In all provenances of *A. littoralis* tested, light and temperature conditions did not significantly affect percent germination, and in only one provenance (Julatten) was a significant interaction between light and temperature detected. In six of the eight *A. torulosa* provenances tested, percent germination was not affected by light or temperature, nor was the interaction of these parameters significant. In the two provenances where a significant effect was detected (Gillies and Kirrama), this was due to a reduced value in only one treatment.

In eight provenances of *A. littoralis*, both temperature and light significantly affected median germination time, with the interaction of temperature and light being significant in three of these provenances (Table 5.8). In the remaining four provenances (including Victoria), only temperature was significant. Two of these provenances were from high altitude sites (Fox 2 and Atherton 3), while the third was from a high rainfall lowland site (Wallaby). No single geographic or climatic parameter differentiated these sites from those at which light was also significant.

In seven of the eight provenances of *A. torulosa* tested, only temperature significantly affected median germination time. In the remaining provenance (Wongabel 2), both temperature and light were significant (Table 5.8). However, the magnitude of difference between light treatments in this provenance was consistently less than 0.7 days.

Table 5.7 Percent germination and seed weight for provenances of *A. littoralis* and *A. torulosa*.

[a] 24 replicates at 3 temperatures and 2 light regimes.

Species	Provenance (Site no.)	Replicate Size[a]	Percent Germination	Seed Weight (mg)
A. littoralis	Atherton 1 (6)	7	73.4	1.85
	Boolbun 1 (4)	20	44.8	1.47
	Coolgara (9)	20	40.5	1.95
	Fox 1 (15)	20	48.7	2.38
	Holdcroft (8)	20	71.5	1.51
	Home Rule (3)	20	49.5	1.85
	Isabella (1)	20	51.2	1.84
	Julatten (5)	10	62.5	1.28
	Kirrama (11)	20	64.7	1.73
	Sullivan (12)	20	41.2	1.78
	Wallaby (2)	8	11.4	1.00
	Victoria	20	46.1	-
	Mean			1.61
A. torulosa	Atherton 3 (C)	10	54.3	3.03
	Boolbun 2 (A)	20	70.7	2.90
	Cardstone (G)	20	75.7	4.22
	Fox 2 (M)	7	55.4	2.86
	Gillies (B)	20	64.8	3.46
	Kirrama (H)	20	70.0	2.79
	Wongabel 1 (D)	20	78.7	3.00
	Wongabel 2 (E)	13	89.2	3.80
	Mean			3.26

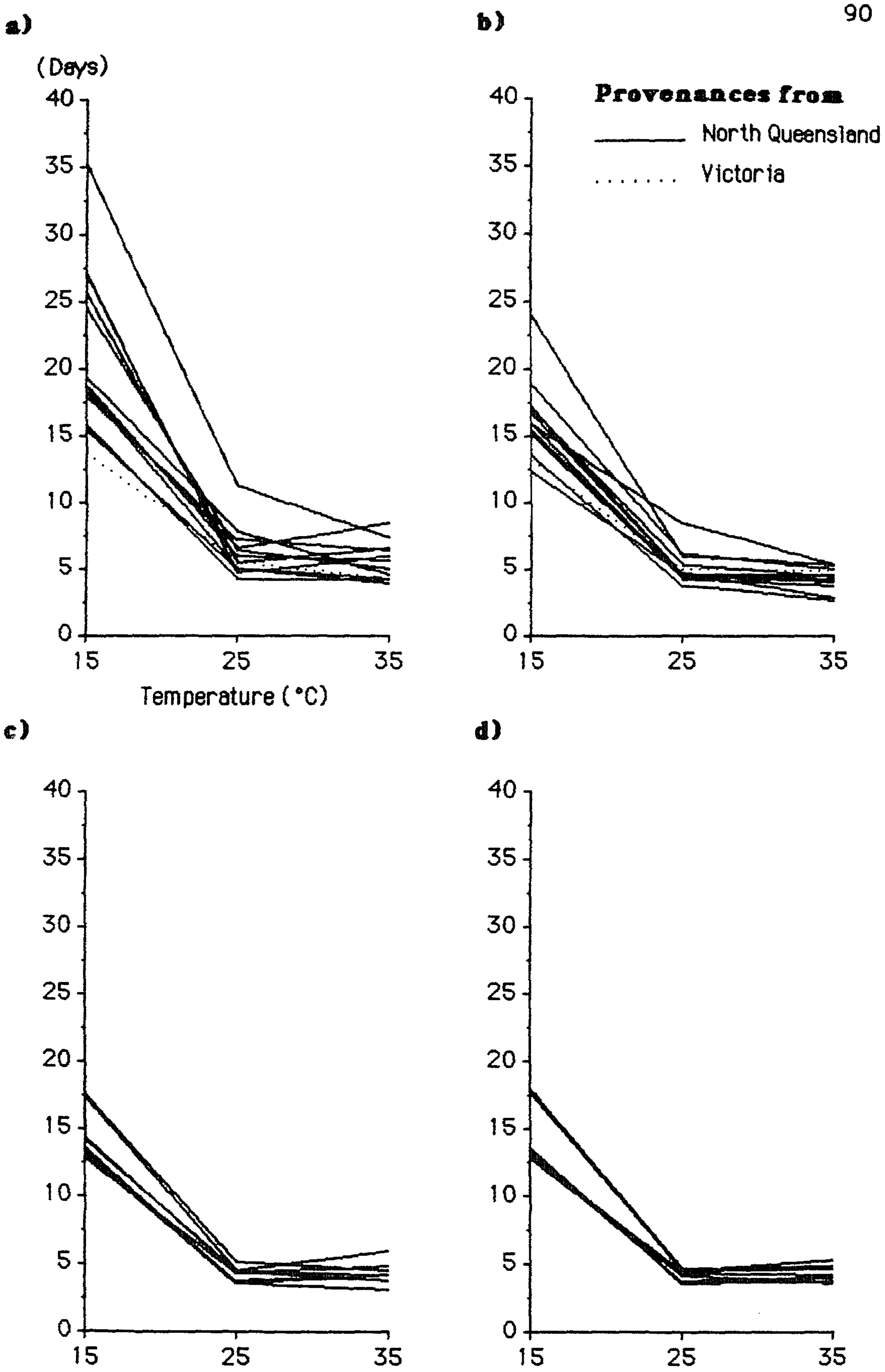


Fig. 5.2 Median germination time of *Allocasuarina* provenances.
A. littoralis - day length: **a)** 0 hours, **b)** 14 hours,
A. torulosa - day length: **c)** 0 hours, **d)** 14 hours.

Table 5.8 F_s values indicating the significance of the effects of temperature and light on median germination time in *A. littoralis* and *A. torulosa*.

n.s. $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	Provenance	Temp (d.f. 2,18)	Light (d.f. 1,18)	Interaction (d.f. 2,18)
A. littoralis	Atherton 1	59.479 ***	0.427 n.s.	1.321 n.s.
	Boolbun 1	567.256 ***	26.745 ***	1.867 n.s.
	Coolgara	2154.968 ***	68.157 ***	9.078 **
	Fox 1	460.069 ***	1.890 n.s.	1.455 n.s.
	Holdcroft	293.110 ***	7.651 **	0.354 n.s.
	Home Rule	88.976 ***	12.227 **	4.569 *
	Isabella	500.919 ***	19.635 ***	18.085 ***
	Julatten	47.567 ***	6.705 *	0.966 n.s.
	Kirrama	134.876 ***	11.004 **	1.008 n.s.
	Sullivan	100.979 ***	18.894 ***	1.090 n.s.
	Wallaby	32.811 ***	2.433 n.s.	0.590 n.s.
	Victoria	40.004 ***	0.025 n.s.	0.590 n.s.
A. torulosa	Atherton 3	107.569 ***	0.013 n.s.	0.010 n.s.
	Boolbun 2	2008.264 ***	0.960 n.s.	2.686 n.s.
	Cardstone	240.666 ***	0.260 n.s.	1.501 n.s.
	Fox 2	282.325 ***	1.330 n.s.	0.622 n.s.
	Gillies	917.772 ***	0.209 n.s.	4.130 n.s.
	Kirrama	591.978 ***	3.098 n.s.	2.812 n.s.
	Wongabel 1	1417.533 ***	0.692 n.s.	1.156 n.s.
	Wongabel 2	2129.645 ***	4.801 *	1.156 n.s.

5.3.5 Field Germination and Early Seedling Survivorship

The first natural germinants were recorded at Kirrama in January 1984 after a period of heavy rain. All natural germination occurred between January and April. A total of 55 seedlings of *A. littoralis* and 101 seedling of *A. torulosa* was recorded. 88% of the *A. torulosa* seedlings were located under a single fecund female of that species. A further 8% were located under another fecund female. In contrast, the *A. littoralis* seedlings were well dispersed, rarely occurring in groups of more than three. However, median distance to the trunk of the nearest potential maternal parent did not reflect the distribution of seedlings and was significantly greater for *A. torulosa* than for *A. littoralis* (2.6 vs 2.0 m, $U = 2074$, $P < 0.01$).

No seedlings of one *Allocasuarina* species were found under the canopy of the other. All seedlings of *A. torulosa* were found directly beneath the canopy of a potential maternal parent. In contrast, only 48% of *A. littoralis* seedlings were found under a canopy of that species, 35% beneath a potential maternal parent. The remaining 52% were found in canopy gaps and along the roadside, where there was no canopy.

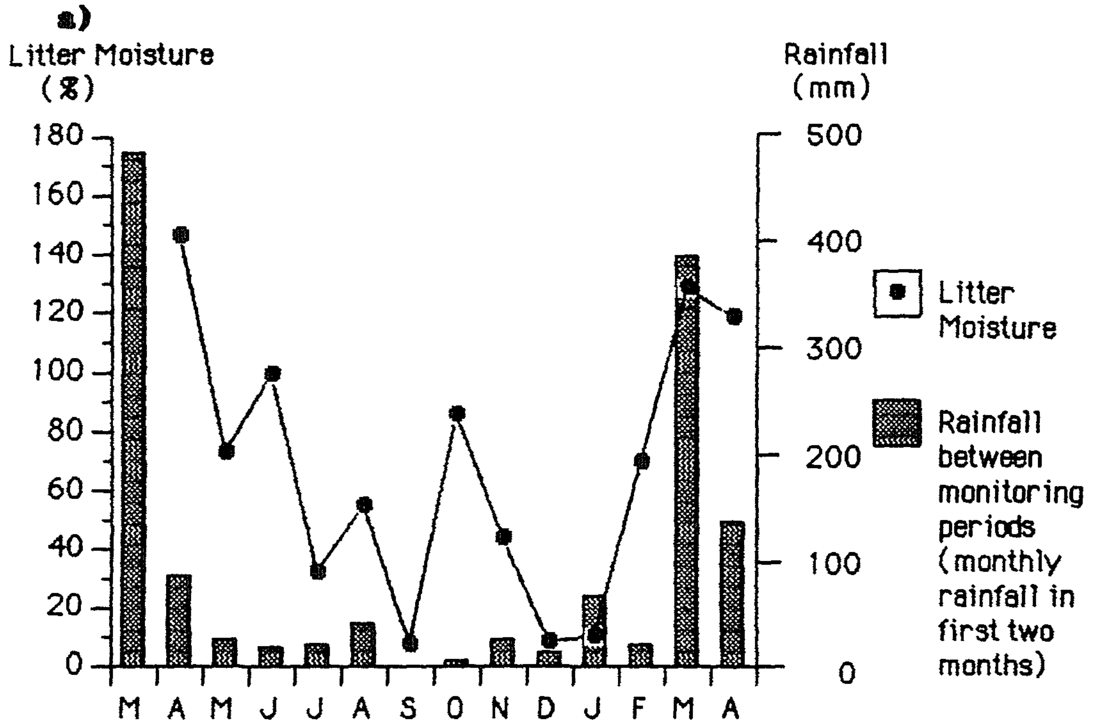
In April 1985, 1.0% of *A. torulosa* seedlings were still alive, compared to 53.7% of *A. littoralis* seedlings. For the latter species, 26.9% of seedlings occurring under the canopy were still alive, compared to 64.3% of seedlings in a canopy gap or open environment.

Although there were heavy falls of rain in the months preceding the field germination experiment, high rainfall did not occur again for 12 months (Fig. 5.3). Within this period, monthly falls exceeding 30 mm occurred only twice, with no rain at all falling in September 1984.

There were no significant differences in the litter moisture values between sub-canopy species or densities. Therefore, litter moisture data were grouped together each month (Fig. 5.3). Sub-canopy density contributed significantly to soil moisture, between May and October, 1984, with higher values under the open sub-canopy. Sub-canopy species did not significantly affect soil moisture. Therefore, soil moisture values of the same sub-canopy density were grouped together (Fig. 5.4). Both litter and soil moisture declined, with some fluctuations, from high values in April to their lowest values in September. They remained generally low between September 1984 and February 1985, peaking with higher rainfall in March/April 85. Fluctuations about these trends appeared to be due to recent rainfall, rather than reflecting consistently higher levels through the month.

Germination was greatest in the first month after seeding and declined each month, until there was no germination in the fifth month (Figs 5.4, 5.5). Germination which occurred in the twelfth month was ignored, as the seed was probably derived from natural seed-fall.

In the protected plots, germination was similar in both species (Table 5.9), except in the open cleared plots, where germination of *A. littoralis* was over three times that of *A. torulosa*. Otherwise, germination was highest in the open plots with ground cover intact and lowest in the closed plots from which the ground cover had been cleared.



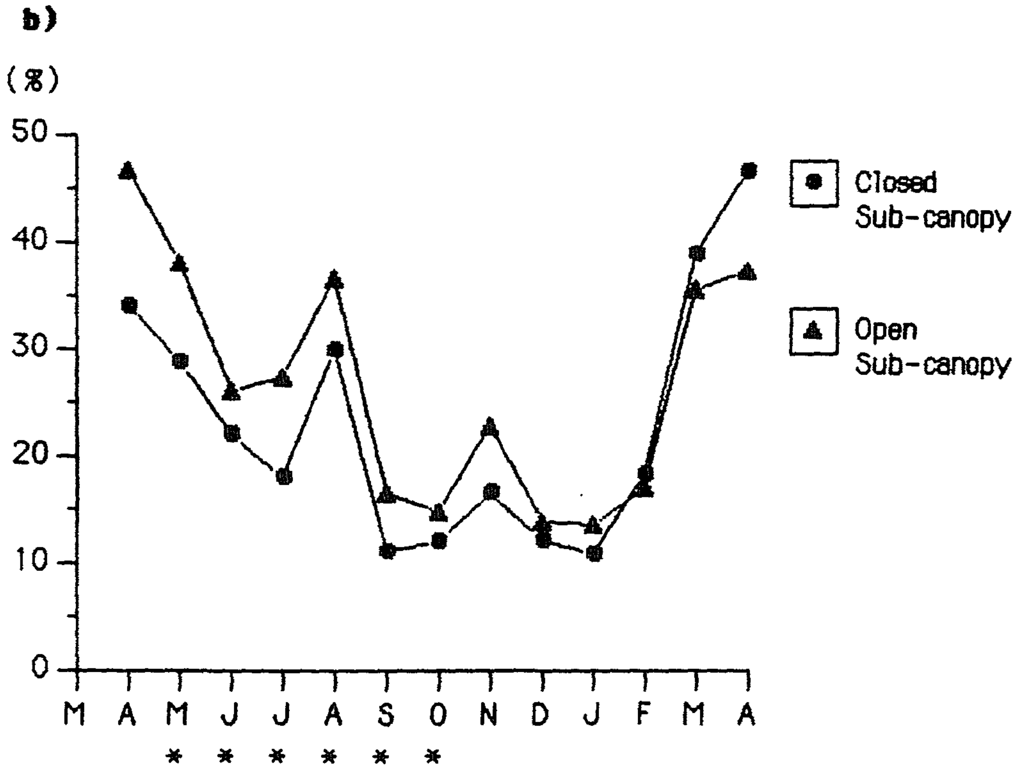


Fig. 3.3. Moisture Statistics Kirrama - March 1984 to April 1985.
a) Rainfall and soil moisture, b) Soil moisture.
Asterisks indicate the months in which moisture levels differ significantly between sub-canopy type.

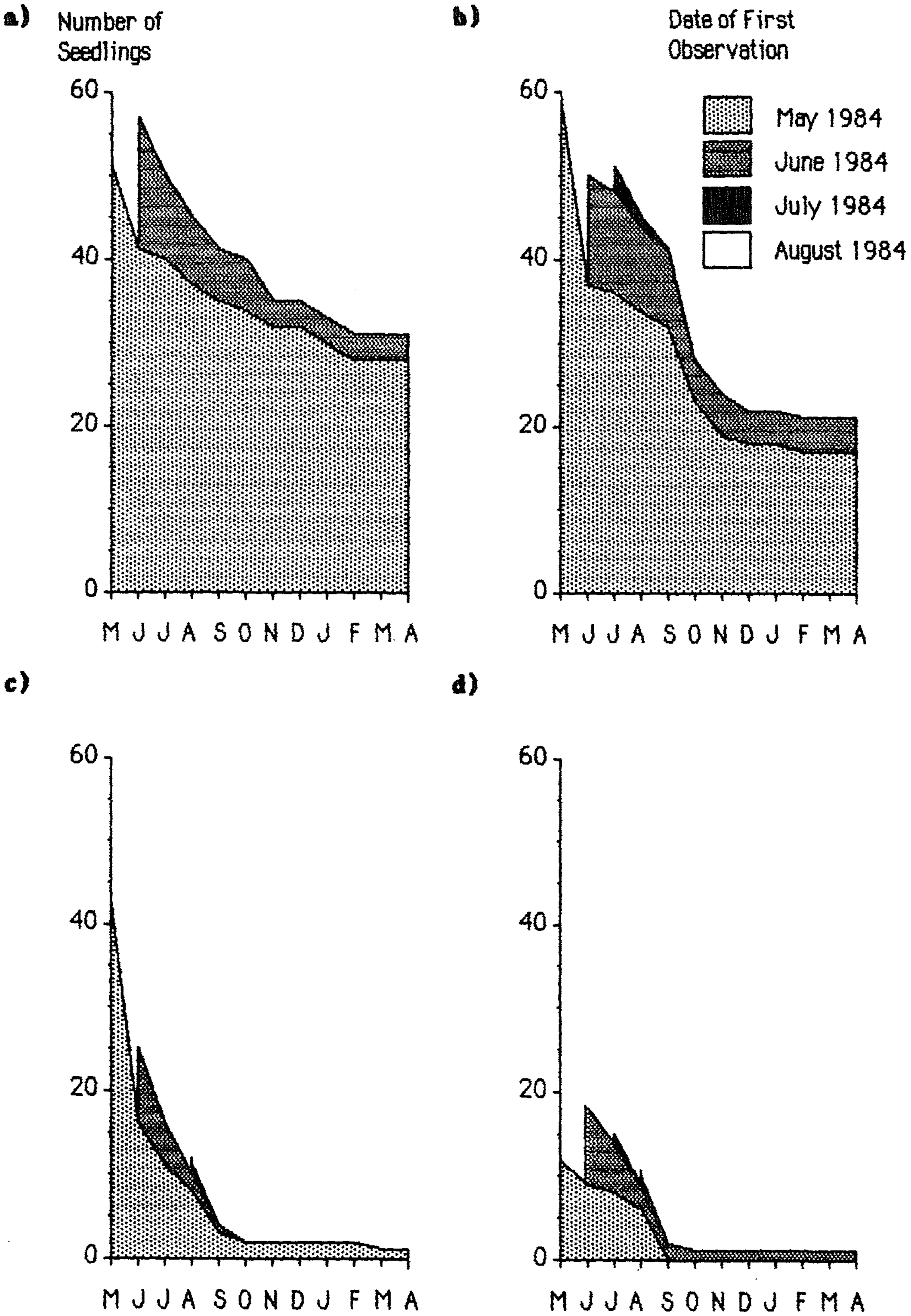


Fig. 5.4 Survivorship of *A. littoralis* seedlings in the field.
Open canopy: **a)** ground cover intact, **b)** ground cover removed,
Closed canopy: **c)** ground cover intact, **d)** ground cover removed.

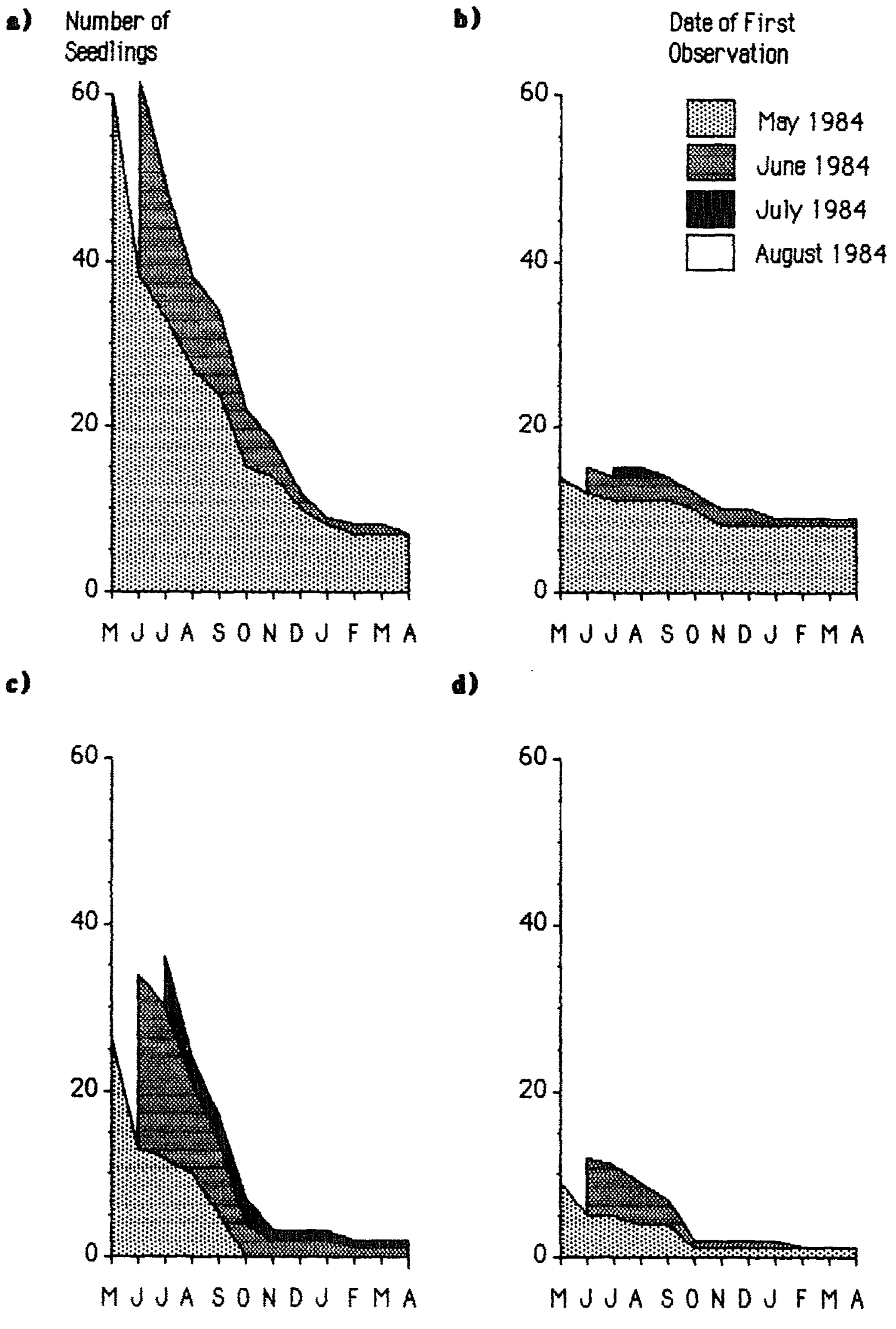


Fig. 5.5 Survivorship of *A. torulosa* seedlings in the field.
Open canopy: **a)** ground cover intact, **b)** ground cover removed,
Closed canopy: **c)** ground cover intact, **d)** ground cover removed.

Table 5.9 Germination of seedlings in experimental plots between April and August 1984.

L = *A. littoralis*, T = *A. torulosa*, S = Sprayed and caged, C = Control.

Treatment:	S	S	S	S	C	C	C	C
Sub-canopy species:	L	L	T	T	L	L	T	T
Seed species:	L	T	L	T	L	T	L	T
Open Sub-canopy								
Ground cover intact	47	50	20	34	1	1	0	6
Ground cover cleared	32	3	43	15	5	0	0	0
Closed Sub-canopy								
Ground cover intact	23	35	30	21	0	1	0	0
Ground cover cleared	13	11	10	1	6	5	0	0

Germination in the exposed plots was low, with only one seedling surviving to the end of the monitoring period (Tables 5.9, 5.10). Low survivorship in these plots was exacerbated by disturbance in early August caused by cows, which trampled and uprooted many seedlings. Seedlings in the exposed plots are thus excluded from the survivorship discussions. Seedlings in the protected plots were not damaged.

Although there were differences in the numbers germinating and proportion surviving under different sub-canopy species, mortality patterns were similar. Therefore, to simplify presentation, otherwise similar plots under different sub-canopy species were bulked to produce cohort survivorship curves (Figs 5.4, 5.5). Mortality of *A. littoralis* seedlings levelled off in September/ October, while in *A. torulosa*, the number of surviving seedlings decreased steadily until the onset of rains in January. Of the seedlings germinating in the protected plots, 25%

of *A. littoralis* and 12.3% of *A. torulosa* seedlings survived to the end of the monitoring period. Seedlings of *A. littoralis* germinating in the first month were more likely to survive than later germinants (28.8% vs 14.29%, $\chi^2 = 4.63$, d.f. 1, $P < 0.05$). While survivorship of *A. torulosa* seedlings germinating in the first month (15.2%) was higher than that of later germinants (7.6%), this difference was not significant ($\chi^2 = 2.21$, d.f. 1, $P > 0.05$).

Table 5.10 Percent survival of seedlings in experimental plots to April 1985.
For explanation of abbreviations see Table 5.9.

Treatment:	S	S	S	S	C	C	C	C
Sub-canopy species:	L	L	T	T	L	L	T	T
Seed species:	L	T	L	T	L	T	L	T
<u>Open Sub-canopy</u>								
Ground cover intact	57.4	14.0	20.0	0.0	0.0	0.0	0.0	0.0
Ground cover cleared	18.8	0.0	34.9	56.3	20.0	0.0	0.0	0.0
<u>Closed Sub-canopy</u>								
Ground cover intact	4.3	5.7	0.0	0.0	0.0	0.0	0.0	0.0
Ground cover cleared	7.7	9.1	0.0	0.0	0.0	0.0	0.0	0.0

The main differences between survivorship of *A. littoralis* and *A. torulosa* seedlings occurred in the open plots where the ground cover had been left intact. In these plots germination had been equally high, but survivorship of *A. littoralis* (46.3%) was considerably higher than in *A. torulosa* (8.3%). In the open, cleared plots, survivorship of *A. torulosa* was approximately twice that of *A. littoralis*. However, as germination was three times higher in *A. littoralis*, a greater number of *A. littoralis* seedlings survived to the end of the monitoring period in these plots. Survivorship was consistently low in all closed sites. While under the *A. littoralis* sub-canopy, there was higher survivorship of both species in the plots in which ground cover was intact, than in which it had been removed, the reverse was true under *A. torulosa*

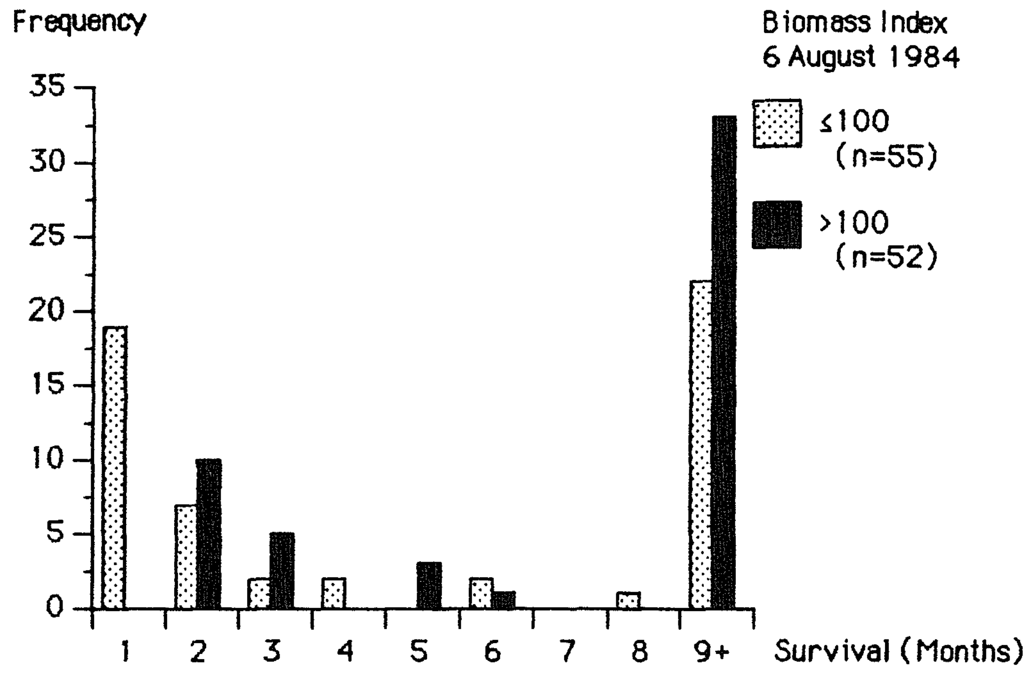
Biomass Index size classes in August 1984 influenced subsequent survival. Those seedlings with B.I. $>$ 100 were likely to survive longer than smaller seedlings (Fig. 5.6), with a larger proportion surviving to the end of the monitoring period. These differences were more pronounced, although statistically less significant, in *A. torulosa* (35% vs 5%, $\chi^2 = 5.89$, d.f. 1, $P < 0.05$) than in *A. littoralis* (63% vs 44%, $\chi^2 = 11.25$, d.f. 1, $P < 0.001$).

5.4 Discussion

5.4.1 Seed Maturation

As seed of both species darkens with maturation, classification of seed into colour stages is artificial, and it is unlikely that seed of the same colour collected at different times will be at exactly the same developmental stage. Changes in seed viability in *A. littoralis* suggest that seed of the November seedlot was in fact more developed than that of the same colour August seedlot, having higher viability in the least mature seed stages. This seems a more likely explanation for the differences between months, than a decline in viability with time after collection, as a similar decline was not noted in the most mature seed stages, and seed stored for six months under various temperatures and humidities still exhibited high viability (Section 5.3.2).

a)



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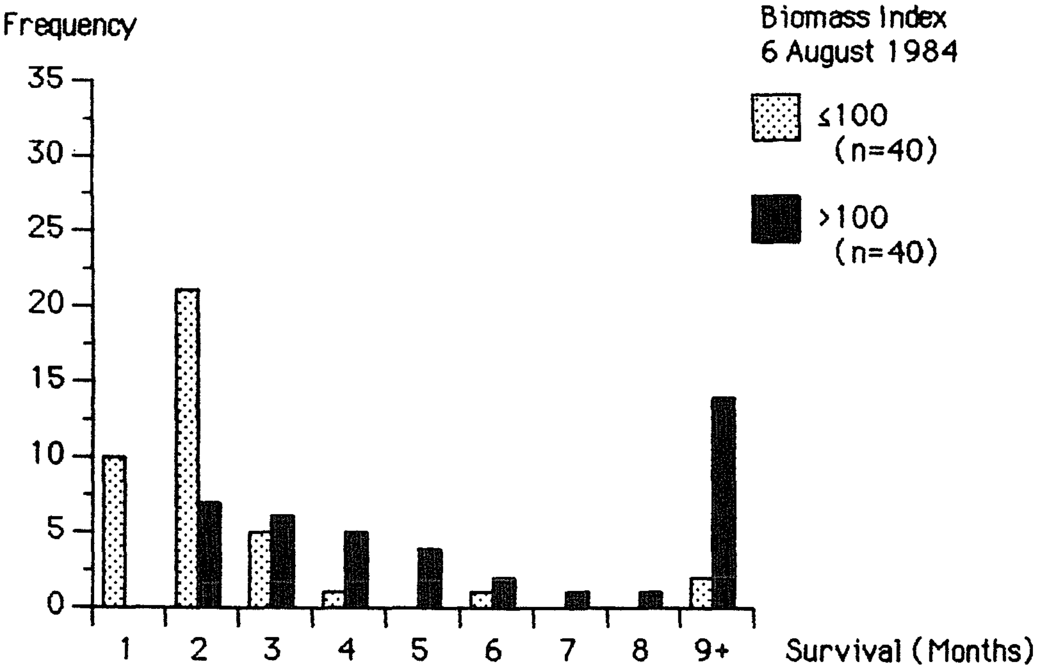


Fig. 5.6. **Survival time of seedlings with a Biomass Index greater than and less than 100 on August 6 1984.**

a) *A. littoralis* **b)** *A. torulosa.*

The decline in viability of the darker stages of *A. littoralis* may indicate a degradation of seed within the cone after maturity is reached. However, any decline does not appear to continue after seed release (Section 5.3.2). The decline does not appear to be caused by hardening as occurs in Acacias (Cavanagh 1980), as it affects only a small percentage of seeds.

Although most seed of *A. littoralis* appears to be released from the canopy within 12 months of flowering, some may be retained for more than one year (Chapter 4). Thus the mature seed stage present in both seedlots of *A. littoralis* may be derived from an earlier flowering season than the less mature seed. Factors affecting viability, such as resource availability and parasite abundance (Andersen 1985b; Harper 1977) may not have been comparable between the two seasons. Hence, the viability of the darkest seed stage may not be directly comparable to that of the other seed stages. Viability of developing *A. torulosa* seed also increases as the seed darkens. That a decline in viability in the last stage was found only in the August seedlot, again suggests that seed viability varies between flowering seasons.

Thus, not all seed shed from the cones of *A. littoralis* and *A. torulosa* will be viable, and as prematurely shed seed has the lowest viability, it will be unlikely to contribute to the seed pool. In contrast to other studies of germination in the Casuarinaceae (Turnbull and Martenz 1982), no evidence was found here for after-ripening being required in either species, as percent germination was no higher in seed which had been stored for four months.

5.4.2 Storage Conditions

The seed of tropical members of the Casuarinaceae has been reported to deteriorate if not held under special storage conditions (Halos 1983; Turnbull and Martenz 1982). However, no reference has been made to the longevity of tropical provenances of the species studied here, and it has been suggested that greater seed viability may be retained in *Allocasuarina* spp. than in other members of the family (Barlow 1983; Turnbull and Martenz 1972). The results of this experiment show that neither storage temperature nor humidity are directly responsible for seed deterioration in *A. littoralis* or *A. torulosa*. However, it seems likely that seed stored in a warm, humid tropical climate may be more prone to pathogenic infection reducing its viability. This is supported by a study by Jones (1967), in which *Casuarina equisetifolia* seed was stored at various moisture contents for two years without loss of viability. The small size of the seed bank beneath stands of *A. littoralis* and *A. torulosa* may be due to such pathogenic attack (Chapter 4).

5.4.2 Moisture Availability

The temporary arrest of germination by dehydration has been termed hydropedesis (Watt 1978) and has been observed in both Australian and exotic pasture species (Gramshaw 1972; Watt 1978, 1982). From this study, it is evident that hydropedesis occurs in *A. littoralis* and *A. torulosa*, with the delay in germination persisting only as long as water is withheld from the seed, and may therefore be a more common phenomena than previously thought. The ability for such seed to germinate lasts for at least two weeks, with only a slight reduction in the viability of *A. torulosa*. The hydropedectic ability of these species compares favourably with those described by Watt (1982), who found that cessation and recommencement of germination is determined by threshold water potentials (Watt 1982).

As hydropedesis will protect seed from death only until radicle emergence, it will prevent germination after periods of moisture availability which are shorter in duration than the time to germination. The longer the initial period of moisture availability, the more seed will have commenced germination, and therefore be exposed to desiccation. Therefore, the more protracted the germination response, the greater will be the protection of the seed bank. A similar conclusion about the function of protracted germination was made by Ladiges (1974a) and Mayer and Poljakoff-Mayber (1982). Thus the most significant effect will be on seed of *A. littoralis* which is in the dark, as would be the case with buried seed, or at low temperatures. Where the initial moist period has been long enough to cause germination of all *A. torulosa* seed, but not of *A. littoralis*, and dehydration is severe enough to cause seedling death, there will be no successful recruitment from the *A. torulosa* seed bank until it is replenished by seed-fall. Thus *A. littoralis* seed is predicted to be more successful than *A. torulosa* in environments where moisture availability is intermittent. Where moisture availability is continuous, seed which has germinated rapidly will have a competitive advantage over later germinants (Harper 1977). As germination of buried *A. littoralis* seed is protracted, it will have a disadvantage in comparison to *A. torulosa* and exposed *A. littoralis* seed in such environments.

Authors who have previously reported hydropedesis, have commented that germination of hydropedectic seed proceeds at a faster rate than that of untreated seed (Gramshaw 1972; Watt 1974, 1978). This study indicates that after two days imbibition followed by periods of moisture stress of up to 14 days, the delay in germination is only equal to the number of days during which moisture was withheld. This suggests that the developmental stage reached after two days imbibition is not reversible. While germination may appear to be faster, when the duration of the initial period of imbibition is taken into account, germination takes the same time as in seed for which germination has not been interrupted. Thus while seed is often considered to be dormant until the emergence of the radicle, this may not always be the case, and can not be assumed without internal examination of the seed.

The floating of seed permits germination of *A. littoralis* and *A. torulosa* where there is standing water by maintaining the moisture gradient essential to germination in most species (Cook 1980). This indicates that imbibition of seed will commence as soon as moisture availability reaches required levels, and that seed is likely to float out of water-logged environments and will be ready to establish once it has been stranded. However, sensitivity to salinity (Clemens *et al.* 1983; El-Lakany and Luard 1982) will prevent germination in saline environments.

Germination tests are usually undertaken on germination pads or, as in the present study, on a bed of vermiculite overlain by filter paper in a petri dish, and effort is made to maintain moisture availability at specific levels (Justice 1972). The floating of seed in dishes of distilled water may prove to be a more convenient method of testing seed germination in the Casuarinaceae, producing comparable germination statistics to those undertaken under more standard conditions.

5.4.4 Seed Source

The main difference in germination characteristics between provenances of *A. littoralis* and *A. torulosa* were the differences between seed viability. Factors affecting seed viability, resource availability (Stephenson 1981) and abundance of seed parasites (Andersen 1985b), will vary from season to season, as well as between sites, and even between neighbouring trees (Badran and El-Lakany 1978). Therefore, little can be concluded from the variation in the viability of different provenances, without repeated sampling. However, the low variation in germination response between provenances of *A. torulosa* may reflect the lower genetic variability in this species than in *A. littoralis* (Barlow 1958, 1959a).

Optimum germination temperatures within the range of 25 to 35°C, are consistent with germination occurring during the northern wet season. The slower germination recorded at 15°C is likely to prevent germination during the dry season, except during periods of extended rainfall, when probability of seedling survival will be high. In some provenances of *A. littoralis* slow germination should ensure that some seed will remain viable within the soil-stored seed bank, after short periods of moisture availability. This again makes *A. littoralis* more suited to less predictably moist environments than is *A. torulosa*. Burial of seeds may be caused by litter fall, disturbance by animals or rain splash, especially in lighter textured soils, and will afford the seed protection from predators (Harper 1977; Wellington and Noble 1985b).

Delayed germination in buried seed in response to dark conditions, again gives many provenances of *A. littoralis* protection against depletion of the seed pool by episodes of rain which are not sustained.

5.4.5 Field Germination and Early Seedling Survivorship

While survivorship of seedlings of a single species increases with seed size (Schaal 1980; Harper 1977), larger seed size in *A. torulosa* than in *A. littoralis* was not reflected in the relative survivorship of seedlings in the field. Higher germination for *A. littoralis* contrasts with the slightly higher seed viability and faster germination rate of *A. torulosa* seed observed elsewhere in this chapter, and may be a result of intermittent moisture availability. The advantage of early germination (Ross and Harper 1972) is emphasized here, with greater survivorship of *A. littoralis* seedlings germinating in the first month, than of later germinants. That significant differences were not also observed in *A. torulosa* is probably a function of the overall low survivorship in this species.

While the restriction of *A. torulosa* seedlings to under the parent canopy could initially be interpreted as indicating an intolerance of open sites in this species, in comparison to *A. littoralis*, whose seedlings are more frequently found in the open, germination trials here showed greater survival of seedlings of both species in open vegetation. Seedling distributions are thus simply a product of seed-fall patterns (Chapter 4). However, that relative survival of naturally occurring seedlings did reflect that of seedlings under experimental conditions, does suggest that higher survivorship of *A. littoralis* seedlings than of *A. torulosa* seedlings.

Low seed germination in the unprotected plots confirms the importance of seed predators in depletion of the seed bank (Chapter 4). However, as mortality in the initial months was extremely high, monthly intervals between observations may have resulted in an underestimate of the numbers of *A. torulosa* germinants. Low apparent germination in the plots from which the ground cover had been cleared may again reflect low survivorship to the first seedling count. Both seeds and seedlings in these plots would have been exposed to dehydration by evaporation, which could kill young germinants, but may also have arrested germination. Greater germination of *A. littoralis* in these plots again suggests this species is better adapted to dry sites than is *A. torulosa*.

The lower moisture level in closed plots compared to the open plots by the first seedling count may have been due to position on the slope, as dense sub-canopies were restricted to the ridge top. However, consumption of water by existing vegetation may also have been involved (c.f. Bowman and Kirkpatrick 1985b). In either case, low moisture availability may have been responsible for the low number of germinants recorded in closed plots.

Survivorship patterns again suggest that *A. littoralis* is better adapted to drier sites, with a large proportion of the seedlings surviving an extremely dry year. Low survivorship in the unprotected plots highlights the hazards posed to seedlings by herbivores and trampling. Low survivorship in the closed, unprotected plots may have been contributed to by crushing beneath heavy litter-fall, or shifting of the litter layer.

5.4.6 Litter Effects

Allelopathy has often been suggested as a cause for vegetation patterns. While the evidence for this is sometimes compelling (Bonner 1950; del Moral *et al.* 1978), there have been several instances where germinating seed has been shown to be sensitive to foliage leachates only in higher concentrations than occur naturally in the field (Stowe 1979). For example, Webb *et al.* (1961) showed that germination of species found growing under *Eremophila mitchellii* was inhibited by the mulched foliage, but not litter, of this species. Withers (1978a) found that powdered green cladodes of *A. littoralis* and *A. verticillata* collected in summer inhibited germination of several species, but that those collected in late autumn did not. The responsible substance did not appear to be released in sufficient concentrations from the litter-fall to inhibit field germination, and no evidence was found for its accumulation in the soil (Withers 1978a), and the effects of other factors, such as shade (Clarke and Hannon 1971), can be too readily attributed to allelopathy.

The results of this thesis indicate that the absence of seedlings in thick mats of cladodes is due to a low survival rate, rather than inhibition of germination. While physical properties of the litter, forming a barrier between seed and soil, and crushing of the seedlings is involved (see also Sydes and Grime 1981a,b; Wither 1978a), a major cause of seedling mortalities appears to be the rapid depletion of soil moisture by competing vegetation in such habitats. Similar conclusions were made by Bowman and Kirkpatrick (1985b) regarding seedling recruitment in *Eucalyptus delegatensis*.

5.4.7 Ecological Consequences of Germination Responses

The ultimate success of a species depends on the progression of individuals through each phase of the life-cycle, which in turn affects the ability of the species to reproduce. The optimum timing of this progression will be determined by the probability of survival in the present phase against the probability of survival in the subsequent phase. Thus the optimum time for germination will be when the probability of seedling survival exceeds that of the probability of seed survival.

The responses of a species' seed bank to any change in environmental conditions may be classified into three categories: continued dormancy, rapid germination, or protracted germination. Continued dormancy is likely where conditions are unfavorable to seedling survival, or where an environmental trigger is required to indicate periods of high probability of surviorship of seedlings, such as the removal of shading vegetation by fire. Rapid germination gives seedlings a competitive advantage over species germinating later, but depletes the seed bank. Protracted germination protects a species from elimination as a result of adverse conditions following germination events (Mayer and Poljakoff-Mayber 1982).

In summary, the most advantageous seed bank responses are:

- continued dormancy (or deferred germination), when probability of seed mortality is low and probability of seedling mortality is high.
- rapid seed germination, when probability of seed mortality is high and probability of seedling mortality is low or unpredictable.

- protracted germination, when probability of seed mortality is low or unpredictable, and probability of seedling mortality is unpredictable.

The major factor identified as detrimental to seed survival in *A. littoralis* and *A. torulosa* is predation by ants and small mammals (Chapter 4), while, in this chapter, moisture availability was identified to be of major importance to early seedling survival. Thus, when the probability of insufficient moisture being available for seedling recruitment exceeds that of seed being harvested, seed germination should not occur.

Buried seed is more likely to escape predation (Wellington and Noble 1985a). Thus, seed germination responses to the absence of light, an indicator of burial, are, indirectly, also responses to low probability of predation. Seed germination is affected by light only in *A. littoralis* in which it is protracted. After moistening, seed of *A. torulosa* germinates rapidly, except at low temperatures, and more rapidly than that of most *A. littoralis* provenances, whose germination becomes more protracted in the absence of light. In both species, germination is arrested if drying occurs before emergence of the radicle, with most seed being available for germination on remoistening.

As seed germination rate in *A. torulosa* after moisteniing is rapid and is not greatly delayed by any factors identified in this study, it appears likely that seedling mortality due to insufficient moisture following germination is of lower significance than seed predation. It is also likely to be of lower significance than it is for individuals of *A. littoralis*, in which absence of light causes germination to become protracted. Thus, the habitats in *A. torulosa* is successful are likely to be wetter than those which favour *A. littoralis*.

The other major difference detected here between the germination patterns of the two species is the markedly slower germination in *A. littoralis* in response to low temperature. The temperature range favourable to the growth of *A. littoralis* and *A. torulosa* is unknown. However, in North Queensland, low temperatures are associated with the dry season, when rains are infrequent and unpredictable. Thus while 100% germination still occurs in both species at 15°C, protracted germination will prevent depletion of the seed bank, should growth sustaining rains not occur. The germination response of *A. littoralis* makes this species more suited to habitats with lower rainfall. That *A. torulosa* has a narrower range of germination responses than *A. littoralis* at any one temperature may again indicate that it is suited to more predictably moist environments.

It might therefore be concluded that *A. littoralis* should have a larger seed bank than *A. torulosa*. That the reverse was found in Chapter 4, does not negate the above conclusions. The inadequacies of the seed bank study have already been described (p. 64), and seed losses to predation were higher under the *A. littoralis* stand.

5.5 Summary

Some seed released from the cones of *A. littoralis* and *A. torulosa* may be inviable due to immaturity. Seed viability increases as seed matures and darkens in colour, although viability of later stages may decline within the cones once full maturity has been reached.

Therefore viability can be approximated from seed colour. The proportion of a seed batch which is viable is likely to vary between trees and seasons, in response to resource availability and abundance of seed parasites during seed development. After-ripening is not required for seed of either species.

Within the temperature range of 15 to 35° C, germination commences once moisture is available. Rapid germination in the light, between 25 and 35° C, minimizes the effects of seed predators, although germination rate in *A. littoralis* is slightly slower than that of *A. torulosa*. Germination is delayed in both species at the lower temperatures, such as those associated with the dry season, thus preventing depletion of the seed bank in short-lived, but not in extended, periods of moisture availability. The delay is more extreme in *A. littoralis*. Germination of *A. littoralis* seed is also delayed in the dark, such as occurs when the seed is buried.

There is little variation in the seed germination rate of *A. torulosa* between provenances, and greater variation in *A. littoralis*. This reflects the broader range of environments in which *A. littoralis* is found, and may be due to its greater genetic variability. However, there is no clear correlation between geographic factors and germination rate.

When moisture supply is interrupted before germination is complete, germination of *A. littoralis* and *A. torulosa* will be arrested, but will recommence with seed re-moistening. Intermittent moisture availability does not greatly reduce seed viability. Germination time is inflexible, and depends on total time of exposure of the seed to sufficient levels of moisture. When waterlogging of soil occurs, *A. littoralis* and *A. torulosa* seed floats, but germination continues normally.

There is no evidence that allelopathy causes differential germination between *A. littoralis* and *A. torulosa*. Mats of cladodes may provide an initially moist environment for germination, but do present a physical barrier to seedling roots, and, as they are only likely to accumulate where competition from *Allocasuarina* species is severe, there is low seedling recruitment in such environments.

Factors responsible for early seedling mortalities include moisture stress, grazing, trampling by animals and crushing by litter-fall. Moisture stress is severe where transpiration rates of competing plants are high, as in closed *Allocasuarina* communities, or where seedlings are exposed to evaporation. Highest recruitment will therefore be in canopy gaps or in open vegetation, where a moist microhabitat is provided by the protection of a grass sward.

Highest levels of seedling recruitment will result from germination occurring when seedling survival probability is high relative to seed survival probability. The more rapid germination of *A. torulosa* will result in high seedling recruitment in this species where moisture levels sufficient to sustain seedling growth usually follow those promoting germination. Thus, *A. torulosa* will be more successful in moist environments, and its seed bank will be easily depleted in drier environments. Conversely, delay of germination of *A. littoralis* seed, after burial or at low temperatures (when seed predation probability is low), protects against depletion of the seed bank in dry environments. *A. littoralis* should therefore be more successful in drier environments.

CHAPTER 6

SURVIVAL, GROWTH AND COMPETITION IN JUVENILE PLANTS

6.1 Introduction

Although the environmental requirements of seedlings may be different from those of adult plants, the factors influencing seedling survivorship will limit the broader distribution of the species. In Chapter 5, light and moisture availability were identified as environmental factors which had different effects on the germination of *A. littoralis* and *A. torulosa*. Seed of *A. littoralis* was able to persist through periods of variable moisture availability with no loss in viability, and protracted germination in the dark appears likely to prevent seed bank depletion by short periods of rain. Germination in *A. torulosa* was rapid under most conditions, and was not affected by dark treatments. These results suggest that *A. littoralis* is adapted to drier environments than *A. torulosa*, which in turn would be more successful under low light intensities. The distribution of *A. littoralis* on apparently xeric sites and of *A. torulosa* on apparently mesic sites supports this conclusion (Chapter 3). However, in North Queensland, both species grow on similar sites receiving 1,000 to 2,000 mm annual rainfall (Chapter 3). Therefore, to better understand the relationship between the two species, the effect of moisture availability and light on seedling survivorship, growth and interspecific competition will be investigated in this chapter.

Analysis of the interactions between moisture availability and light regime on the survival and growth of *A. littoralis* in Victoria indicated that the species was both drought avoiding and tolerant of low light levels (Withers 1978b, 1979a,b). However, the Victorian provenance grew at rainfall levels (603 mm; Withers and Ashton 1977) that were considerably lower than those experienced by North Queensland provenances (Chapter 3). In order to compare the relative drought avoidance of northern provenances of *A. littoralis* with those from Victoria, as well as with *A. torulosa* from North Queensland, the response of plant transpiration rate to declining soil moisture is measured.

Ability of plants to perform under high or low light intensities is affected by the orientation of their foliage (Hadfield 1975). The cladodes of *A. littoralis* have been decribed as erect and those of *A. torulosa* as pendulous (Doran and Hall 1983), suggesting that *A. littoralis* is adapted to higher light intensities than is *A. torulosa*. In seedlings, angle of foliage appears to be related to cladode length (pers. obs.). Therefore, measurements are made of the average cladode length in seedlings of *A. littoralis* and *A. torulosa*.

6.2 Methods

The following experiments were undertaken on the campus of James Cook University, Townsville (146° 43' 15" E, 19° 19' 30" S, 30 m) The climate of Townsville is warm, with high levels of solar radiation, reaching maximum levels from October to December (Fig 6.1). Relative light intensities (R.L.I.) were measured as a percentage of full midday sunlight (1,600 to 1,650 μM m^{-2} s^{-1} at 400-700 nm).

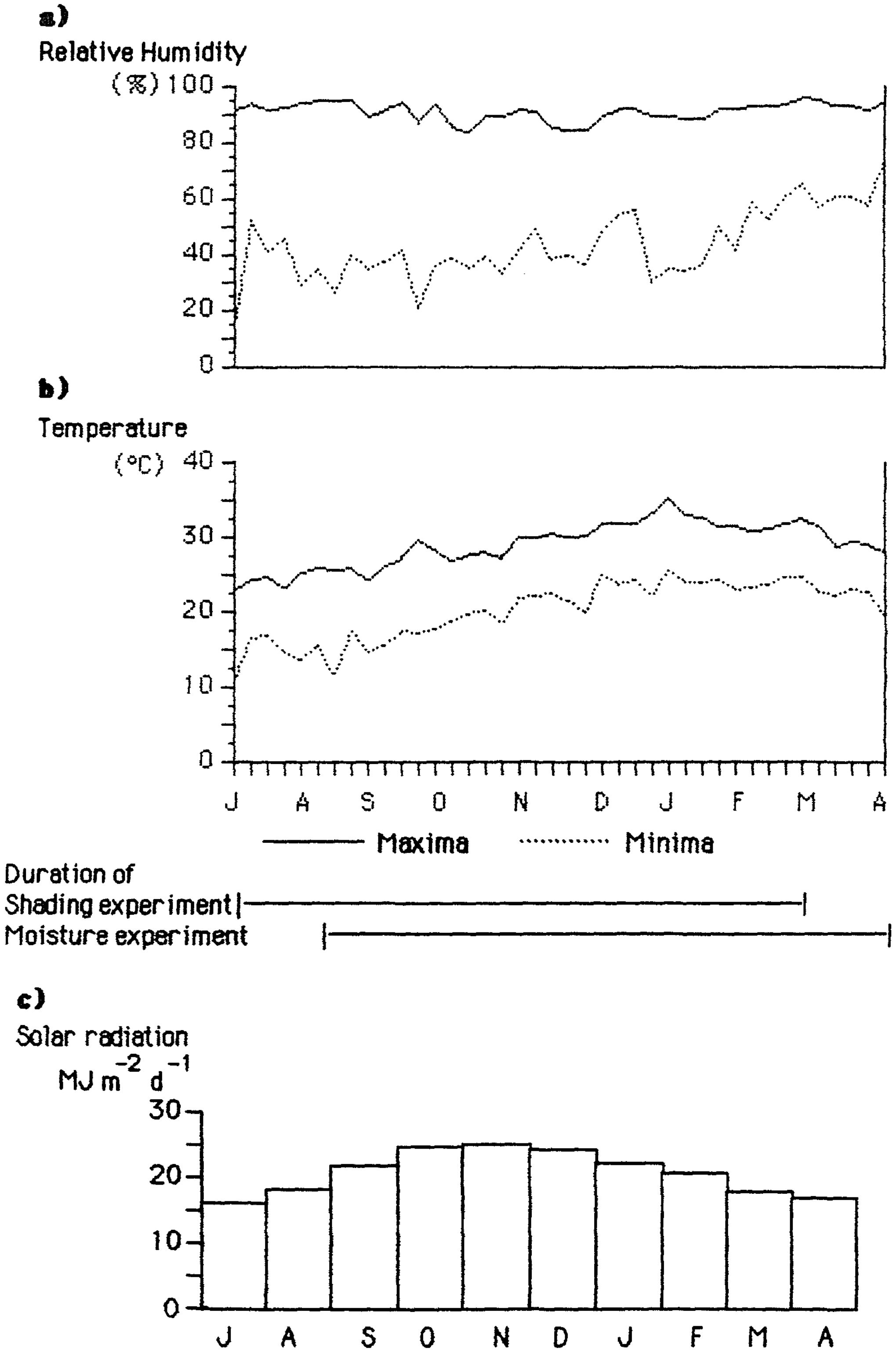


Fig. 6.1 Weather statistics for James Cook University.
a) Mean weekly relative humidity, July 1984 - April 1985.
b) Mean weekly temperature, July 1984 - April 1985.
c) Mean monthly solar radiation totals, July to April.

Seedlings for these experiments were grown for six months under glasshouse conditions (20-26°C, 10% R.L.I.) in mixed, sieved topsoil (clay loam) obtained from beneath stands of *A. littoralis* and *A. torulosa* at the Kirrama study site, and watered to field capacity three times weekly.

6.2.1 Description of Plant Parameters

In order to assess the relationship between plant height an average cladode length, plant height, shoot number and total shoot length were measured for 111 six month old plants of each of *A. littoralis* and *A. torulosa*. Average cladode length was calculated for each of the above plants, and tested for regression against plant height (Sokal and Rohlf 1969 p 419).

For subsequent experiments in this chapter, it was necessary to have a measure of plant biomass, to assess transpiration in relation to plant size and to enable plants of similar size to be paired in competition experiments. The absence of distinct photosynthetic units makes measurement of growth rates in live juvenile casuarinas difficult. As cladode diameter is relatively constant, photosynthetic area will be proportional to total cladode length (Withers 1979a). Total cladode length, however, is time-consuming to measure and damage to the plant is likely to occur during measurement. Therefore, the product of shoot number and plant height was tested for linear and power curve regression (Sokal and Rohlf 1969 p 419) against the total shoot length.

6.2.2 Moisture Stress

Nine one year-old plants of each species were transplanted singly into pots containing approximately 2 kg of Kirrama topsoil (dry weight). After two months, the soil was brought to field capacity (≈ 30%) by soaking the pots for twenty minutes, then draining for thirty minutes. Each pot was then placed in a strong clear plastic bag and sealed with paraffin wax around the base of the plant, with the plants' shoots exposed, and not watered further. Four controls were similarly prepared with the plant being replaced by a dead woody stem. Very little water was lost from the control pots, indicating that the sealing technique was successful. The pots were weighed daily between 500 hrs and 630 hrs on an Ohaus Triple Beam Balance to determine transpiration rate.

Plant height and shoot number were recorded at the commencement of the experiment. Total shoot length was calculated from the regression equations obtained in Section 6.2.1. Photosynthetic area was calculated on a half cylinder basis following Ashton *et al.* (1975) and Withers (1978b). At the conclusion of the experiment, dry weights of shoots and soil were obtained, after drying to a constant weight at 60°C. Daily changes in soil moisture were also determined. Transpiration rates were calculated in relation to individual plants, unit area and unit weight of shoots. As the smaller plants maintained a high transpiration rate for longer than larger plants, the plants of each species were subdivided into three groups on the basis of size (Table 6.1). Mean daily transpiration rate was calculated separately for each group.

Table 6.1 Mean size of plants used in plant desiccation experiment.

S - small, M - medium, L - large.

Species	*A. littoralis*			*A. torulosa*		
Average size	S	M	L	S	M	L
Shoot weight (g)	1.25	1.98	3.09	1.87	2.58	2.64
Estimated shoot length (mm)	5140	9500	22400	8740	11180	15680

As daily transpiration rate showed a high degree of variation, mean daily transpiration per unit area and weight was calculated for each week. Regression equations were calculated for these measures against the soil moisture at the commencement of each week, and the significance of these equations was tested (Sokal and Rohlf 1969 p 430) and analysis of covariance (Snedecor 1956) used to test the difference in slope in these equations. The experiment was continued for 8 weeks, when it was terminated because of time constraints. At this stage few of the plants exhibited any shoot death, and none had died completely. Therefore, as direct measurement of soil moisture at plant death could not be made, this was calculated from the above-mentioned regression equations.

6.2.3 Effect of Moisture on Survival, Growth and Competition

Two seedlings of similar shoot length were planted in each of 121 pots (15 cm high, 12 cm diameter), in commercial topsoil. Nine pots of each pure species combination (*A. littoralis* with *A. littoralis* or *A. torulosa* with *A. torulosa*) and 18 pots of the mixed species combination (*A. littoralis* with *A. torulosa*) were placed in each of two moisture treatments (watered to field capacity or with ≈ 100 ml, three times a week). The plants were placed in a shade-house at 30% R.L.I. and ambient temperature conditions. Species combinations were randomly arranged within treatments in alternating lines of 10 pots of each treatment. Each pot was fertilized with 100 ml of 1 g/l Aquasol ™ fertilizer at the time of each measurement.

The plants were harvested at 33 weeks and dried to constant weight at 60°C. Shoots and roots were weighed separately on a Sauter balance. Relative shoot weight (shoot weight/ (shoot weight + root weight)), plant weight and relative total weight (weight of plant 1/ (weight of plant 1 + weight of plant 2)) were calculated for each plant. Three way analysis of variance was undertaken to determine the effect of species, companion species and treatment on plant survivorship.

To identify the separate effects of species, companion species and treatment on plant parameters, two way analysis of variance was undertaken initially for each species, and then for each treatment. The effect of species combination and treatment on total plant weight per pot was tested with a two way analysis of variance. Replacement diagrams (De Wit 1960, 1971) were constructed to illustrate any deviation of yields in mixed species pots from those predicted by single species pots.

6.2.4 Effect of Shading on Survival, Growth and Competition

Two seedlings of similar shoot length were planted in each of 121 pots (15cm high, 12 cm diameter), in Kirrama topsoil (clay loam. Nine to 12 pots of each single species combination (*A. littoralis* with

A. littoralis and *A. torulosa* with *A. torulosa*) and 18 to 21 pots of the mixed species combination (*A. littoralis* with *A. torulosa*) were placed randomly in two blocks in each of three shade treatments (100%, 10 and 1% natural sunlight), produced using various thicknesses of Sarlon shade cloth over enclosures 1.2 m high x 2 m x 4 m. Within these enclosures, pots were randomly arranged in blocks inside two 20 cm high frames which were covered in 1 cm mesh wire, to prevent cane toads *Bufo marina* from damaging the seedlings.

The plants were harvested at 35 weeks and dried to a constant weight at 60°C. Measurement of plant parameters, analyses and construction of replacement diagrams are the same as outlined in Section 6.2.3.

6.3 Results

6.3.1 Plant Parameters

In plants of similar height, average cladode length was greater in *A. torulosa* than in *A. littoralis*. A linear relationship was found between average shoot length and plant height in both species (Fig. 6.2). This relationship was described by the following regression equations:

for *A. littoralis*:

$L = 0.0850H + 8.5201$, ($F_s = 4968$, d.f. 1,109, $P < 0.001$),

and for *A. torulosa*:

$L = 0.1819H + 8.8848$, ($F_s = 863$, d.f. 1,109, $P < 0.001$),

where L = Average shoot length (mm)

and H = Plant height (mm).

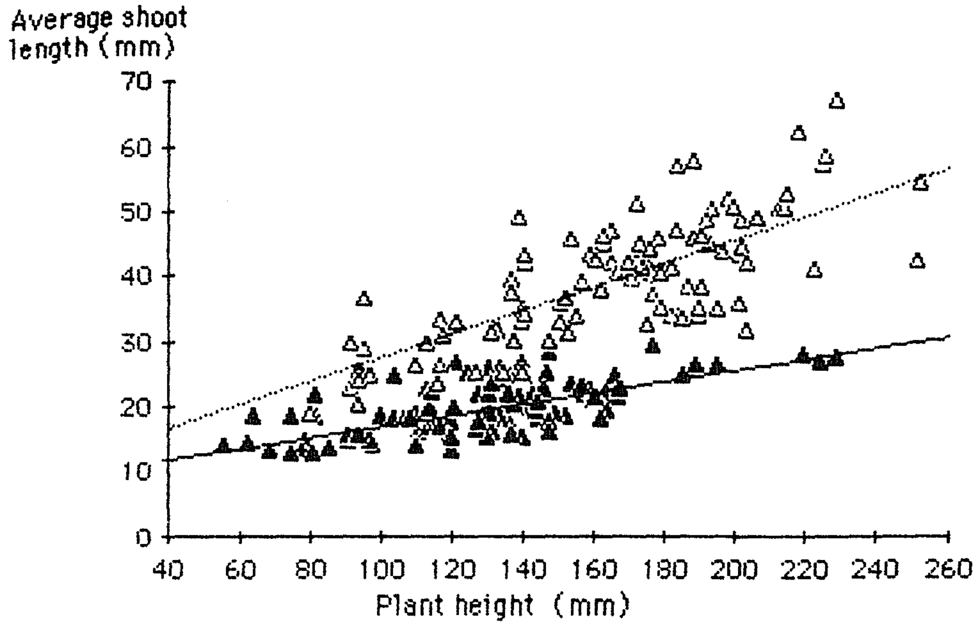


Fig. 6.2 **Relationship between average shoot length and plant height.**

Observations: ▲ *A. littoralis*, △ *A. torulosa*,

Regression lines: — *A. littoralis*, ······ *A. torulosa*.

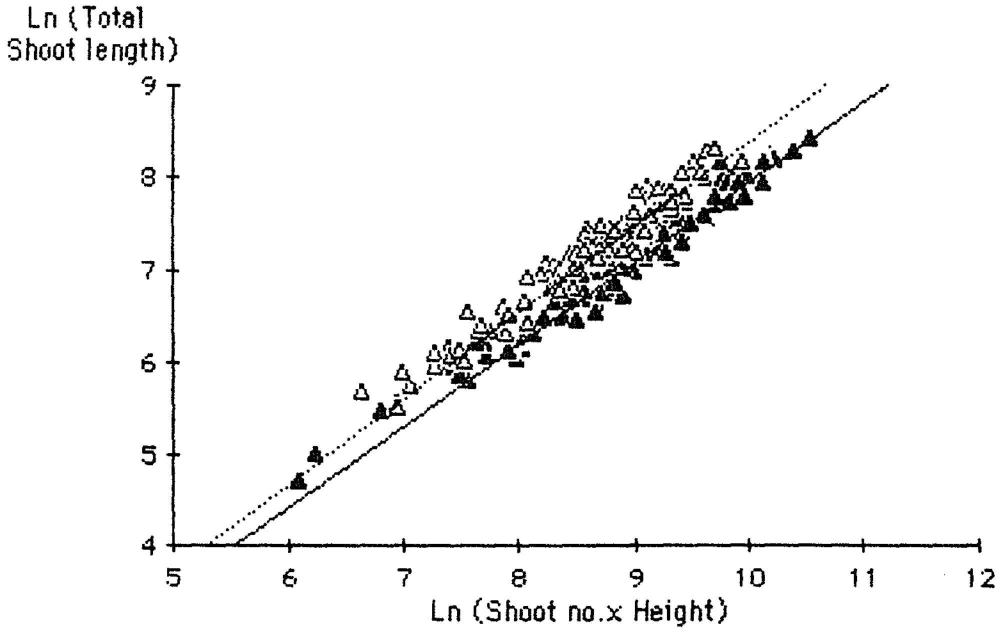


Fig. 6.3 **Relationship between ln (total shoot length) and ln (shoot no. x height).**

Observations: ▲ *A. littoralis*, △ *A. torulosa*,

Regression lines: — *A. littoralis*, ······ *A. torulosa*.

Analysis of covariance indicated that the increase in average cladode length with increasing plant height was significantly greater in *A. torulosa* than in *A. littoralis* ($F_s = 24.196$, d.f. 1,218, $P < 0.001$).

Linear regressions between total shoot length and the product of shoot no. by plant height were significant for both *A. littoralis* plants ($F_s = 1730$, d.f. 1,109, $P < 0.001$) and *A. torulosa* plants ($F_s = 977$, d.f. 1,109, $P < 0.001$). However, as variation from the regression line increased with plant size, in both species, the regressions were strengthened by translation to power curve relationships which were described by the following equations (Fig 6.3):

for *A. littoralis*:

$$T = 0.6280 \times (SxH)^{0.8422}, \quad (F_s = 2419, \text{ d.f. } 1,109, P < 0.001)$$

and for *A. torulosa*:

$$T = 0.6175 \times (SxH)^{0.8873}, \quad (F_s = 1617, \text{ d.f. } 1,109, P < 0.001),$$

where T = Total shoot length (mm),
S = Shoot no.,
and H = Plant height (mm).

6.3.2 Moisture Stress

Plants in the smallest size grouping were not visibly damaged by the experiment. Although most plants in the medium and large groupings were severely damaged by the lack of water, suffering up to 90% death of photosynthetic area, none were completely killed by the experiment.

Changes in daily transpiration per plant were similar between the two species (Fig. 6.4). There was a rise in transpiration rate over the first two to four days, then a decline, the rate of which was dependent on plant size. The smallest size groups took nearly four weeks to reach 20% of initial rate, while this level was reached by the medium plants in two to three weeks,

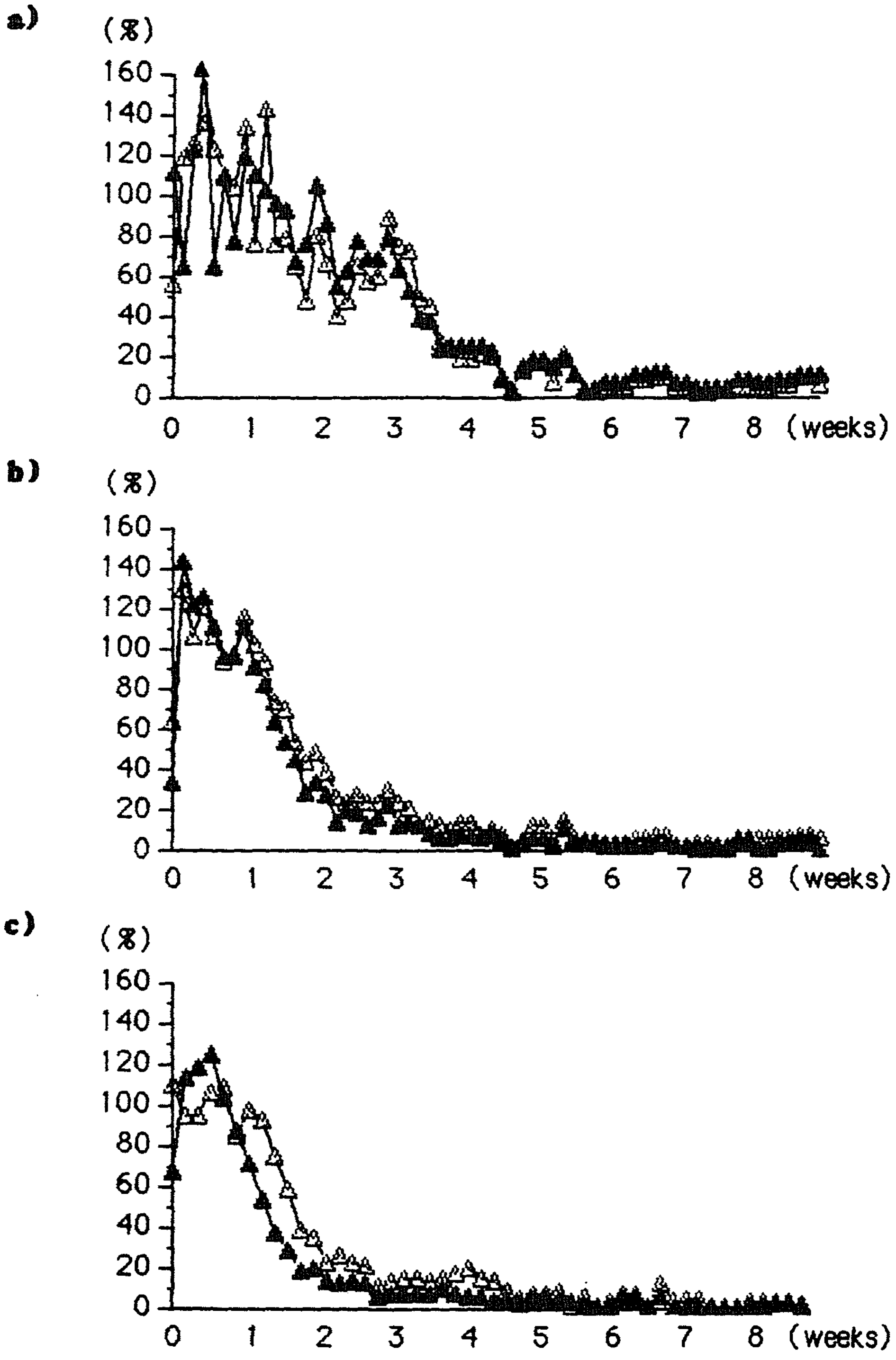


Fig. 6.4 **Changes in daily transpiration per plant from field capacity without further watering, as a percentage of initial rate.**

a) small plants, **b)** medium plants, **c)** large plants.

▲ *A. littoralis*, △ *A. torulosa*.

and by the large plants in approximately two weeks. In the medium and large groups, the reduction in transpiration was faster in *A. littoralis* than in *A. torulosa*, with the result that daily transpiration per plant of *A. littoralis* was slightly lower than that of *A. torulosa* for most of the experiment. It appears that plant size has a greater influence on daily transpiration per plant than does the species of the plant.

However, the relationship between transpiration rate per unit area or weight of cladode indicate marked differences between the two species, with *A. littoralis* having a greater transpiration rate, throughout the range of soil moisture levels examined, but reducing at a faster rate than did *A. torulosa* (Fig. 6.5). The relationship between transpiration per half cylinder area of cladode and soil moisture was described by the following regression equations:

for *A. littoralis*:

$U_a = 1.0770M - 5.6606$, ($F_S = 306$, d.f. 1, 70, $P < 0.001$)

and for *A. torulosa*:

$U_a = 0.7871M - 5.2386$, ($F_S = 210$, d.f. 1, 70, $P < 0.001$)

where U_a = water use ($g\ dm^{-2}\ d^{-1}$)
and M = soil moisture (%).

These equations estimate transpiration will be 32.0 and 22.3 $g\ dm^{-2}\ d^{-1}$ at field capacity (35%), and will cease at a soil moisture of 6.6% and of 5.3% in *A. littoralis* and *A. torulosa* respectively, and that transpiration rate per unit area at all soil moisture levels would be higher in *A. littoralis* than in *A. torulosa* (Fig 6.5a). Analysis of covariance indicated that the decline in transpiration with decreasing soil moisture was steeper in *A. littoralis* than in *A. torulosa* ($F_S = 12.396$, d.f. 1, 140, $P < 0.001$).

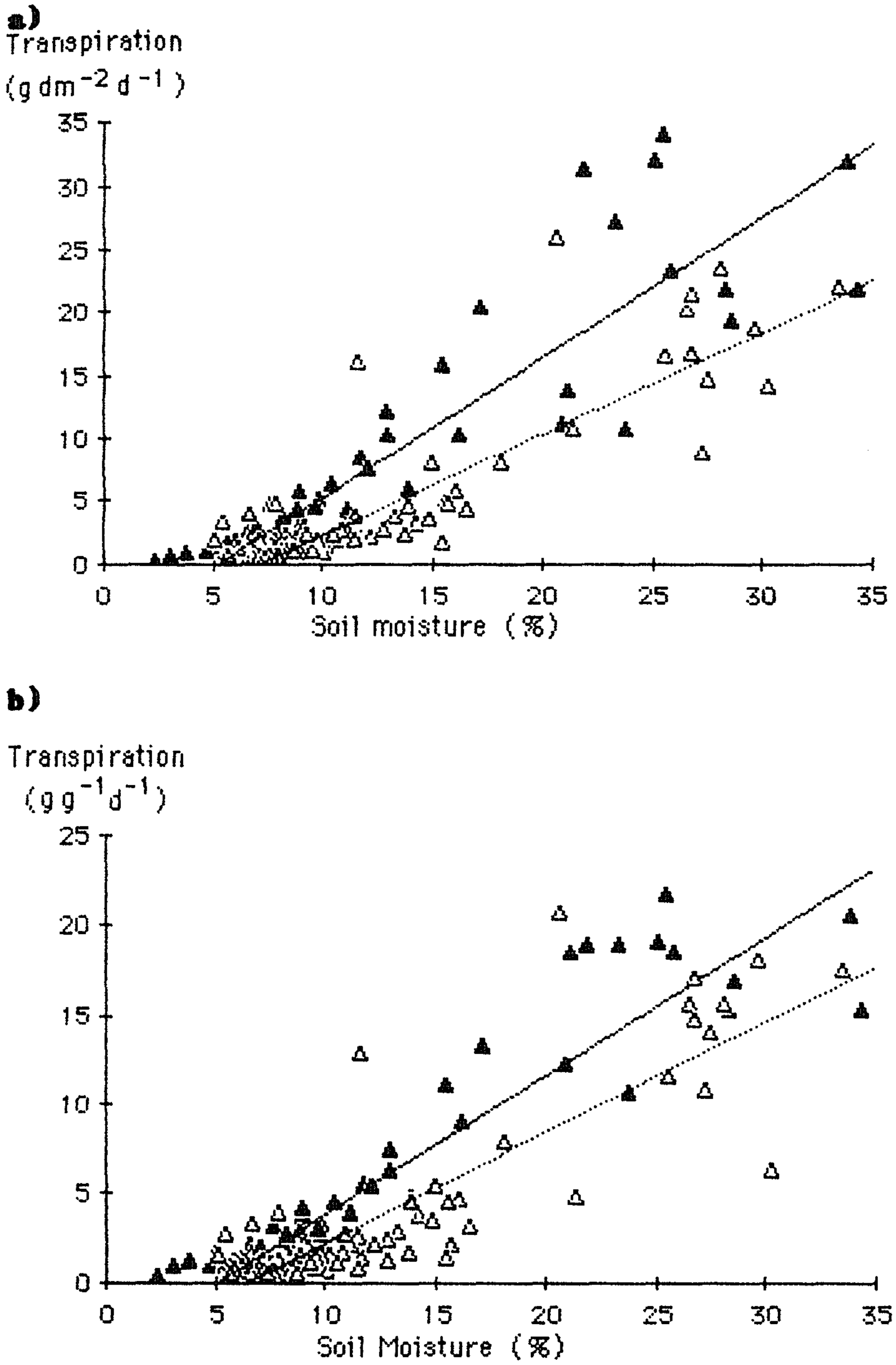


Fig. 6.5 **Relationship between transpiration rate and soil moisture.**

a) g dm^{-2} d^{-1}, **b)** g g^{-1} d^{-1}.

Observations: ▲ *A. littoralis*, △ *A. torulosa*,

Regression lines: —— *A. littoralis*, ······ *A. torulosa*.

The relationship between transpiration shoot dry weight and soil moisture was described by the following regression equations:

for *A. littoralis*:

$$U_d = 0.7763M - 3.9574, \quad (F_S = 485,\ d.f.\ 1, 70,\ P < 0.001)$$

and for *A. torulosa*:

$$U_d = 0.6171M - 4.0804, \quad (F_S = 185,\ d.f.\ 1, 70,\ P < 0.001)$$

where U_d = water use ($g\ g^{-1}\ d^{-1}$)
and M = soil moisture (%).

These equations estimate transpiration will be 23.2 and 17.5 $g\ g^{-1}\ d^{-1}$ at field capacity (35%), and will cease at a soil moisture of 5.1% and of 6.6% in *A. littoralis* and *A. torulosa* respectively, and that transpiration rate per unit area at all soil moisture levels would be higher in *A. littoralis* than in *A. torulosa* (Fig 6.5b). Analysis of covariance again indicated that the decline in transpiration with decreasing soil moisture was steeper in *A. littoralis* than in *A. torulosa* ($F_S = 7.757$, d.f. 1, 140, $P < 0.01$).

6.3.3 Effect of Moisture on Survival, Growth and Competition

While there were no plant deaths in the wet treatment, survivorship in the dry treatment was higher for *A. littoralis* than *A. torulosa* (Table 6.2). As survivorship of *A. torulosa* was lowest when grown with *A. littoralis*, interference from *A. littoralis* plants is suggested. However, three way analysis of variance did not indicate that survivorship of any group of plants was significantly higher than that of any other group.

Table 6.2 Plant survivorship under two moisture regimes.

Treatment	Wet		Dry	
Species	A.l	A.t	A.l	A.t
Companion species				
A. littoralis (A.l)	100.0	100.0	88.9	61.1
A. torulosa (A.t)	100.0	100.0	83.3	88.9

The effect of moisture treatments on each species varied between parameters (Table 6.3). Companion species did not affect any plant parameter, although in the wet treatment, plants of both species had a significantly greater root investment in mixed species pots. Therefore, no distinction has been made between plants in single species pots and mixed species pots (Table 6.4).

Mean combined biomass of plants in the wet treatment was significantly higher than that in the dry treatment (Fig. 6.6, F_S = 14.381, d.f. 1,59, $P < 0.001$), but no species combination was significantly heavier than any other (F_S = 0.029, d.f. 2,59, $P > 0.05$). There were no significant differences between the shoot weight or total plant weight of *A. littoralis* and *A. torulosa* in either treatment. Therefore, on average, each species constituted an equal proportion of the total biomass in each mixed species pot. However, *A. littoralis* had the greater root weight in both treatments, and, assuming similar root morphology, should therefore have greater access to moisture. While shoot and total plant weight were significantly greater in the wet than the dry treatment in both species, root weight was significantly

Table 6.3 F-ratios calculated from analysis of variance, indicating effect of factors on plant parameters, under two moisture regimes.

S Shoot weight, R Root weight, P Plant weight,
S/P Shoot weight/ Plant weight,
P/T Plant weight/(Combined plant weight),
^{a} Angular transformation before analysis,
*** P < 0.001, ** P < 0.01, * P < 0.05, - not significant.

Species/Treatment Factor		S	R	P	S/P^a	P/T^a
A. littoralis d.f. 1,60						
Moisture regime	F_s	9.734	11.768	11.421	0.224	0.027
	P	**	**	**	-	-
Companion species	F_s	0.075	0.050	0.071	0.005	0.810
	P	-	-	-	-	-
Interaction	F_s	0.097	1.380	0.432	0.990	0.061
	P	-	-	-	-	-
A. torulosa d.f. 1,62						
Moisture regime	F_s	8.028	3.861	6.949	4.509	0.012
	P	**	-	*	*	-
Companion species	F_s	0.015	0.533	0.023	2.010	0.533
	P	-	-	-	-	-
Interaction	F_s	0.038	0.684	0.018	1.133	0.833
	P	-	-	-	-	-
Wet treatment d.f. 1,68						
Species	F_s	0.195	11.080	2.409	27.812	0.531
	P	-	**	-	***	-
Companion species	F_s	0.029	0.086	0.000	1.392	0.531
	P	-	-	-	-	-
Interaction	F_s	0.030	1.144	0.086	4.556	0.000
	P	-	-	-	*	-
Dry treatment d.f. 1,54						
Species	F_s	0.392	4.766	1.271	1.533	0.551
	P	-	*	-	-	-
Companion species	F_s	0.095	0.602	0.214	0.211	0.779
	P	-	-	-	-	-
Interaction	F_s	0.046	1.030	0.219	0.064	0.000
	P	-	-	-	-	-

greater only in *A. littoralis* (Tables 6.3, 6.4). This affected relative shoot weight, which was greater in the wet treatment than in the dry treatment in *A. torulosa*, but not in *A. littoralis* (Tables 6.3, 6.4). Therefore, only in the wet treatment, was the relative shoot weight of *A. littoralis* significantly lower (and therefore root : shoot ratio higher) than that of *A. torulosa*.

As weights of all plants in the mixed species pots were close to expected values, there was no evidence for interference between species (Fig. 6.6). Although the weights of *A. littoralis* in the mixed species pots in the dry treatment were slightly lower than expected (Fig. 6.6), they were not significantly so. Some plants in this experiment showed signs of nutrient deficiency, with cladodes turning yellow. This yellowing disappeared on the addition of the fertilizer used.

Table 6.4 Plant parameters under two moisture regimes.

For significance of differences between values, refer to Table 6.3.
A.l, *A. littoralis*; A.t, *A. torulosa*.
^{a} Calculated for mixed species pots only.

Treatment	Wet		Dry	
Species	A.l	A.t	A.l	A.t
Plant parameter				
Shoot weight(g)	2.39	2.22	1.73	1.60
Root weight (g)	1.29	0.92	0.92	0.72
Shoot/ Plant weight	0.64	0.72	0.65	0.68
Plant weight (g)	3.60	3.14	2.67	2.31
Relative total weight^a	0.53	0.47	0.55	0.45

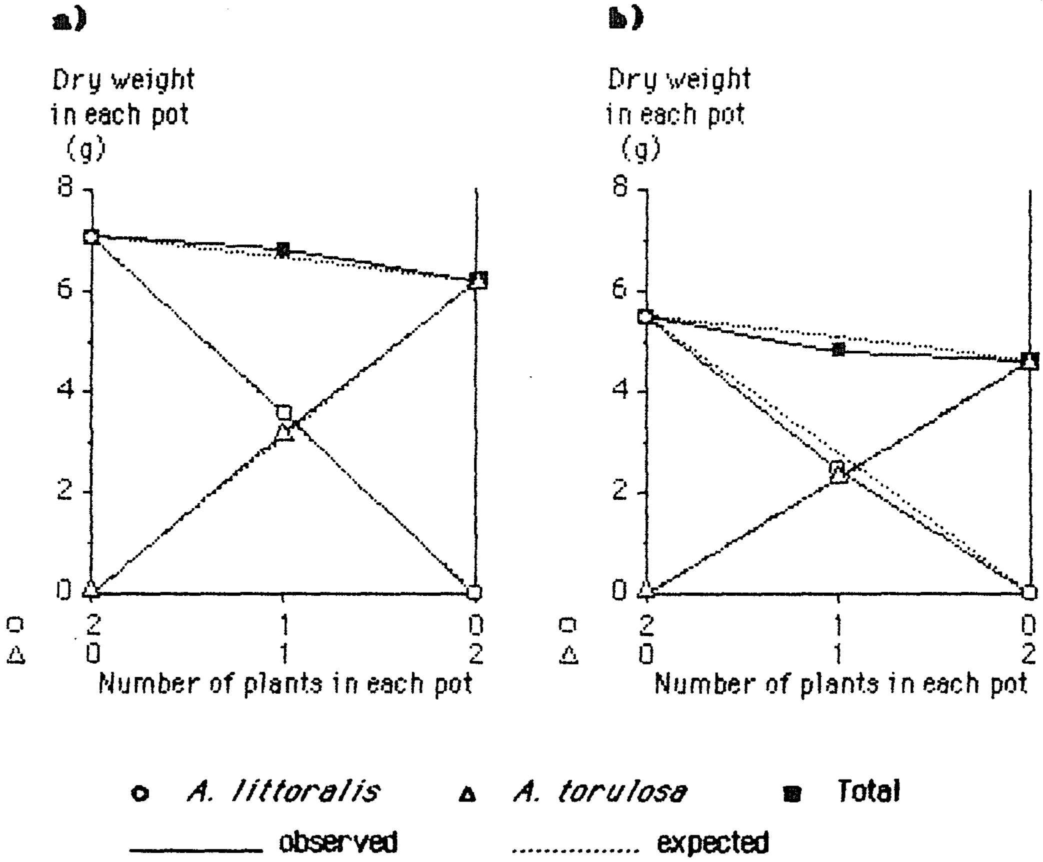


Fig. 6.6 **Dry matter production in relation to species composition under two moisture regimes.**

a) Wet treatment, **b)** Dry treatment.

6.3.4 Effect of Shading on Survival, Growth and Competition

Survivorship in the 10% and 1% sunlight treatment was greater than 90% for both species (Table 6.5). Survivorship in the full sunlight treatment was lower in both species, with the survival of *A. littoralis* about twice that of *A. torulosa*. Due to poor condition and low sample sizes, plants in the full sunlight treatment were excluded from further analysis. As survivorship of each species was similar in single and mixed species pots, there was no evidence of competition induced mortality. Three way analysis of variance identified a significant effect of shade treatment on plant survivorship ($F_S = 63.869$, d.f. 2,2, $P < 0.05$), but did not distinguish between species ($F_S = 11.917$, d.f. 1,2, $P > 0.05$).

In the full sunlight, *A. torulosa* plants developed reddish-purple pigments, which were assumed to be anthocyanin, a pigment usually produced in response to ultraviolet radiation stress (Levitt 1980).

Table 6.5 Plant survivorship under three shade treatments.

	100%		10%		1%	
	A.l	A.t	A.l	A.t	A.l	A.t
Survivorship (%)						
with A.l	77.8	40.9	100.0	90.5	100.0	100.0
with A.t	70.0	31.8	100.0	100.0	94.4	94.4

The effect of light intensities on each species varied between parameters (Table 6.6). Companion species did not affect any plant parameter in the 1% shade treatment. Therefore, no distinction has been made between plants in single species pots and mixed species pots, for this treatment (Table 6.7).

As the biomass indices indicated that the plants in this experiment were initially about one third the size of the plants in the moisture experiment (Section 6.3.2), the biomass production in this experiment was proportional to that in the moisture experiment. Plants in the present experiment did not exhibit visible signs of nutrient deficiency, suggesting that either the topsoil from the Kirrama site had a higher nutrient status than did the commercial topsoil or the smaller size of the plants prevented exhaustion of the soil nutrient reserves.

Combined biomass production in the 10% and 1% R.L.I. was similar (Fig. 6.7, $F_S = 0.0663$, d.f. 1,69, $P > 0.05$), no species combination was significantly heavier than any other ($F_S = 0.613$, d.f. 2,69, $P > 0.05$), and differences between individual plant weights in the two shade treatments were not significant for either species (Table 6.6).

However, the response of all individual plant parameters to relative light intensity significantly differed between species. While average total plant weight of *A. littoralis* was greater in the high light treatment than in the low light treatment, the reverse was true for *A. torulosa*. Only plant weights in the higher light treatment were affected by the species with which the plant was grown. In both species, plants grown with *A. torulosa* were heavier than those grown with

Table 6.6 F-ratios calculated from analysis of variance, indicating effect of factors on plant parameters, in two light intensities.

S Shoot weight, R Root weight, P Plant weight,
S/P Shoot weight/ Plant weight,
P/T Plant weight/(Plant weight + companion plant weight),
^{a} Angular transformation before analysis,
*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, - not significant.

Species/Treatment Factor		S	R	P	S/P^a	P/T^a
A. littoralis d.f. 1,71						
Shade	F_s	0.296	8.169	1.825	26.060	4.193
	P	-	**	-	***	*
Companion	F_s	2.832	1.727	2.716	0.041	1.688
species	P	-	-	-	-	-
Interaction	F_s	2.317	3.596	3.072	0.123	4.393
	P	-	-	-	-	*
A. torulosa d.f. 1,71						
Shade	F_s	4.962	3.233	1.781	25.614	4.151
	P	*	-	-	***	*
Companion	F_s	0.058	0.453	0.130	0.170	1.979
species	P	-	-	-	-	-
Interaction	F_s	1.058	1.917	1.383	0.870	4.752
	P	-	-	-	-	*
10% sunlight d.f. 1,70						
Species	F_s	4.867	15.207	8.826	12.512	12.007
	P	*	***	**	***	***
Companion	F_s	7.531	5.570	7.796	0.439	12 .661
species	P	**	*	**	-	***
Interaction	F_s	1.924	1.415	2.152	0.288	0.000
	P	-	-	-	-	-
1% sunlight d.f. 1,72						
Species	F_s	0.393	5.847	0.008	25.664	0.430
	P	-	*	-	***	-
Companion	F_s	0.059	0.510	0.131	0.409	0.591
species	P	-	-	-	-	-
Interaction	F_s	0.158	0.022	0.076	0.000	0.000
	P	-	-	-	-	-

A. littoralis. Competitive interference from *A. littoralis* is indicated by the departure of weights from expected values in mixed species pots in the higher light intensity (Fig. 6.7). This effect extended to root and shoot weight. In the lower light treatment, there was no significant difference between the total weights of the two species. The relative shoot weight of *A. torulosa* was consistently higher than that of *A. littoralis*, and thus the root : shoot ratio lower, although both increased at the lower light intensity.

Table 6.7 Plant parameters under two shade treatments.

[a] Companion species not separated in 1% R.L.I. treatment, except for relative total weight, where measures refer to plants grown in mixed species pots only.

Relative light intensity	10%				1%	
Species	A.l	A.t	A.l	A.t	A.l	A.t
Companion species[a]	A.l	A.l	A.t	A.t		
Shoot weight(g)	0.77	0.69	1.16	0.82	0.90	0.98
Root weight (g)	0.36	0.22	0.55	0.28	0.29	0.19
Shoot/ Plant weight	0.69	0.77	0.69	0.75	0.78	0.84
Plant weight (g)	1.12	0.91	1.73	1.10	1.19	1.17
Relative total weight	0.50	0.66	0.34	0.50	0.46	0.54

6.4 Discussion

6.4.1 Moisture Availability

The initial rise in transpiration rate observed in this experiment is consistent with release from waterlogging (Jarvis and Jarvis 1963b).

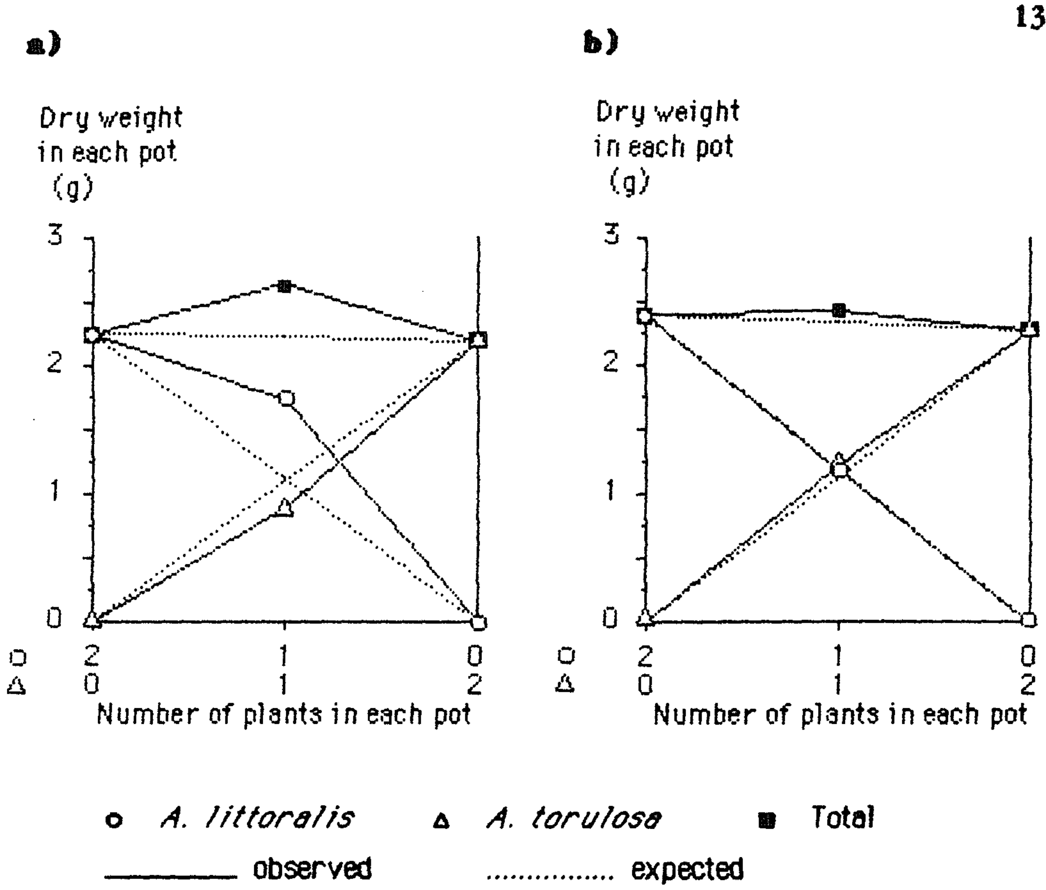


Fig. 6.7 **Dry matter production in relation to species composition under two light regimes.**
a) 10% sunlight. b) 1% sunlight.

Although other studies have found a strong relationship between transpiration rate and temperature conditions (Ladiges 1974b), under the relatively stable temperature conditions of this experiment, it is clear that transpiration rate is closely linked to soil moisture. This suggests that the apparent sudden decline in transpiration rate observed in other studies (Ashton *et al.* 1975; Quraishi and Kramer 1970; Withers 1978b), is an artefact of the declining rate of change of transpiration with soil moisture, from the initially high levels limited by waterlogging. This experiment also indicates that the rate at which the decline occurs is related to the ratio between pot to plant size. Thus with a high ratio, the decline may occur over a period of weeks, such as in the smaller plants in the present study, whereas when the ratio is low, the decline may occur within 24 hrs. The rate will also depend on environmental conditions, such as temperature and light conditions (Gleadow and Rowan 1982).

Rapid decline in transpiration has been interpreted as indicating sudden stomatal closure in response to a threshold level of moisture stress, with moisture loss shifting from mainly stomatal to cuticular transpiration (Quraishi and Kramer 1970; Withers 1978b). However, rather than there being sudden stomatal closure, stomatal conductance appears to decline gradually and constantly with declining leaf water potential from a threshold level (Ludlow 1980).

Ability to obtain soil moisture reserves at high availability, enabling rapid growth rates and depriving neighbours, appears to be more important in competition for moisture than a superior ability to use water at low availability, as water content does not change much in soils of low moisture content (Donald 1963). Therefore the ability of

A. littoralis to transpire at a greater rate than *A. torulosa* both at high and low moisture availability should endow this species with a competitive advantage in moisture limited environments. Similar differences in transpiration were found for the drought avoiding *A. verticillata* in comparison to the drought sensitive *Eucalyptus* spp. by Ashton *et al.* (1975), although the results of their experiments were inconsistent.

Transpiration rates of *A. littoralis* in Victoria (Withers 1978b, 1979b) were also similar to those reported in the present study. Thus, the tolerance of lower rainfall levels by *A. littoralis* at higher latitudes (Chapter 3), appears to be due to the effect of season of rainfall on moisture availability, with higher annual rainfall required to sustain plant growth in the tropics than in the temperate region (H.A. Nix pers. comm.), rather than to differences in the inherent water relations of northern and southern provenances.

The greater drought tolerance of *A. littoralis* over *A. torulosa* suggested by transpiration rates was paralleled by the relative survivorship of the two species under the drier regime. However, among surviving plant pairs, *A. littoralis* did not appear to be competitively superior to *A. torulosa*. Conformity of plant yields in mixed species pots to those predicted from yields of single species pots (Fig. 6.6) indicated that, although the two species were drawing on a common moisture resource, neither species was dominant. Lower biomass of both species in the dry treatment compared to the wet treatment, indicated that moisture was limiting in both species. That biomass production in *A. littoralis* and *A. torulosa* was not significantly different suggests that these species will be similarly affected by moisture deficits.

However, plant architecture should favour *A. littoralis* over *A. torulosa*. A higher root : shoot ratio in *A. littoralis* is characteristic of greater drought avoidance (Jarvis and Jarvis 1963a; Ladiges 1974a). Despite the fact that root : shoot ratio in *A. littoralis* was significantly greater than that of *A. torulosa* only in the wet treatment, the significantly greater root mass in both treatments, would result in it having access to more moisture in the field (Donald 1963). Furthermore, where moisture availability is seasonal and the majority of growth occurs when moisture availability is not limiting, root : shoot ratios would be likely to be characteristic of the wet treatment, i.e. higher in *A. littoralis* than in *A. torulosa*. Thus, as moisture becomes limiting, *A. littoralis* will have access to a larger volume of soil from which it can draw moisture. Therefore, it is expected that *A. littoralis* will be more successful in environments with seasonal moisture availability. This may be the reason that, although both species are found in areas which receive 1,000 to 2,000 mm annual rainfall, *A. littoralis* predominates on the apparently drier sites, and *A. torulosa* on the apparently wetter sites. That competitive dominance was not exhibited by *A. littoralis* over *A. torulosa* in the dry treatment may simply indicate that seasonality of moisture availability is more important than total supply.

In the field, *A. littoralis* plants may actually receive more moisture than those of *A. torulosa* because of foliage characteristics. The erect foliage of *A. littoralis* would tend to direct water towards the plant's root system; Withers (1978a) found that stands of *A. littoralis* intercepted up to 40% of rainfall, with stem flow directing the water to the base of the plant. By contrast, the horizontal to pendulous foliage of *A. torulosa* would rapidly drain water away from the plant, possibly directing moisture away from the plant's root system. Thus pendulous cladodes may have a similar function to the drip tips of rainforest leaves (Richards 1952), allowing rapid drainage. This would be beneficial under moist conditions, to minimize fungal attack of the foliage (Cohen 1981), but disadvantageous in dry conditions.

6.4.2 Light Intensity

Low survival rate of *A. torulosa* in full sunlight, and development of anthocyanin pigments, supports the conclusion made in Chapter 5, of a low level of light tolerance in *A. torulosa*. Low survival may be contributed to by intolerance of ultraviolet light (Levitt 1980), high cladode temperature or soil heating and drying. Both heat stress and drought stress may be caused by high foliage temperatures, producing direct heat damage and inordinate loss of moisture (Levitt 1980).

A linear increase in leaf surface temperature of approximately 2° C per 1 J cm^{-2} min^{-1} solar radiation has been demonstrated for *Camellia sinensis* var. *assamica* at an ambient temperature of 30°C (Hadfield 1975). Mean daily solar radiation at Townsville of 20.06 MJ m^{-2} d^{-1} (Fig 6.1c), or approximately 2.9 J cm^{-2} min^{-1}, over a 12 hr day, would raise leaf temperature in *C. sinensis* var. *assamica* an average 5.8° C above ambient temperature, the rise being greater during the middle of the day, and less towards dawn and dusk. A reduction of light intensity to 10% and 1% would reduce this increase to

0.57° C and 0.057° C respectively. Hence, only plants in the full sunlight treatment would be likely to have experienced foliage temperatures significantly above ambient air temperatures. Daily maximum temperatures exceeded 30°C regularly from the eleventh week of the experiment (Fig 6.1b). Therefore foliage temperatures in the exposed treatment may have reached lethal temperatures.

The cladodes of *Allocasuarina* species are less affected by the heating by sunlight than are leaves (Withers 1978b) and needle-shaped leaves are more efficient at dissipating heat (Gates 1965). Therefore, the effect of insolation on cladodes would be less than that on *C. sinensis* var. *assamica*. Among plants with a similar leaf form, angle of incidence to the sun appears to be the most important factor determining the effect of insolation on foliage temperature (Hadfield 1975). Thus, seedlings of *A. littoralis*, with more erect cladodes and a greater angle of incidence to the midday sun than *A. torulosa*, may be less affected by solar radiation. Differences in reflectivity of foliage may also contribute to or counteract foliage temperature differences. However, no data on this factor are available for the Casuarinaceae. In some North Queensland populations of *A. littoralis*, glaucous foliage (pers. obs.) may afford further protection from insolation, although reflectivity in the visible spectrum may not be paralleled by that in the infrared range (Gates and Tantraporn 1952). If transpiration rate of *A. littoralis* exceeds that of *A. torulosa* in the field as well as under glasshouse conditions, the cooling effects of transpiration (Hadfield 1975) should result in a further reduction in its cladode temperature.

Although the light intensity in the moisture experiment was 30%, the effects of intense sunlight were not exhibited in that experiment.

This is likely to be a result of the absence of direct light, as light intensity was reduced by opaque plastic, rather than a cloth mesh. Therefore, plants in the moisture experiment would have been protected from the effects of insolation and ultraviolet radiation.

Under a particular set of environmental conditions, plant growth is closely related to net photosynthetic rate (Chabot 1978). Therefore, biomass of *A. littoralis* and *A. torulosa* at 10% and 1% R.L.I. are likely to reflect relative photosynthetic rates at those light levels. As biomass production was similar at 10% and 1% R.L.I., photosynthetic rates occurring at 10% sunlight do not appear to have been greater than those at 1% sunlight for either species. Shade tolerant plants show little increase in photosynthetic rates with increasing levels of light intensity (Boardman 1977), but increase the area of their photosynthetic tissue, although without increasing shoot weight (Evans and Hughes 1961). Both species appear to be shade tolerant, as they had significantly greater shoot : root ratios, and similar total biomass at 1% R.L.I. than at 10% R.L.I.

The significantly greater resource allocation to shoot biomass at the lower light intensity may be due to increased availability of moisture, or an indication that light is limiting to plant growth (Brouwer 1962). That allocation to shoots was consistently greater in *A. torulosa* suggests that, except where moisture is limiting, this species should have a competitive advantage over *A. littoralis*. However, such an advantage was not demonstrated at the light levels used in this experiment. Shade tolerant plants may increase their Leaf Area Ratio, without adjusting root : shoot ratio, or despite an increase in root : shoot ratio (Evans and Hughes 1961; Hiroi and Monsi 1963; Jarvis 1964). However, cladodes may be less morphologically versatile, in which case an decrease in root : shoot ratio may be the only means by which photosynthetic area can be increased in cladode bearing plants.

The photosynthetic compensation point of *A. littoralis* in Victoria was found to be 27 μM m^{-2} s^{-1} (Withers 1979b), or equivalent to 1.7% R.L.I. at Townsville, and similar to that used in the lowest light treatment. In this study, there was no indication that either species was close to its photosynthetic compensation point at 1% R.L.I., as the performance of both species was similar as at the higher light level.

As the total biomass production of each pot of plants was not significantly affected by species composition at either light intensity, *A. littoralis* and *A. torulosa* can be considered to be drawing on a common pool of resources, and thus to be in direct competition with each other (de Wit 1960; Hall 1974). Under the lowest light intensity used here, the interspecific competitive abilities of *A. littoralis* and *A. torulosa* were equivalent to their intraspecific competitive abilities. However, greater biomass of *A. littoralis* than of *A. torulosa* indicates *A. littoralis* has a greater competitive ability at the higher light level. This may be afforded by the greater investment by *A. littoralis* in root biomass resulting in a superior ability to exploit moisture supplies. Although in the 1% sunlight treatment *A. littoralis* had a similarly greater investment in roots than *A. torulosa*, moisture supply was less likely to be limiting as evaporative loss from this treatment by the dense shade cloth may have been reduced.

While the artificial shade produced in this experiment would have reduced moisture stress due to evaporative losses, that produced by dense sub-canopies of *Allocasuarina* spp. was associated with low soil moisture due to competition from established plants (Chapter 5). Under such conditions, survivorship of both species was extremely low (Chapter 5).

These results suggest that when plants of *A. littoralis* and *A. torulosa* are grown in close proximity under medium to high light intensity, those of *A. littoralis* will be more successful. Seedling architecture suggests that *A. torulosa* plants will be more successful at low light levels, but the performance of this species was not superior to that of *A. littoralis* under the conditions used in this study.

6.5 Summary

The results of the experiments in this chapter suggest that where moisture availability is limiting or highly seasonal, *A. littoralis* will be favoured over *A. torulosa* because of its greater root : shoot ratio and transpiration rate, and its erect foliage, which minimizes insolation and solar radiation effects and maximizes stemflow. Conversely, *A. torulosa* may be favoured in environments where light is limiting, because of its greater investment in shoots and the horizontal foliage of its seedlings, which will maximize light interception, although this was not supported by experimental evidence.

CHAPTER 7

POPULATION STRUCTURE AND REPRODUCTION

7.1 Introduction

The age-structure of a plant population is the consequence of both recruitment and loss of individuals, and therefore cannot alone be used as a record of the population's history (Harper 1977). Where there is no means of determining plant age, such as in the Casuarinaceae, population structure must be described in terms of size-class frequency. Size-classes are also dependent on growth, which is influenced by competition and site quality, presenting further difficulty to the reconstruction of population history (Hartshorn 1975). However, there have been several attempts to determine recruitment patterns from size-class structure alone, both in the Casuarinaceae (e.g. Chesterfield and Parsons 1985; Hazard and Parsons 1977) and in other species (Johnson and Bell 1975). Woolfrey (1985) concluded that a reverse J-distribution of *C. cunninghamiana* gave no indication of recruitment patterns. Harper (1977 p 601) argues that size-class distributions are better used to predict future population development, and such has been attempted with transition matrices (Lefkovitch 1965; Leslie 1945). However, as transition matrices assume the continuation of the same environmental conditions from the period of observation to that of prediction, their predictions can rapidly depart from reality (Enright and Ogden 1979). Absence of smaller size-classes is likely to indicate lack of recent recruitment (Harper 1977). This has been shown in some Casuarinaceae populations (Chesterfield and Parsons 1985; Withers and Ashton 1977). If growth rates are known, it may be possible to estimate time spent in each part of the plant life cycle.

Information may also be obtained about differential mortality between the sexes of dioecious plants (Lloyd 1973). Populations of dioecious plants are composed of two sub-populations, a female population and a male population, which may have different growth (Grant and Mitton 1979) and mortality rates (Lloyd and Webb 1977). The relative size of these sub-populations, or sex ratio, may deviate from 1 : 1 (female : male), even when that of the seed populations does not (Putwain and Harper 1972). Although the overall sex ratios of *C. cunninghamiana* populations in the Australian Capital Territory were found to be 1 : 1, females predominated on mesic sites, and males on xeric sites (Woolfrey 1985). Similar trends have been found in other genera (Fox and Harrison 1981; Freeman *et al.* 1976), and sex ratios have also been found to vary with other environmental factors (Cox 1981; Grant and Mitton 1979).

Differences between species and sexes, in growth and mortality rates, and hence sex ratios, are likely to be linked to the proportion of resources allocated to reproduction, and hence not available for growth (Darwin 1877; Gadgil and Solbrig 1972; Lloyd and Webb 1977; Primack 1979). Natural selection will favour the reproductive effort which maximizes offspring recruitment, with disturbance believed to favour a large reproductive effort, and competition or stress to favour a small reproductive effort (Abrahamson and Gadgil 1973; Gadgil and Solbrig 1972; Grime 1977, 1979).

Reproductive schedules may vary between species and sexes with regard to age or size at first reproduction (Harper and White 1974), frequency, seasonality and duration of flowering and fruiting (Lloyd and Webb 1977), and in the relationship between reproductive output and tree size (Enright 1982; Harper and White 1974; Hartshorn 1975; Sarukhán 1980). Although optimal reproductive schedules will depend on environmental conditions (Barclay and Gregory 1982; Grime 1977; Noble and Slatyer 1980; Schaffer 1974a; Stearns 1977), closely related species are likely to have similar nutrient requirements, and therefore different reproductive schedules may be necessary if they are to co-exist in the same environment (Fleming 1985; Forcier 1975; Rogers and Westman 1979).

Different reproductive efforts may be selected for in the two sexes of the same species. Reproductive effort of females may exceed that of males, because of the cost of nurturing the developing embryo and associated structures (Lloyd and Webb 1977; Stephenson and Bertin 1983). However, in anemophilous species, male and female reproductive efforts appear to be equivalent, because inefficient pollen transfer requires extra pollen production (Givnish 1980; Lemen 1980). In such cases, the sexes could be expected to exhibit similar growth and mortality rates, resulting in a homogeneous, 1 : 1 sex ratio. However, differential growth rates (Grant and Mitton 1979), sex ratios departing from 1 : 1 (Crawford and Balfour 1983) and microdistributional differences (Freeman *et al.* 1976; Grant and Mitton 1979; Woolfrey 1985) have all been demonstrated in anemophilous, dioecious species.

Direct measurement of reproductive effort in tree species presents difficulties, and there has been considerable debate about quantification of resource allocation (Abrahamson and Caswell 1982; Thompson and Stewart 1981). Leaf litter-fall appears to parallel periods of leaf growth in many Australian species (Specht and Brouwer 1975), including *Allocasuarina* spp. (Hannon 1958), and while production and litter-fall may be out of phase in other components (Rogers and Westman 1981; Specht *et al.* 1981), it is possible to relate litter-fall to reproductive productivity if information is concurrently collected on periods of growth and abscission (Ashton 1975a,b,c; Milton and Moll 1982).

In this chapter, the reproductive schedules of *A. littoralis* and *A. torulosa*, both female and male, are examined in relation to population structure and distribution. Lengths of flowering seasons, and the relationships between tree size and fecundity, are determined by monitoring individuals bearing flowers or cones. Litter-fall phenology at Kirrama is monitored as an indicator of reproductive effort. Relative growth rates, mortality rates, and sex ratios are determined and related to reproductive effort.

7.2 Methods

7.2.1 Population Structure and Plant Growth at Kirrama

The 40 x 100 m grid at Kirrama, described in Chapter 4, in which the understorey of the eastern half of the grid was dominated by *A. littoralis*, and that of the western half by *A. torulosa*, was used for monitoring population structure and plant growth. The grid was divided into 40 10 x 10 m plots, within which all individuals of *A. littoralis* and *A. torulosa* were tagged and sexed. Girth at a height of 1.2 m was recorded in July 1982 and July 1984, and converted to diameter (DBH), before further analysis. A size-class distribution was produced for each species, using consecutive 4 cm DBH size-class intervals. Plants in the smallest size-class were only included if they persisted for a minimum of 12 months. Measures of skewness and kurtosis, g_1 and g_2, were applied to determine deviation of these distributions from normality (Sokal and Rohlf 1969 p 116).

As some cones persist on female trees for over 12 months, (Chapter 4), and observation as at Kirrama indicated that most sexually mature female plants bore reproductive structures throughout the year, plants with no reproductive structures throughout the monitoring period were combined with males in the calculation of female : male sex ratios. The sex ratio was calculated for each size-class and plot, and deviation from 1 : 1 was tested using a chi-square test (Sokal and Rohlf 1969 p 561). To test whether sex ratio was influenced by site factors, plots were grouped into four levels relative to position from top of slope. Heterogeneity of sex ratio between these samples was tested by comparison of summed and squared chi-squared measures (Putwain and Harper 1972; Sokal and Rohlf 1969 p 581). Differences in the sex ratios between the smaller and larger size-classes, and between *A. littoralis* and *A. torulosa* were tested with a Chi-squared test for independent samples (Siegel 1956 p 175).

Relative growth rates were calculated as follows (after Harper 1977 p 28):

$$\mathrm{RGR} = \frac{\log_{10} \mathrm{DBH}_2 - \log_{10} \mathrm{DBH}_1}{t_2 - t_1}$$

Where RGR = Relative growth rate,

DBH_1 = Diameter at 1.2 m at time t_1,

DBH_2 = Diameter at 1.2 m at time t_2,

t_1 = October 1982

and t_2 = October 1984

Two-way analysis of variance (Sokal and Rohlf 1969 p 333) was undertaken to test the effect of size-class and sexual activity on relative growth rates.

Each species' population was divided into smaller size-classes (ten 1 cm DBH size-classes up to 10 cm, 10-15 cm, 15-30 cm and 30-60 cm) for calculation of maximum relative growth rates. Regressions were calculated for the highest three growth rates in each size-class against the inverse of the midpoint of each size-class (Sokal and Rohlf 1969 p 430). The difference between the regression was tested (Sokal and Rohlf 1969 p 450), and the intercept between the two lines calculated. Growth of plants from 1 cm DBH was thus predicted.

7.2.2 Structure of North Queensland Populations

Sites of *A. littoralis* and *A. torulosa* which represented a wide range of habitats and vegetation associations in North Queensland were subjectively selected from vegetation maps (Tracey and Webb 1975) and reconnaissance. At each site, a quadrat of 50 to 1260 m^2 was subjectively located to include a minimum of 30 individuals of the particular species concerned. In three cases, only 29 individuals could be located. Where plants were too widely dispersed, transects were employed. Girth at a height of 1.2 m was measured, and, where possible, sex was determined.

For each population, size-class distributions and sex ratios were calculated and analysed (see Section 7.2.3). Heterogeneity of sex ratios between populations was tested by pooling all North Queensland populations of each species, excluding Kirrama, and comparing summed and pooled chi-square values. Differences in pooled sex ratios between species, and with Kirrama sex ratios, were tested with a chi-squared test for independent samples (Siegel 1956 p 175).

7.2.3 Phenology at Kirrama

Litter-fall phenology was monitored within the grid at Kirrama, using the traps (also used for seed-fall monitoring in Chapter 4) randomly located in the 10 x 10 m plots of Section 7.2.1. The traps were emptied at three to eight week intervals, from 27 July 1982 to 4 August 1984, and the contents placed in paper bags and dried for three days at 60°C to prevent decomposition, before sorting. As it was not practicable to sort all components to species level, traps were designated as either *A. littoralis* or *A. torulosa* on the basis of the vegetation surrounding the litter traps, from records made of all trees of either *A. littoralis* or *A. torulosa* with foliage above a line of 45° projected from the top of the trap, to a distance of 3 m.

All non-*Allocasuarina* litter was bulked. *Allocasuarina* litter was sorted into male inflorescences, female inflorescences, cladodes and twigs, which were not identified to species level, and immature and mature cones which were identified to species level. Pollen losses were assumed to be an insignificant component of the dry weight of male inflorescences. Inflorescences included both those in bud and those in flower. Immature cones were those in which the styles had withered, and some elongation had occurred, but from which seed release was impossible. Mature cones were those that were capable of releasing seed, which was determined by comparison with detached cones. All categories were separately bagged, then dried to a constant weight, or for a minimum of 3 days, at 60°C. Samples were then weighed on a Sauter balance and converted to g m^{-2} d^{-1}. Female reproductive structures were counted. Totals were calculated for vegetative and reproductive components of litter-fall. Seed-fall was described in Chapter 4.

To determine the timing of the developmental sequence of cone maturation, fifty-six immature cones of each species (from a total of six shoots on five *A. littoralis* plants, and ten shoots on four *A. torulosa* plants) were marked at Kirrama in September 1983, and their development followed until March 1985. The number of shoots tagged was limited by accessibility. For the timing of cone initiation, a monthly tally was made of all new reproductive structures on these shoots for 12 months From March 1984. Female reproductive structures were classified as in the litter-trap contents. However, open cones, in which any bracteolar valves had opened, were also recorded.

In August 1983, approximately 100 individuals of each species, of representative sizes were tagged at the Kirrama study site. These plants were monitored for flowering and fruitin on a monthly basis until April 1985 (excludind December 1983 and February 1985). Trees positively identified as male were divided into 4 cm DBH size-classes, and the proportion of each size class in flower each month calculated. Mean cone load over the monitoring period was calculated for female trees and related to DBH.

7.3 Results

7.3.1 Population Structure and Plant Growth at Kirrama

The frequency distribution of 4 cm DBH size-classes of both *A. littoralis* and *A. torulosa* at Kirrama were reverse J-shaped, with only *A. torulosa* individuals exceeding 32 cm DBH (Fig. 7.1). Many of the *A. torulosa* in the smallest size-classes were resprouts from persistent lignotubers, which bore remnants of dead or damaged shoots.

In *A. littoralis*, the sex of 95.7% of the population, including all plants over 4 cm DBH, was determined. The sex ratio of individuals > 4 cm DBH was significantly biased towards males in the overall population and at all four levels down the slope (as determined by insignificant heterogeneity) (Table 7.1). There was no significant difference between the sex ratio of plants from 4 to 8 cm DBH (1 : 1.60, n = 104) and those greater than 8 cm DBH (1 : 2.11, n = 56) (χ^2 = 0.629, d.f. 1, P > 0.05).

There was a steady increase in the proportion of *A. torulosa* for which sex could be determined, from 1.06%, for plants less than 4 cm DBH, to 100% of those greater than 16 cm DBH. The sex of 95.5% of individuals over 12 cm DBH (n = 46) was determined, with a sex ratio of 1 : 1.09. Sex ratio for individuals greater than 12 cm DBH did not significantly depart from 1 : 1, and was homogeneous at the four levels down the slope (Table 7.1). There was no significant difference between the sex ratio of plants from 12 to 24 cm DBH (1 : 2.08, n = 37) and those greater than 24 cm DBH (1 : 1.09, n = 44) (χ^2 = 1.947, d.f. 1, P > 0.05).

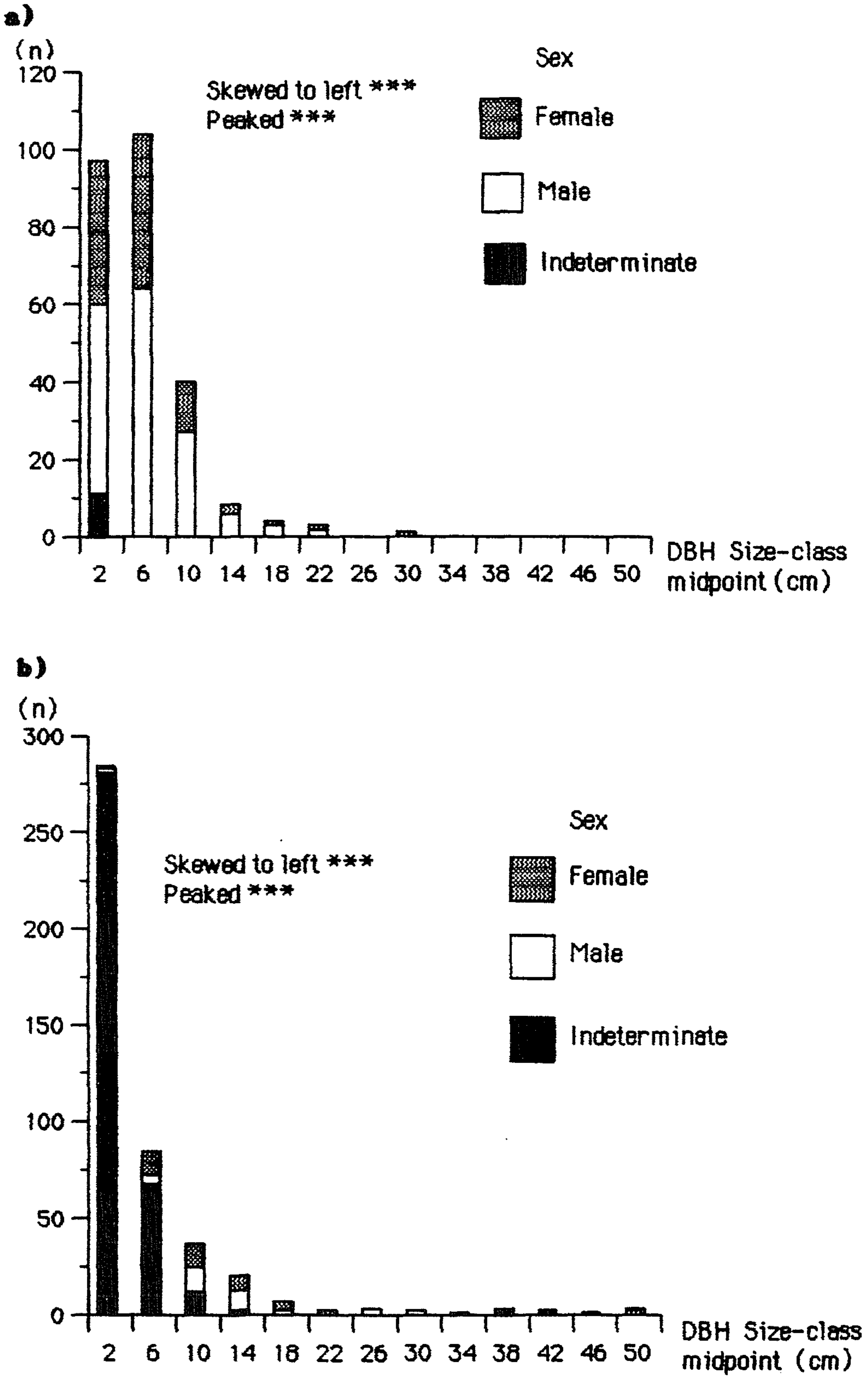


Fig. 7.1 **Stand Structure at Kirrama.**
a) *A. littoralis*, **b)** *A. torulosa*.
Significance of deviations from normality: *** $P < 0.001$.

That the sex ratio of *A. torulosa* was not significantly different to that of *A. littoralis* ($\chi^2 = 2.379$, d.f. 1, $P > 0.05$) suggests small sample sizes may have prevented detection of a significant departure in *A. torulosa*. Surface soil and litter moisture measurements recorded in Chapter 5 showed that moisture availability was greater in the lower sites. Therefore, there was no evidence of moisture availability influencing sex ratio in either species at Kirrama.

The observed mortality of *A. littoralis* over the two year period was 2.72% (Table 7.2), with slightly higher mortality of females (3.16%) than of males (1.99%), and highest mortality in plants greater than 8 cm DBH. Observed mortality of *A. torulosa* was 4.68% (Table 7.2), with mortality of females (4.34%) and plants of indeterminate sex (4.96%) higher than that of males (2.44%). Mortality rate was highest for plants less than 4 cm DBH. Some of the smaller individuals of *A. torulosa* were uprooted by feral pigs, *Sus scrofa*. There were no mortalities in the 4 - 8 cm DBH size-class, in either species.

Table 7.1 Departure of sex ratio from 1 : 1 for mature size-classes of *A. littoralis* and *A. torulosa* at Kirrama.

Four samples per species, stratified relative to position on slope.

Species	No. of Plants		Sum of n χ^2	P	Pooled χ^2	P	Heterogeneity χ^2	P
	f	m/u						
A. littoralis	55	101	13.64	< 0.01	13.56	< 0.001	0.08	n.s.
A. torulosa	22	24	1.02	n.s.	0.09	n.s.	0.93	n.s.

Table 7.2 Mortality over 2 years at Kirrama

Size-class (cm) DBH	*A. littoralis* n	*A. littoralis* Mortality (%)	*A. torulosa* n	*A. torulosa* Mortality (%)
< 4	97	3.09	284	6.33
4 - 8	104	0.00	85	0.00
> 8	56	5.36	80	3.75
Total	257	2.72	449	4.68

In *A. littoralis*, relative growth rate was affected by size-class (F_S = 33.640, d.f. 5,5, $P < 0.001$), but not sex (male vs female F_S = 0.003, d.f. 1,5, $P > 0.05$). There were too few individuals of indeterminate sex in *A. littoralis* for the effect of sexual inactivity to be tested in this species. In *A. torulosa*, relative growth rate was affected by size-class (F_S = 9.040, d.f. 4,4, $P < 0.001$), but not sex (male vs female F_S = 3.438, d.f. 1,4 $P > 0.05$) or sexual inactivity (F_S = 0.205, d.f. 1,3, $P > 0.05$). The high incidence of negative growth of smaller individuals of *A. torulosa* (Fig. 7.2) was caused by stem death followed by resprouting.

Maximum relative growth rate showed an inverse relationship with plant size, represented by the following equations:

$RGR = 0.0034 + (0.2629/(DBH_I))$, ($F_s$ = 809.088, d.f. 1,24, $P < 0.001$)
for *A. littoralis*

and

$RGR = 0.0111 + (0.1717/(DBH_I))$, ($F_s$ = 581.751, d.f. 1,26, $P < 0.001$)
for *A. torulosa*.

where RGR = relative growth rate
and DBH_I = initial diameter at 1.2 m (cm).

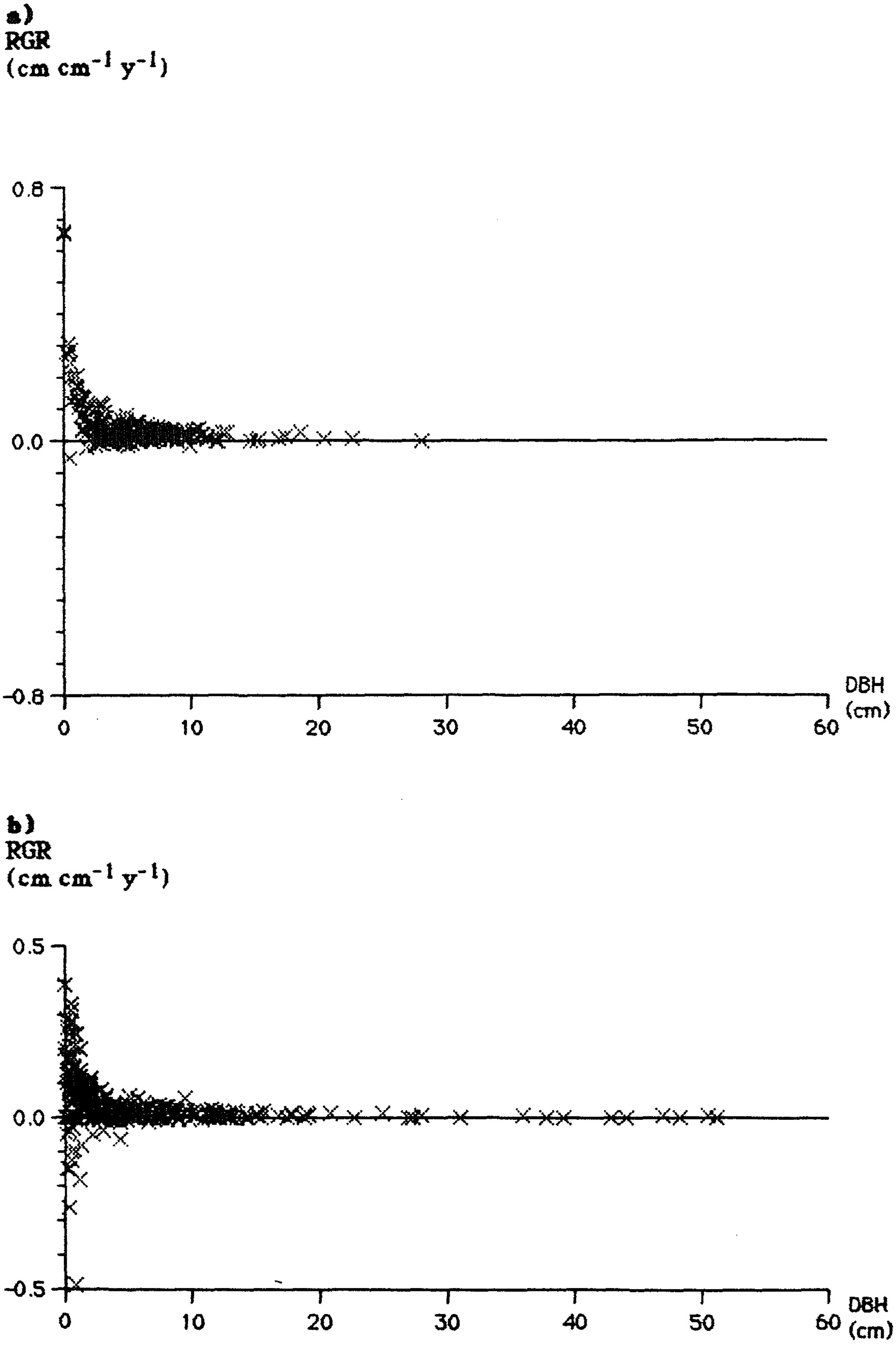


Fig. 7.2 **Relative growth rates (RGR) versus diameter at 1.2 m (DBH) at Kirrama**
a) *A. littoralis*, **b)** *A. torulosa*.

Maximum growth rate curves of *A. littoralis* and *A. torulosa* were significantly different ($F_S = 61.943$, d.f. 1,21, $P < 0.001$), with *A. littoralis* growth rates exceeding those of *A. torulosa* in plants of DBH less than 11.84 cm, and being exceeded in larger plants. These growth rates predict that for plants of an initial DBH of 1 cm, *A. littoralis* plants will be larger than *A. torulosa* of the same age for the following 40 years, after which *A. torulosa* plants will exceed those of *A. littoralis* with the difference in size increasing with time.

7.3.2 Structure of North Queensland Populations

The North Queensland populations of *A. littoralis* and *A. torulosa* which were studied are listed in Table 7.3. The shape of frequency distributions varied markedly between sites in both species (Figs 7.3, 7.4). Five populations of the 13 *A. littoralis* populations were normally distributed. The remaining populations were dominated by the smaller size-classes; three also being peaked (leptokurtic). Six of the 14 *A. torulosa* populations were normally distributed, five were dominated by smaller size-classes, two of which were also leptokurtic, and the remaining three populations had bimodal distributions.

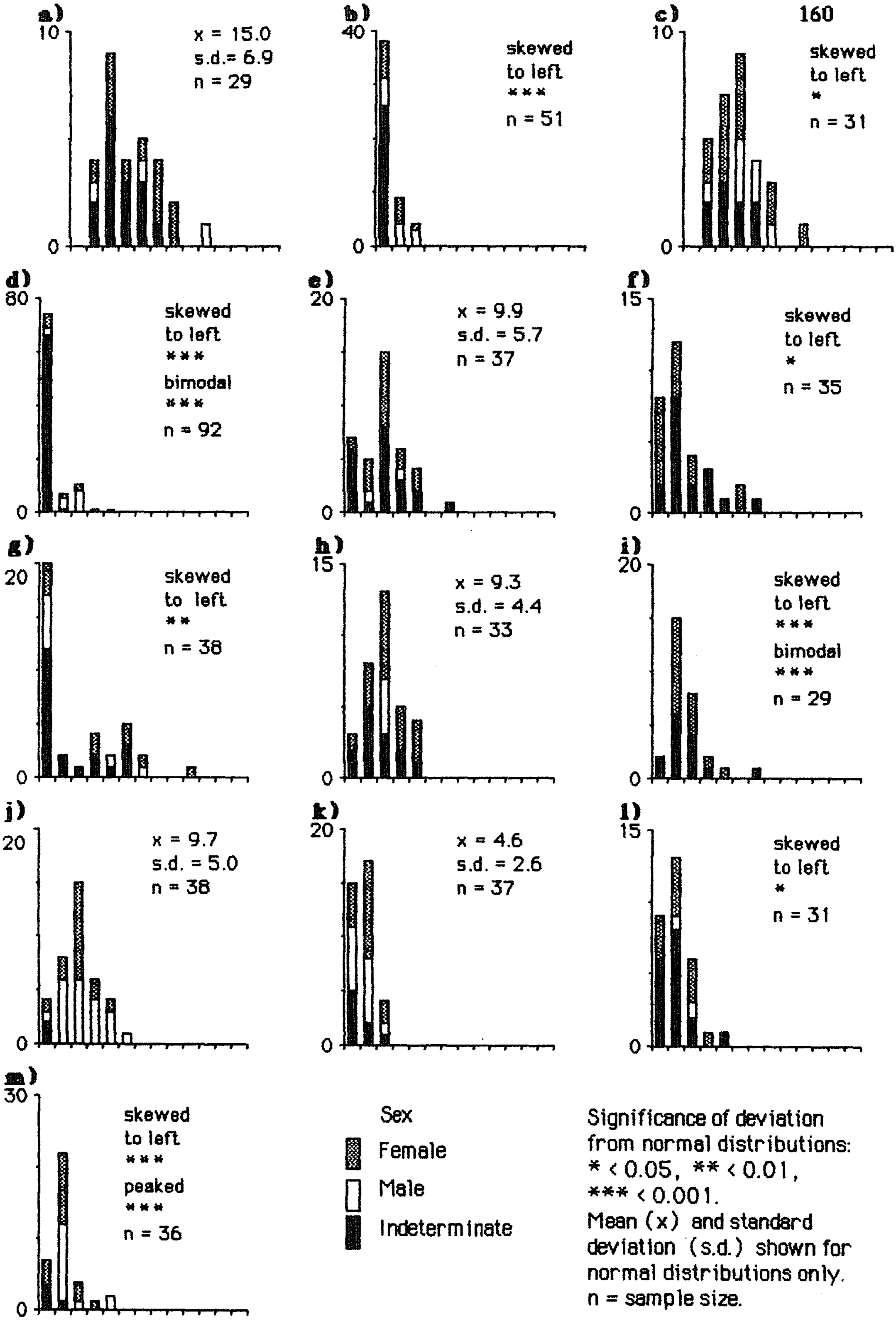
Maximum tree size in *A. torulosa* populations generally exceeded that of *A. littoralis*. 10.5% of *A. littoralis* and 25% of *A. torulosa* plants were larger than 16 cm DBH. Mean DBH in normally distributed populations ranged from 4.6 to 15.0 cm (average 9.6) in *A. littoralis* and from 5.9 to 32.5 (average 15.6) in *A. torulosa*.

Table 7.3 Description of North Queensland Populations

A. littoralis			*A. torulosa*		
	Density (no. m^{-2})			Density (no. m^{-2})	
Site	All	> 4 cm DBH	Site	All	> 4 cm DBH
Isabella	no plot		Boolbun 2	659	401
Wallaby	2993	2064	Gillies	424	413
Home Rule	466	214	Atherton 3	278	278
Boolbun 1	445	445	Wongabel 1	4600	2900
Julatten	2028	1888	Wongabel 2	798	798
Atherton 1	240	240	Wild River	327	14b
Holdcroft	620	460	Cardstone	no plot	
Coolgara	1276	250	Kennedy	1227	659
Bilyana	3110	793	Oak Hills 2	940	463
Sullivan	2711	1579	Wallaman 2	18849	3968
Oak Hills 1	969	867	Fox 2	1152	485
Wallaman 1	7143	5754	Paluma 1	667	435
Fox 1	509	415	Bluewater	741	525
			Elliot	1425	739

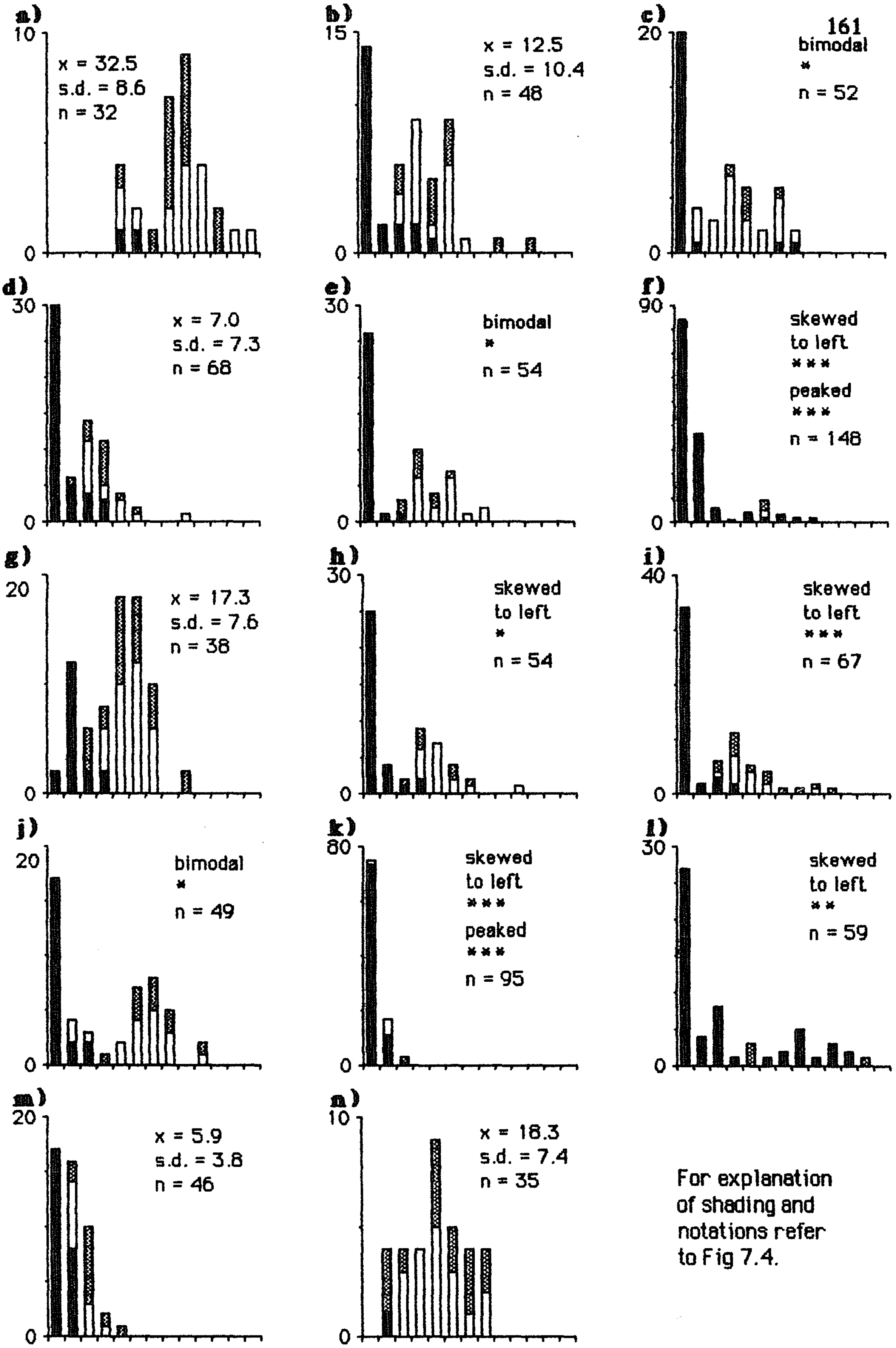
A large number of seedlings observed in the survey of sites were in beds of charcoal. Many of the other plants in the smallest size classes in *A. torulosa* were resprouts from persistent lignotubers.

Sex ratios were calculated for plants greater than 4 cm and 12 cm DBH in *A. littoralis* and *A. torulosa* respectively, assuming from Section 7.3.1 that the majority of females in these classes (referred to as mature size-classes) could be determined. Females comprised 42.4% ± 1.7% of the mature size-classes in *A. littoralis* ($n = 323$), and 37.5 ± 1.7% in *A. torulosa* ($n = 439$), resulting in sex ratios of 1 : 1.36 and 1 : 1.67 respectively. Sex ratio significantly departed from 1 : 1 in



Significance of deviation from normal distributions: * < 0.05, ** < 0.01, *** < 0.001.
Mean (x) and standard deviation (s.d.) shown for normal distributions only.
n = sample size.

Fig 7.3 Size-class distributions for North Queensland populations of *A. littoralis*. a) Atherton 1, **b)** Bilyana, **c)** Boolbun 1, **d)** Coolgara, **e)** Fox 1, **f)** Holdcroft, **g)** Home Rule, **h)** Isabella, **i)** Julatten, **j)** Oak Hills, **k)** Sullivan, **l)** Wallaby, **m)** Wallaman.
Vertical axes - number of individuals.
Horizontal axes - diameter at 1.2 m size-class in 4 cm intervals.



For explanation of shading and notations refer to Fig 7.4.

Fig 7.4 Size-class distributions of North Queensland populations of *A. torulosa*. **a)** Atherton 2, **b)** Bluewater, **c)** Boolbun 2, **d)** Cardstone, **e)** Elliott, **f)** Fox 2, **g)** Gillies, **h)** Kennedy, **i)** Oak Hills 2, **j)** Paluma, **k)** Wallaman, **l)** Wild River, **m)** Wongabel 1, **n)** Wongabel 2.
Vertical axes - number of individuals.
Horizontal axes - diameter at 1.2 m size-class in 4 cm intervals.

one *A. littoralis* (Coolgara, 1 : 2.80, χ^2 = 4.263, d.f. 1, $P < 0.05$), and five *A. torulosa* populations (d.f. 1, Bluewater, 1 : 2.25, χ^2 = 3.846, $P < 0.05$, Boolbun-2, 1 : 3.80, χ^2 = 8.167, $P < 0.001$, Elliot, 1 : 2.43, χ^2 = 4.167, $P < 0.05$, Kennedy, 1 : 2.83, χ^2 = 5.261, $P < 0.05$ and Wild River, 1 : 3.75, χ^2 = 6.368, $P < 0.05$).

The summed sex ratio did not significantly depart from 1 : 1 in *A. littoralis*, but the pooled sex ratio was biased against females (Table 7.4). However, as sex ratio was not significantly heterogeneous, this discrepancy appears to be due to the sample sizes of individual sites being too small to enable the significance to be detected. In the mature size-classes, sex ratio was relatively constant (Fig. 7.5), and there was no significant difference between the sex ratio of plants between 4 to 16 cm DBH (n = 258) and those greater than 16 cm DBH (n = 55) (χ^2 = 0.032, d.f. 1, $P > 0.05$).

For *A. torulosa* both the summed and pooled sex ratios were biased against females, and sex ratio was homogeneous among the sites (Table 7.4). In the mature size-classes, sex ratio was relatively constant (Fig. 7.5), and there was no significant difference between the sex ratio of plants between 12 to 24 cm DBH (n = 185) and those greater than 24 cm DBH (n = 83) (χ^2 = 0.811, d.f. 1, $P > 0.05$).

The pooled sex ratios of *A. littoralis* and *A. torulosa* were not significantly different (χ^2 = 0.032, d.f. 1, $P > 0.05$), nor was the pooled sex ratio of *A. littoralis* significantly different from the sex ratio of *A. littoralis* at Kirrama (χ^2 = 2.907, d.f. 1, $P > 0.05$), or the pooled sex ratio of *A. torulosa* significantly different from the sex ratio of *A. torulosa* at Kirrama (χ^2 = 2.348, d.f. 1, $P > 0.05$).

Table 7.4 Departure of sex ratio from 1 : 1 for mature size classes in 13 North Queensland populations of *A. littoralis* and *A. torulosa*.

(No *A. torulosa* at Wallaman were > 12 cm DBH).

Species	No. of Plants f	m/u	Sum of n χ^2	P	Pooled χ^2	P	Heterogen -eity χ^2	P
A. littoralis	139	181	13.73	n.s.	5.51	<0.05	8.21	n.s.
A. torulosa	106	188	32.55	<0.01	22.87	<0.001	9.68	n.s.

7.3.3 Phenology at Kirrama

On the basis of the surrounding vegetation, 19 traps were designated as *A. littoralis*, and 18 as *A. torulosa*. Data from a further three traps, surrounded by both species, were not included in this chapter. Male and female trees in the mature size-classes occurred with similar frequency within 3 m of the litter-traps, with 26 of each sex of *A. littoralis* around *A. littoralis* traps, and 18 female, 19 male and 4 indeterminate *A. torulosa* around *A. torulosa* traps. All trees of *A. torulosa* greater than 16 cm DBH could be sexed, with 8 of each sex occurring within 3 m of *A. torulosa* traps.

The major species contributing to non-*Allocasuarina* litter-fall were *Eucalyptus intermedia*, *E. tereticornis* and *E. grandis*. Litter-fall of these species (Fig. 7.6) was similar in traps under *A. littoralis* and *A. torulosa* (1.27 vs 1.34 g m^{-2} d^{-1}), and between years (1.37 vs

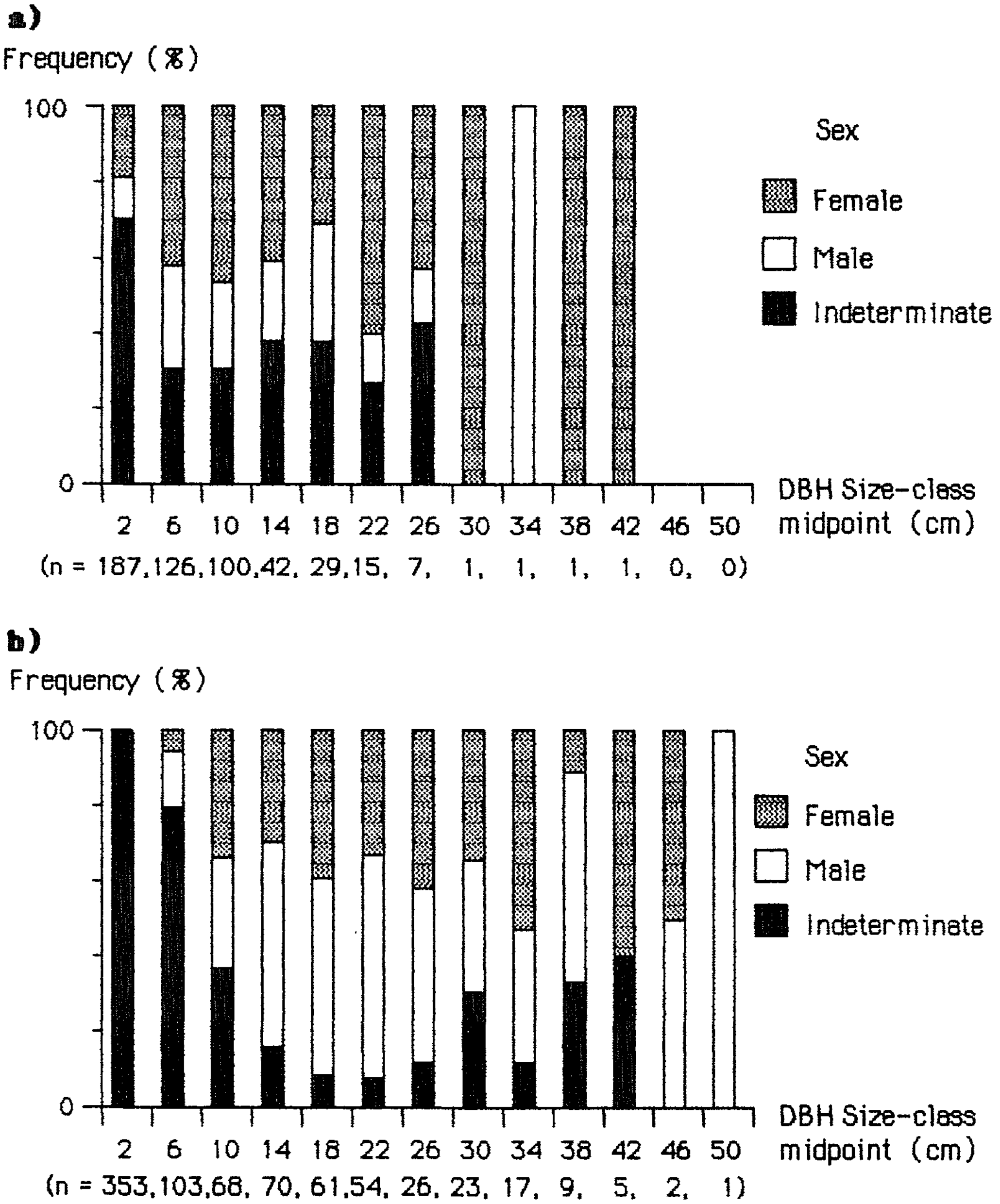


Fig. 7.3 Sex ratios in North Queensland populations.

a) *A. littoralis*, **b)** *A. torulosa*.

Sample sizes in parentheses.

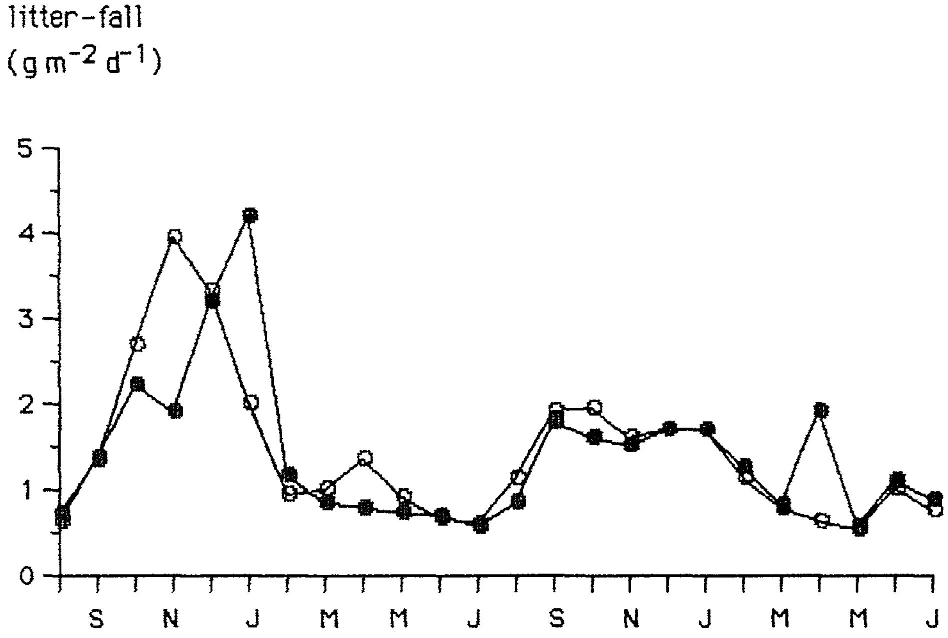


Fig. 7.6 **Total non-*Allocasuarina* litter-fall.**

Kirrama August 1982 to July 1984.

● *A. littoralis* traps,
○ *A. torulosa* traps.

1.24 g m^{-2} d^{-1}). Peak production in the first year occurred from November to December, due to large quantities of bark and wood. There was no major peak in the second year, but high levels were recorded from September to January. Minor peaks also occurred in April of the first year under *A. torulosa*, due to large quantities of *E. intermedia* leaves, and under *A. littoralis* in the second year, due to a *Eucalyptus* branch falling into a single trap.

While total litter-fall of *Allocasuarina* spp. per unit area was lower in *A. littoralis* than in *A. torulosa* (0.42 vs 0.83 g m^{-2} d^{-1}), seasonality was similar (Fig. 7.7). Major peaks in September/October each year were the result of heavy cladode-fall. Secondary peaks, in both species, followed the main flowering periods. There was little difference between years in the vegetative litter-fall of either *A. littoralis* (0.30 vs 0.33 g m^{-2} d^{-1}) or *A. torulosa* (0.75 vs 0.61 g m^{-2} d^{-1}).

Reproductive litter-fall of *A. littoralis* was greatest from November / December and August, peaking in March (Year 1) and May (Year 2). In *A. torulosa*, there was no definite reproductive peak in the first year, but a major peak occurred in May of the second. The reproductive portion of total litter-fall was 30.5% in *A. littoralis*, and 19.0% in *A. torulosa*. The ratio between reproductive litter-fall in the first and second years was 54.9% in *A. littoralis* and 56.0% in *A. torulosa*.

Male and female reproductive litter-fall was similar when averaged over the two year period in both species, but differed between the two years (Table 7.5). In *A. littoralis*, Male reproductive litter-fall exceeded that of females in the first year, and female exceeded male in the second. The reverse was true for *A. torulosa*.

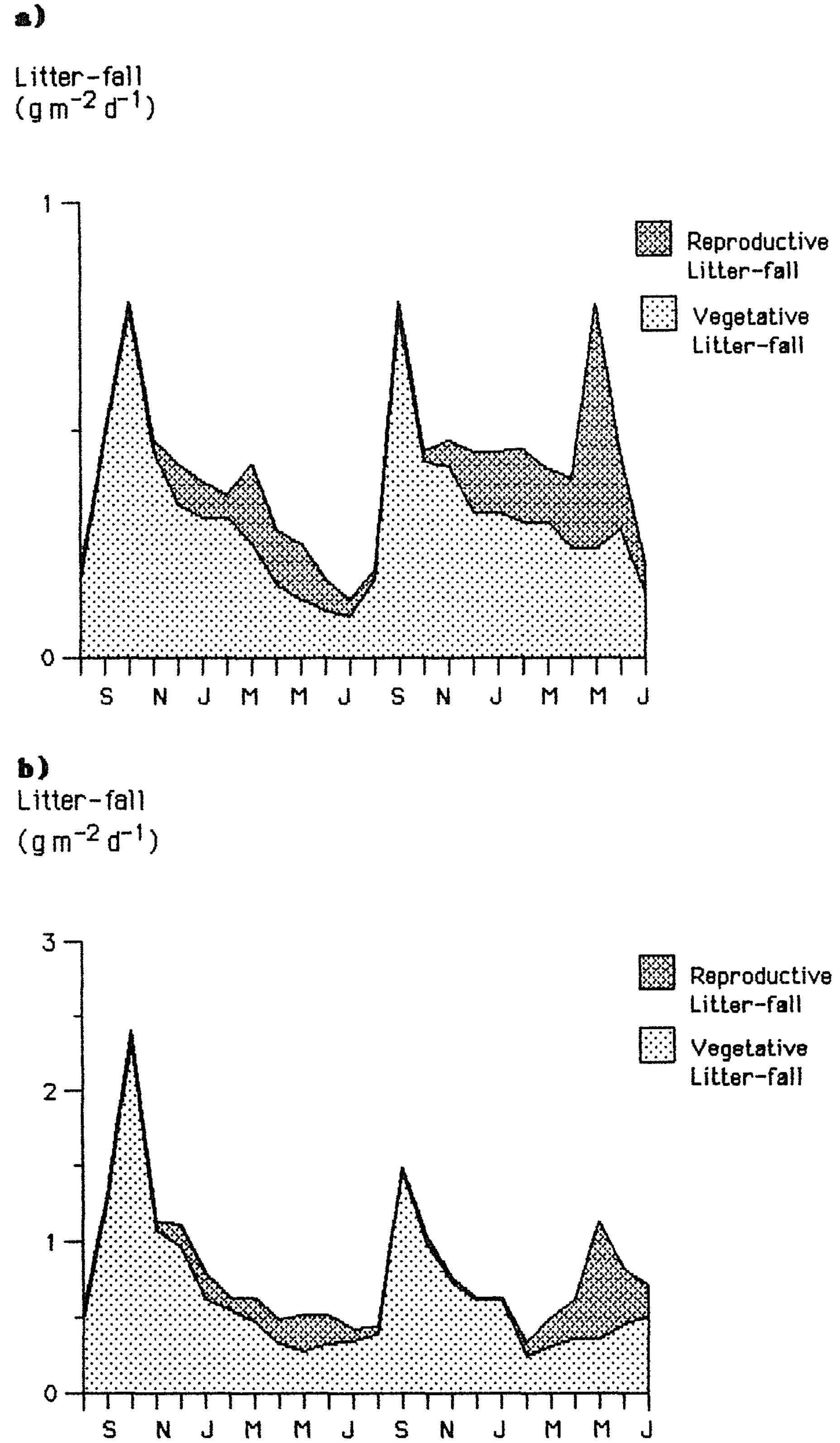


Fig. 7.7 **Litter-fall from *Allocasuarina* spp.**

August 1982 to July 1984.

a) *A. littoralis.* **b)** *A. torulosa.*

Table 7.5 Female and male reproductive litter-fall.

Species	Sex	Year 1	Year 2	Total	Total
		(	$g\ m^{-2}\ d^{-1}$	)	(%)
A. littoralis	Female	0.01	0.08	0.05	0.50
	Male	0.06	0.05	0.05	0.50
A. torulosa	Female	0.09	0.08	0.08	0.53
	Male	0.04	0.09	0.07	0.47

Male inflorescences accounted for 50% and 47% of total reproductive output in *A. littoralis* and *A. torulosa* respectively (Table 7.5). In *A. littoralis*, inflorescences were numerically the most important component of female litter-fall (Table 7.6). However, female inflorescences along with immature cones accounted for a minor proportion of litter-fall by dry weight (Fig. 7.8a). Mature cone-fall was largely restricted to a peak from April to July in the second year. In *A. torulosa*, inflorescences accounted for approximately half the female reproductive structures shed over the two years (Table 7.6). However, cones were the major component of litter-fall by dry weight (Fig. 7.8b).

Although the proportion of female reproductive structures persisting to maturity was similar between species (Table 7.6), earlier abortion in *A. littoralis* resulted in a smaller dry-matter investment for each successfully developed mature cone, with mature cones accounting for 96% and 78% by weight of the female reproductive litter-fall of *A. littoralis* and *A. torulosa* respectively.

Table 7.6 Numerical breakdown of female reproductive litter-fall.

Species	Reproductive Structure	Year 1 no.m^{-2}d^{-1}(%)	Year 2 no.m^{-2}d^{-1}(%)	Mean no.m^{-2}d^{-1}(%)
A. littoralis				
	Inflorescences	0.231 (90.2)	0.251 (69.7)	0.241 (78.2)
	Immature Cones	0.015 (5.9)	0.017 (4.6)	0.016 (5.1)
	Mature Cones	0.010 (3.9)	0.092 (25.7)	0.051 (16.6)
A. torulosa				
	Inflorescences	0.090 (41.7)	0.117 (59.5)	0.104 (50.6)
	Immature Cones	0.099 (45.9)	0.031 (15.6)	0.065 (31.5)
	Mature Cones	0.027 (12.4)	0.049 (24.9)	0.038 (18.3)

In the second year, there was an increase in mature cone-fall (Fig. 7.8) and seed-fall (Chapter 4) for both species. This was coincident with a decline in immature cone-fall in *A. torulosa*, and with female inflorescence-fall in *A. littoralis*. During the second year there was a dramatic increase in male inflorescence production in *A. torulosa*, but not in *A. littoralis*.

In *A. littoralis*, the peak of female inflorescence abortion occurred during that of male inflorescence abscission: from December to April / May (Fig. 7.9a). Most *A. torulosa*, inflorescences were shed between March and June, coinciding with major periods of male inflorescence abscission (Fig. 7.9b). During the first year, however, three peaks in female inflorescence abscission occurred in the absence of male inflorescences.

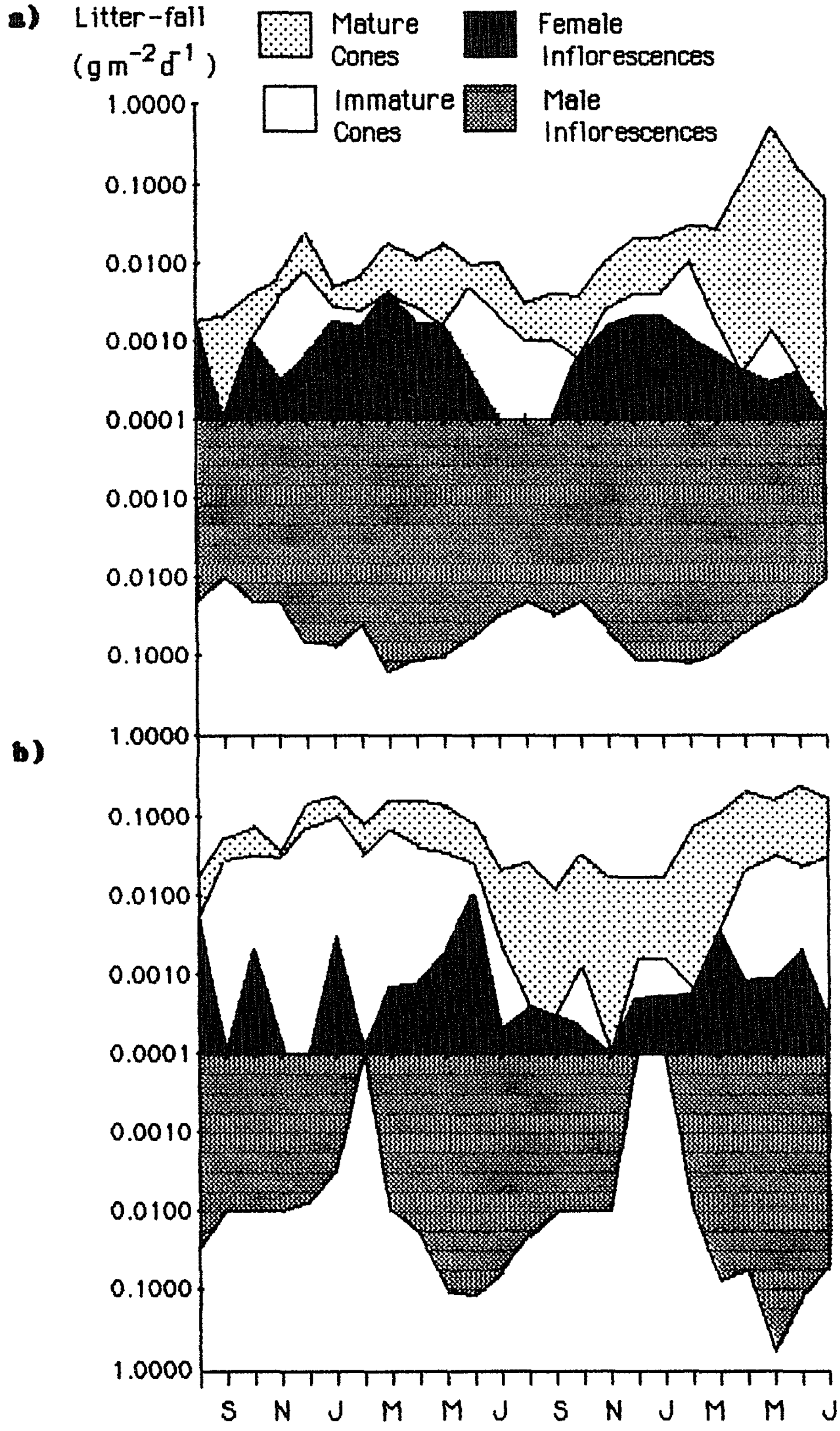


Fig. 7.8 **Comparison between components of female and male reproductive litter-fall.**
August 1982 to July 1984.
a) *A. littoralis*, **b)** *A. torulosa*.

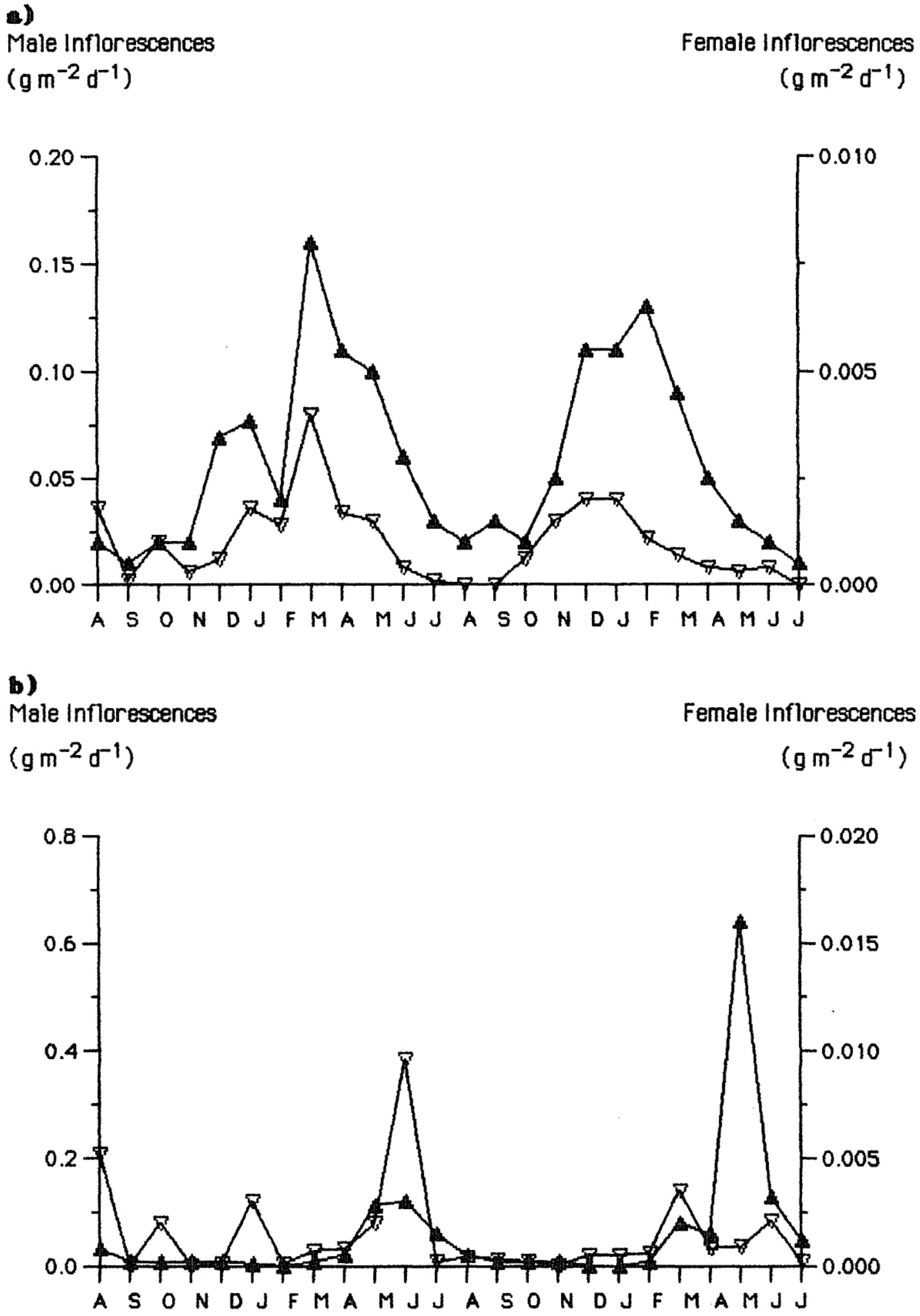


Fig. 7.9 **Inflorescence abscission.**
August 1982 to July 1984.
a) *A. littoralis* **b)** *A. torulosa*
▲ **Male inflorescences,** ▽ **Female inflorescences.**

In both species, immature cones that had been marked during September 1983 reached maturity between the following November and February. About one-third of the cones were still retained by the parent plants of both species 18 months later (Fig 7.10). A tendency, suggested in the litter-fall, for cone abscission in *A. torulosa* to be more protracted than that of *A. littoralis* was confirmed from the tagged shoots, although the main period of shedding in *A. littoralis* occurred in January, rather than in May. Very few opened mature cones were observed on the tagged shoots, indicating that cones were abscised before dehiscence, or soon afterwards. However, older, open cones were observed in the canopies of both species.

Most development of *A. littoralis* inflorescences occurred in January, with minor peaks in September and March (Fig 7.11a). Inflorescences that did not develop into cones were soon aborted. Peak transition between inflorescence and cone development coincided with the peak abscission of inflorescences recorded in the litter traps. Maturation success rates could not be determined from tagged shoots, as it was not known whether changes in inflorescence numbers monitored on marked shoots between visits were due to development or abortion. However, the cone tallies suggested low rates of immature cone abortion.

A. torulosa inflorescences remained in bud for several months. There was a steady increase in the number of inflorescences between July and January (Fig 7.11b). The main period of cone development, from March to July, coincided with the peak period of inflorescence abscission recorded in the litter traps. There a gradual increase in the number of mature cones from July to January, preceding the main

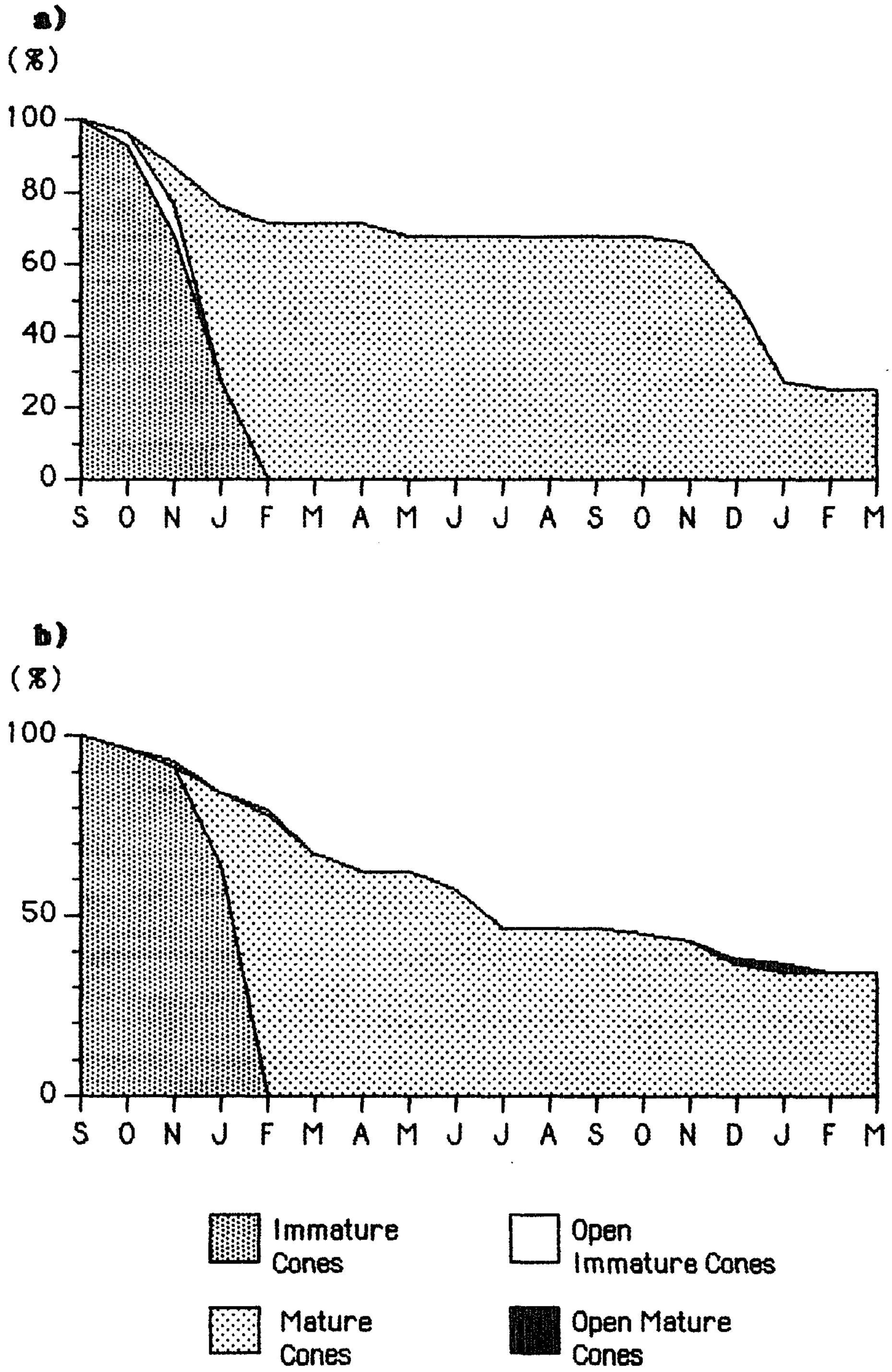


Fig. 7.10 **Fate of Immature Cones present on Trees in September 1983.**

a) *A. littoralis* (n = 56). **b)** *A. torulosa* (n = 56).

No data for December 1983

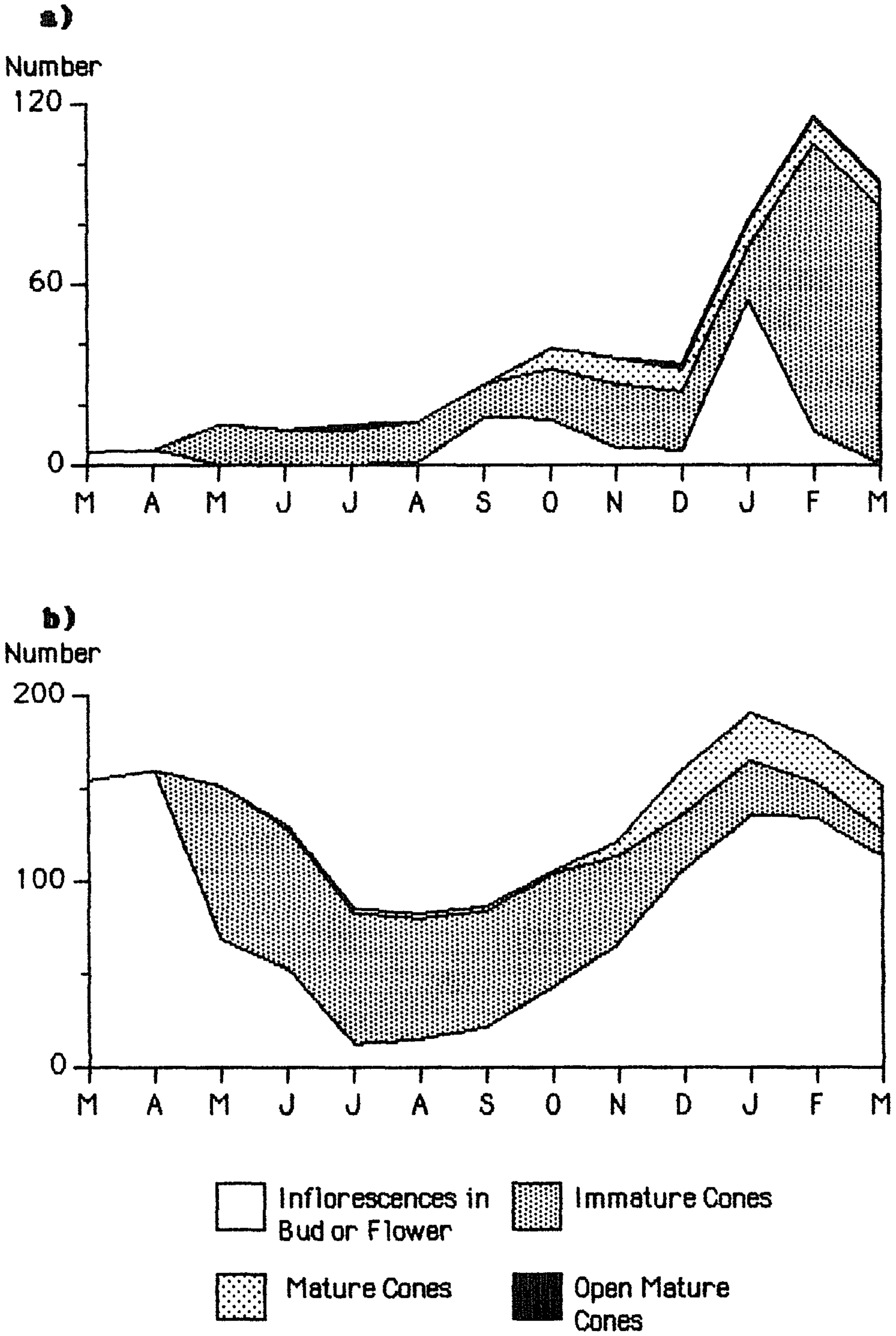


Fig. 7.11 **Monthly tally of reproductive structures developing during or after March 1984.**

a) *A. littoralis*; **b)** *A. torulosa*.

period of cone abscission recorded in the litter traps. Greater reduction in immature cones than increases in mature cones support the finding from litter-fall of high immature cone abortion rates. However, high abortion rates of inflorescences are also suggested.

The flowering period of male *A. littoralis*, as indicated by percentage of plants in flower, extended through most of the year, peaking from November to April with little variation between years (Fig 7.12a). Male flowering occurred in all size-classes. The number of flowering individuals classed as smaller than 1.2 m high increased in the second flowering period due to plant maturation. In 12 of the 19 visits, all identified males over 8 cm DBH were in flower. The reduced incidence of flowering in August and September is in agreement with the low levels of inflorescences shed during this period. In *A. torulosa*, flowering was restricted to the months between February and July, except for two large trees where a small number of inflorescences were noted in November and December 1984 (Fig. 7.12b). Heavy flowering in 1984 coincided with a period of heavy male inflorescence production as measured in litter-fall. The flowering period of 1985 appeared as though it would be lighter in intensity, and was later in starting. There was no flowering in plants of less than 8 cm DBH, and in only one month were all identified males in flower.

Cone production in *A. littoralis* increased rapidly with plant size, reaching a maximum of 1,000 at about 15 cm DBH (Fig. 7.13a). In *A. torulosa*, a maximum of just under 1,000 cones was attained by trees with a DBH of greater than 20 cm (Fig. 7.13b). Below this size, trees carried a crop of between 1 and 300 cones, and few individuals under

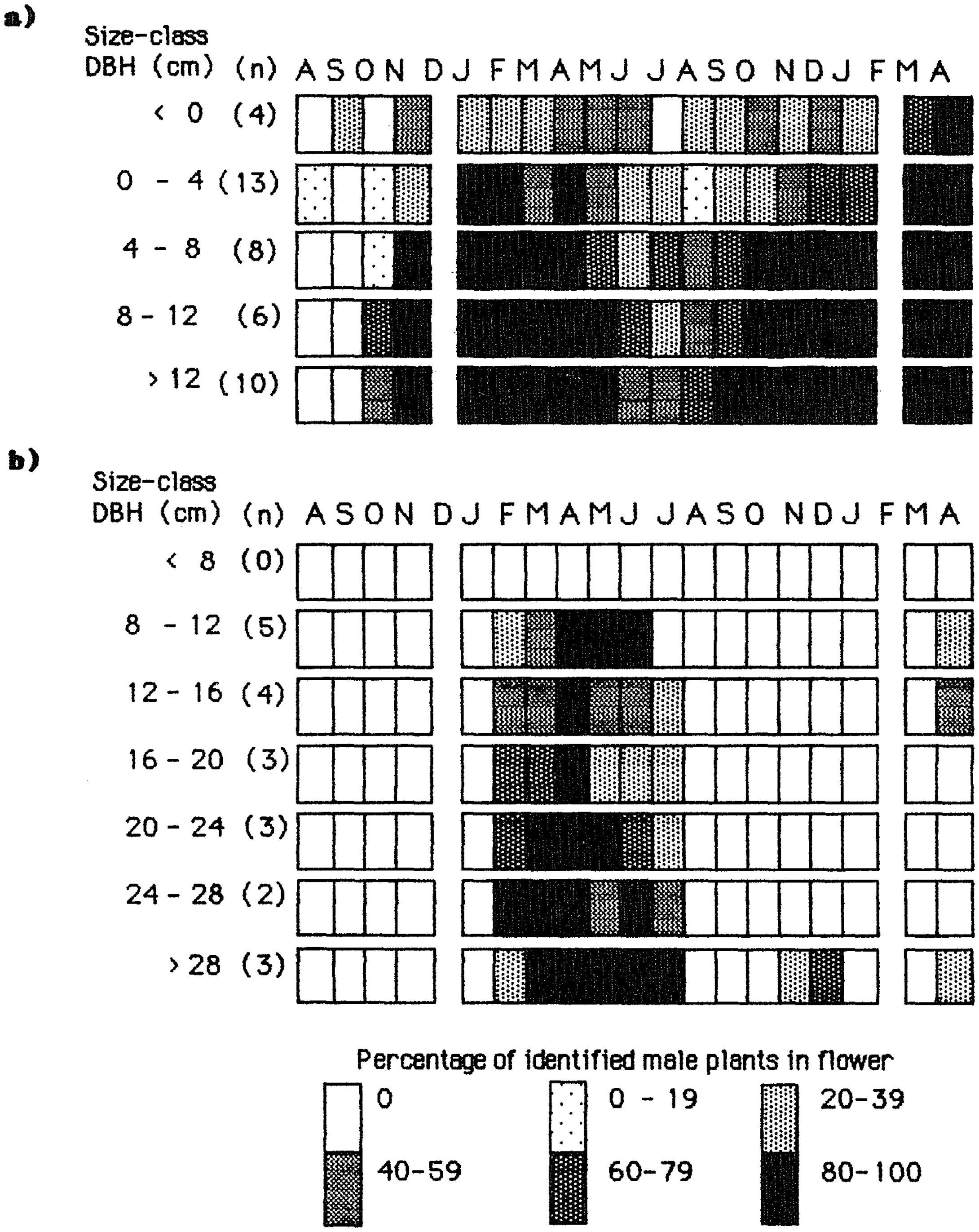


Fig. 7.12 **Percentage of male plants in flower.**

August 1983 to April 1985.

No records for December 1983 or February 1985.

a) *A. littoralis*, **b)** *A. torulosa*.

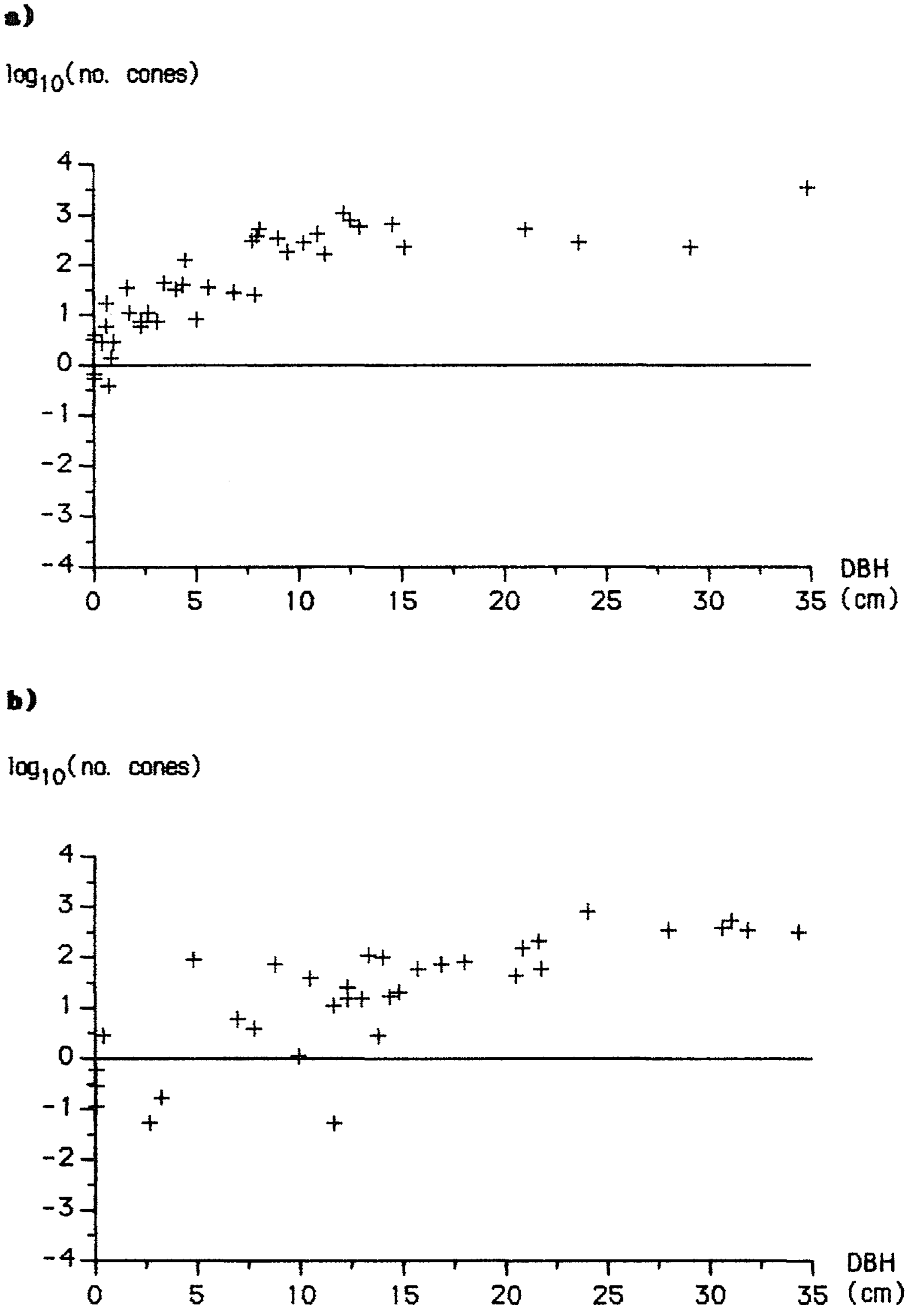


Fig. 7.13 **Mean cone load in relation to tree size.**

a) *A. littoralis* **b)** *A. torulosa.*

5 cm DBH showed any sign of sexual reproduction. By multiplying maximum cone load with average seed number per cone (Chapter 4), maximum seed crop is calculated as 39,300 in *A. littoralis* and 11,500 in *A. torulosa*.

7.4 Discussion

7.4.1 Structure of North Queensland Populations

There was no evidence in either *A. littoralis* or *A. torulosa* of convergence to a stable population structure, as has been suggested for uneven-aged stands by Leak (1964). *A. littoralis* and *A. torulosa* populations in North Queensland, varied from either normally distributed to skewed to the left, (some of the latter also being peaked). Less frequent were bimodal populations of *A. torulosa*. Populations at Kirrama, being peaked and skewed to the left, fell within the range of population structures observed elsewhere in North Queensland. Measurements made at Kirrama are therefore considered applicable to the interpretation of the structure of North Queensland populations.

While it is not possible to determine recruitment patterns from size-class distributions alone, an absence of smaller individuals, as was apparent in two North Queensland populations of each *A. littoralis* and *A. torulosa*, indicates a lack of recent recruitment (Harper 1977; Chesterfield and Parsons 1985). These populations were in open woodland with a grassy understorey, in which fire, with or without cattle grazing, appeared to cause frequent disturbance. However, it cannot be assumed that such fire regimes will prevent regeneration in the long term, as many of the other sites had similar regimes.

Otherwise, *A. torulosa* populations were distinguished from *A. littoralis* populations by two factors: a predominance of individuals in the smallest size-class, (sometimes resulting in a bimodal distribution), and the frequent occurrence of plants in the size-classes over 40 cm DBH. Ford (1975) and Mohler *et al.* (1978) found that bimodality in size-class distributions was characteristic of mature even-aged, monocultures of forests, when relative growth rate increases with size, with competition from the larger individuals suppressing the smaller individuals. However, bimodality does not usually develop in such stands until the smaller size-classes are absent (Ford 1975; Mohler *et al.* 1978). It seems unlikely *A. torulosa* would grow in even-aged stands. Seed is not stored for long periods in the soil (Chapter 5), and, as seed is not effectively transported away from the canopy of the maternal parent (Chapter 4), patches of dense regeneration would be limited to beneath existing stands. There are no records of massive death of existing *A. torulosa* stands, and many plants will survive after fire (Chapter 8). Furthermore, growth rates show an inverse relationship with plant size. Other studies have shown that bimodality may result from growth rate characteristics alone (Turner and Rabinowitz 1983). Therefore, bimodality in these stands may be due either to growth rates or to the persistence of small individuals, as suggested by the high frequency of lignotuber resprouts. Stems of such plants appear fragile, and are frequently damaged. However, in a canopy gap, or in the absence of disturbance, recruitment to the larger size-classes may occur. Such a regeneration pool of small plants is relatively common in lignotuberous *Eucalyptus* spp. (Bowman and Kirkpatrick 1986a; Campbell 1956; Henry and Florence 1966; Incoll 1979; Rotherman 1983). In *E. delegatensis*, suppression of seedlings and saplings is related to distance from adult tree, and although corresponding to light penetration levels, appears to be caused by depletion of soil moisture by existing plants, and seedlings responded well to removal of root competition (Bowman and Kirkpatrick 1986a,b). In *E. marginata*, persistence as lignotuberous seedlings enables root development to reach the water table (Campbell 1956).

The lower relative frequency of small individuals in *A. littoralis* may be caused by lower germination success, higher mortality or more rapid recruitment into the larger size-classes. Germination rates of *A. littoralis* are similar to those of *A. torulosa*, and there is lower mortality within the first year after germination (Chapter 5). Observed mortality of *A. littoralis* at Kirrama was lower than that of *A. torulosa*, and growth rates of small plants were higher. Hence, it appears that there is more rapid recruitment of individuals of less than 4 cm DBH to the larger size-classes in *A. littoralis*. While basal swellings were noted in pot seedlings (Chapter 6), rapid shoot growth may pre-empt the development of large lignotubers in this species.

The absence of individuals of *A. littoralis* of greater than 40 cm DBH, and the preponderance of plants of less than 16 cm DBH, appears to be due to the slower growth rates of larger plants and a higher adult mortality, as were observed at Kirrama, in comparison to *A. torulosa*.

Reasons for the prevalence of seedlings in charcoal beds are investigated in Chapter 8.

7.4.2 Growth and Mortality Rates

The only published records of *A. littoralis* growth rates were of seedlings at Ocean Grove, Victoria, which grew to less than 40 cm high in two years (Withers 1978a). In field trials in Israel, *A. torulosa* grew to a DBH of 12-18 cm in six years at Ilanot, and 0-2 cm in five years in the Negev Desert, and was recommended for afforestation programs as a fast growing species on red sandy loams, as growth rates of this species exceeded that of many other Casuarinaceae spp. (Karschon 1962). In comparison, amximum growth rates at Kirrama predict that six years after planting at 1 cm DBH, *A. littoralis* would reach 5.36 cm, and *A. tourlosa* would reach 4.06 cm. Thus field growth rates of both species are lower thjan those of *A. torulosa* planted on the red sandy loam of Ilonat, but exceed that on desert calcareous loess. If the initially faster growth rates of *A. littoralis* are repeated elsewhere, this species will be suitable for revegetation programs where rapid short-term firewood production, or land stabilization is required. However, where long-term production of timber is required, *A. tourlosa* would eventually yield greater volumes.

Growth rates may vary between sites (Abott and Loneragan 1983; Enright 1982; Wardle 1970) and provenances (Burgess 1975; El-Lakany and Shepherd 1983). A complex quadratic relationship was found in *C. glauca* between stem diameter at one year and latitude of seed origin (El-lakany and Shepherd 1983). Hence, maximum growth rates measured from two years' growth at Kirrama are likely to depart significantly from growth rates elsewhere in North Queensland, and will not necessarily be representative of long term growth at Kirrama. However, they provide some insight into North Queensland populations.

Few North Queensland populations of *A. littoralis* contained individuals greater than 24 cm DBH. According to the maximum growth rate curves for Kirrama, these plants would be less than 30 years old. Similarly, most *A. torulosa* plants were less than 32 cm DBH, or 41 years old. The largest plant at Kirrama would be 34 years old, for *A. littoralis*, and 53 years old for *A. torulosa*. these predictions suggest that *A. torulosa* has greater longevity than *A. littoralis*, and that the size of an *A. littoralis* plant is not exceeded, within its life time, by that of an *A. torulosa* of the same age. The dry weather prevailing during the observation period means that these predictions are likely to be underestimated of growth, and while such figures must be treated with caution, even large deviations from the growth rate predictions would result in similar findings about relative longevity.

Higher adult mortality of *A. littoralis* observed at Kirrama corroborates these predictions, and lower juvenile mortality is supported by the survival of first year experimental seedlings, as noted in Chapter 5. Thus *A. littoralis* has lower juvenile mortality, a higher juvenile growth rate, a higher adult mortality and lower adult growth rate than *A. torulosa*. The apparently bimodal pattern of mortality in relation to plant size may be due to a shift in the factors responsible for mortality; while small plants are vulnerable to disturbance and moisture stress (Chapter 5), mortality risks of larger plants are associated with their high load of respiratory tissue and disease prone material (Harper 1977).

7.4.3 Sex Ratios

As no differences were detected between the sex ratios of Kirrama and other North Queensland sex ratios, the latter were taken to represent the actual sex ratios, namely 1 : 1.36 in *A. littoralis*, and 1 : 1.67 in *A. torulosa*. While both are biased towards males, the bias may be exaggerated in *A. torulosa*, for which the sex of less than 100% of plants in the mature size-classes could be determined at Kirrama.

Male-biased sex ratios occur in numerous plant taxa (Godley 1964; Lloyd 1973), although seed set is maximized by female-biased sex ratios (Kaplan 1972; Lloyd 1974). However, it is unlikely that maximum seed set could be selected for as seed crop size is generally limited by resource availability rather than pollination (Stephenson 1981), and selection for maximum seed quality is expected to select against maximum seed crop (Lloyd 1974). Mechanisms that have been proposed as possible causes of biased sex ratios include differential pollen production, competition between male and female pollen, competition between male and female sporophytes resulting in differential mortality of embryos, juvenile plants or sexually mature plants (Godley 1964; Lloyd 1974).

In *A. littoralis* and *A. torulosa* at Kirrama, there was no evidence from the relative growth rates of differential vigour in reproductively mature male and female plants. Although slightly higher female mortality rates were observed at Kirrama, the constant sex ratio through the mature size-classes suggests they were not sufficiently different to produce a male-biased sex ratio. Sex-linked differences which have been observed in some taxa before reproductive maturity, are more pronounced once reproductive maturity is reached (Lloyd and

Webb 1977). This suggests that the sex ratios were male-biased at germination. Further work is necessary to determine the cause of male-biased sex ratios in *A. littoralis* and *A. torulosa*.

That sex ratios were homogeneous between sites of different rainfall, moisture availability, density, altitude and latitude contrasts with microdistributional differences observed in other wind-pollinated taxa, including *C. cunninghamiana*, in which females were found to predominate on wetter sites (Woolfrey 1985). However, this does not negate the possibility of niche differentiation between the sexes, which may be attained by differences in architecture and seasonality of growth (Putwain and Harper 1972; Stephenson and Bertin 1983).

7.4.4 Vegetative Phenology

Peaks in monthly litter-fall coincide with or follow periods of shoot growth in a diversity of Australian sclerophyllous vegetation communities (Ashton 1975a,c; Hannon 1958; Milton and Moll 1982; Specht and Groves 1966). As scarce nutrients are withdrawn from shoots before abscission - in *A. littoralis* (Fraser 1948) among other species - it appears that shoot abscission is largely regulated by the rate at which nutrients are required for new growth (Specht *et al.* 1981), although extreme climatic conditions may also cause shoot abscission (Ashton *et al* 1975). Specht and Brouwer (1975) have used seasonal patterns of litter-fall as an indication of growth periods in many Australian communities.

Despite variation in rainfall patterns, seasonal patterns of litter-fall of *A. littoralis* and *A. torulosa* were similar between years.

Maximum shoot abscission in both species corresponded with hot, dry weather of September and October, when the photosynthetic index at Townsville is at a minimum, but when new shoot growth of deciduous tropical tree species occurs (Specht and Brouwer 1975).

The canopy species, which dominated the non-*Allocasuarina* littore, may be deeper rooted than *A. littoralis* and *A. torulosa*, which are subcanopy species. If this is the case, then *A. littoralis* and *A. tourlosa* may be exposed to greater heterogeneity of resources than the canopy species. Nevertheless, similar patterns of litter-fall by the canopy species recorded in traps located in stands of *A. littoralis* and *A. torulosa* suggest homogeneous resource availability across the site. Therefore, differences between *A. littoralis* and *A. torulosa* litter-fall seem unlikely to be due to major differences in resource availability. The greater total litter-fall of *A. torulosa* may be due to the greater density and canopy cover of this species, but may also have been caused by the faster adult growth rates resulting in greater foliage production and subsequent foliage shedding. Differences in litter-fall may also result from differential investment in roots and shoots as observed in Chapter 6

7.4.3 Reproductive Phenology

Frankie *et al.* (1974) observed that wind pollinated plants usually flower in the dry season, when the dispersal of pollen is most efficient. However, the major flowering peaks recorded in this study for both *A. littoralis* and *A. torulosa* were towards the end of the wet season. However, the high vagility and abundant production of pollen, characteristic of the family (Kershaw 1970), may enable successful pollination under adverse, wet conditions. Flowering during the summer and autumn months, may reflect the warm-temperate origin of these species, which is suggested in *A. littoralis* by the restriction of diploid populations to the warm temperate and subtropical regions (Barlow 1958). However, no data are available to determine relative flowering success of warm-temperate and North Queensland populations.

Male inflorescence production measured in monthly litter-fall corresponded with the proportion of male trees in flower for the year these records overlapped (August 1983 to July 1984). Thus, almost three years of male flowering records are available. These suggest that intensity of male flowering in *A. littoralis* shows little variation from year to year. Litter-fall and the proportions of male trees in flower records suggest that 1984 was a heavier flowering year than 1983 or 1985 respectively. This may indicate a two or more year cycle, or that there is great fluctuation in fmale flower abundance from year to year in response to environmental conditions.

Although events were recorded slightly later in the litter-fall, close correspondence between peak periods of reproductive activity indicated by litter-fall and direct observation confirms the value of litter-fall for recording reproductive phenology, already suggested by the studies of Ashton (1975b,c) for *Eucalyptus regnans* and Milton and Moll (1982) for *Acacia* spp.

Abortion of female inflorescences and cones, as monitored in the litter traps, corresponded with the production of inflorescences and cones on the tagged shoots. While litter-fall records suggest that the proportion of *A. littoralis* structures aborted at this stage was higher than in *A. torulosa*, observations of tagged shoots suggested the reverse. The greater incidence of *A. littoralis* inflorescence abortion indicated by the litter-fall than by the tagged shoots can be accounted for by the rapid development and maturation of inflorescences. Some of the small, slender buds of *A. torulosa* may not have been detected in the litter-fall. It is therefore possible that the litter trap data provided a more accurate estimate of inflorescence production in *A. littoralis* than in *A. torulosa*. Both sources of data indicated that more immature cones were shed in *A. torulosa* than in *A. littoralis*, and that abscission of mature cones was more protracted in *A. torulosa*. However, in *A. littoralis*, the major period of cone abscission from the tagged shoots was five months earlier than that recorded in the litter-fall. As cone development was monitored outside the grid in which litter-fall was collected, this may indicate variation in the major period of seed and cone fall across the site. It may also indicate variation in timing of cone abscission with cone age, as monitoring of the tagged shoots only recorded abscission of cones less than one year old, while the litter-fall would have included cones of all ages. However, the tagged shoots suggested that first year cones should dominate the cones in the litter-fall.

The proportion of female inflorescences that initiated cones (21.8 and 49.8%), inflorescences that mature into cones (16.6% and 18.3%) and initiated cones that mature (76.1% and 36.9%) in *A. littoralis* and *A. torulosa*, are higher than in most other species for which comparable measurements have been made (Stephenson 1981). Although the proportion of inflorescences recorded as reaching maturity were similar in both species, the greater loss of immature cones in *A. torulosa*, results in a larger dry-matter investment per cone reaching maturity in this species. The difference would be greater if counts of *A. torulosa* inflorescences in the litter-fall were under-estimates.

The tagged shoots showed that different components of female reproductive litter-fall originate from different flowering seasons, with most cones being derived from flowering which occurred within the previous three months, immature cones from flowering between three and ten months previously, and the majority of mature cones from flowering between one and two years previously. Thus, the contribution of each component to the total female litter-fall in any one year does not correspond with the flowering success of a single year.

If the majority of immature cones shed in the first year of monitoring and of mature cones shed in the second year are derived from early 1982, conditions favourable for maximum seed set in both species are indicated for the flowering season of that year. Approximately twice the number of *A. torulosa* cones was aborted in the first year, than was shed as mature cones in the second, and the majority of premature abortions occurred during an extended dry season, suggesting moisture availability was a limiting factor. This dry period appeared to have little effect on *A. littoralis*, for which six times as many mature cones were shed in the second year, than the number of immature cones prematurely aborted in the first year. The low mature cone-fall and seed-fall in the first year of monitoring suggests low seed set from the 1981 flowering for both species.

Premature abortion of female reproductive structures may be caused by inadequate pollination, genetic abnormalities, insect attack or resource limitations (Andersen 1985b; Bierzychudek 1981; Louda

1982a,b; Stephenson 1981). Although dry conditions were implicated in the greater abortion rates of immature cones of *A. torulosa* than *A. littoralis*, the specific causes of abortion of inflorescences and immature cones in these species are unknown.

Peak periods of flower production in many species, are separated by the time taken for seed maturation (Stephenson 1981), or for flowers to develop (Ashton 1975b). As the period between flower initiation and seed-fall in *A. littoralis* and *A. torulosa* is approximately two years, then female flowering peaks could be expected to be about two years apart. This is suggested in both species by the alternation of a year of high seed-fall with one of lower seed-fall, and in *A. torulosa*, by the periodicity of male flowering and the coincidence of high seed-fall and male flower production. Seed production may also vary with climatic conditions during or preceding bud initiation (Harper 1977).

That the cone load of female trees, and propensity to flower in male trees, increase with size to a constant level suggests the absence of a significant post-reproductive period in either *A. littoralis* or *A. torulosa*. Similar fecundity schedules have been described for *Citrus* spp. (Savage 1966), but reproductive senescence has been noted in *A. verticillata* (Hueneke 1976), and in the tropical trees, *Pentaclethra macroloba* (Hartshorn 1975) and *Astrocaryum mexicanum* (Sarukhán 1980).

Despite differences between the components of reproductive output, peak periods of vegetative growth and reproductive output in *A. littoralis* and *A. torulosa* coincide. Therefore, it appears likely that these species would be competing for similar resources at the same time.

This may be one factor contributing to their mutually exclusive microdistributions.

7.4.6 Comparison of Reproductive Effort between Species

The use of dry-matter as a measure of resource allocation has been criticized by Thompson and Stewart (1981), who argue against the use of non-limiting resources. Mineral nutrients and moisture are likely to be the most important factors limiting above ground growth, as they are acquired through the root system (Brouwer 1962). However, which nutrients limit growth in *A. littoralis* and *A. torulosa* has not been determined, and it cannot be assumed that nitrogen and phosphorus are limiting, as their acquisition is assisted by symbiotic relationships (Bowen 1981; Coyne 1983). Therefore, no single nutrient, or group of nutrients, could be identified as more appropriate than dry-matter as a measure of reproductive allocation, and allocation of dry-matter is no less likely to be correlated to allocation of limiting nutrients than are non-limiting mineral nutrients (Abrahamson and Caswell 1982).

Thompson and Stewart (1981) further argue that reproductive structures should not contribute to the resource measured, such as occurs with the contribution of the photosynthetic shoots of male inflorescences to dry-matter production. However, it is expected that the relative photosynthetic contribution will be similar between *A. littoralis* and *A. torulosa*, therefore justifying comparison of dry-matter litter-fall between these species.

The greater reproductive component of litter-fall, longer flowering period, earlier reproductive maturity, greater propensity of individuals to flower, and heavier cone load in *A. littoralis* suggests that this species has a larger reproductive effort than *A. torulosa*. Species with higher reproductive efforts are expected to have slower adult growth rates and higher adult mortality than those with lower reproductive efforts (Gadgil and Solbrig 1972). Both are characteristics of *A. littoralis* in relation to *A. torulosa*. Grime (1977, 1979) proposed that a higher reproductive effort promotes a species' survival in more disturbed environments, and lower reproductive effort is more suited to competitive or stressful environments. This theory suggests that *A. littoralis* is better adapted to survive disturbance, and *A. torulosa* to survive competition and stress. This model will be discussed in Chapter 9 in conjunction with life-history characteristics described in this and other chapters.

7.4.7 Comparison of Reproductive Effort between Sexes

Reproductive effort of males and females in anemophilous dioecious species is thought to be equivalent (Givnish 1980; Lemen 1980). If equal contribution to the litter traps could be assumed, equality of reproductive effort of the sexes is suggested in both species by the ratios between male and female reproductive litter-fall. However, although male and female trees had similar representation in the vicinity of the litter traps, it was not possible to determine the contribution of each sex to the vegetative litter-fall. Therefore the reproductive component of productivities could not be determined relative to total output for each sex. However, one important feature of the litter-fall is that, in both species, female reproductive effort was larger than that of male in one year of this study and smaller in the other year. Thus a study of litter-fall over only one year, such as undertaken by Lemen (1980), could give misleading results for species in which relative reproductive activity varied between years.

Although not conclusively established, a two year reproductive cycle in *A. littoralis* females and in both sexes of *A. torulosa* was suggested. Therefore two years' litter-fall data may be sufficient for an assessment of relative reproductive effort of the sexes. Average reproductive litter-fall over the two years of this study suggests a similarity of reproductive effort of the sexes in both species. Equality of reproductive effort is further suggested by the absence of differences between the growth rates of male and female plants over the two year period in either species, indicating a similarity between the sexes in the resources allocated to growth. As neither sex predominates on better sites, neither sex is likely to experience greater resource availability. Therefore, the growth rate data suggest that relative allocation of resources to reproductive output is similar between sexes. The absence of effective differences in the mortality between sexes gives further support to the conclusion of equal reproductive effort between the sexes.

Similarity of growth rates (indicating a similarity of resources allocated to growth) between sexually active and inactive plants of *A. torulosa* suggests that non-reproduction is due to limited resource availability. Repression of reproduction by resource limitation has been noted in other species (Harper and Ogden 1970). Thus a threshold of resource availability, above which plants may allocate excess resources to reproduction, is suggested in *A. torulosa*. In *A. littoralis*, higher allocation of resources to reproduction will permit reproduction under conditions which could prevent reproduction in *A. torulosa*.

7.5 Summary

Structure of *A. littoralis* and *A. torulosa* populations indicates little about their history, except where lack of recent regeneration is indicated by an absence of individuals in the smaller size-classes. Small *A. torulosa* may persistently resprout from lignotubers. Thus large numbers in the smallest size-class of *A. torulosa* do not necessarily indicate recent recruitment. *A. littoralis* individuals do not generally persist as suppressed lignotubers, but are more rapidly recruited to the larger size-classes. *A. littoralis* at Kirrama has a greater growth rate than *A. torulosa* up to about 12 cm DBH, after which *A. torulosa* growth rate is faster. Predicted maximum growth rates of *A. torulosa* exceed those of *A. littoralis* at about 40 years. However, *A. littoralis* appear to live to only 30 yrs and *A. torulosa* to about 50 yrs.

Sexual maturity is reached at an earlier age and size-class in *A. littoralis* than in *A. torulosa*, with most plants of *A. littoralis* at Kirrama reaching sexual maturity at less than 4 cm DBH and of *A. torulosa* at more than 12 cm DBH. There is no difference between the growth rates of male and female individuals in either species, and little difference in mortality rates, such that sex ratio in mature size-classes is constant. There is no evidence of niche differentiation between the sexes of either species, with sex ratio remaining homogeneous, and male-biased, across a variety of sites. The bias towards males in the sex ratio appears to be in place before plants reach sexual maturity, and the cause is not apparent.

Litter-fall phenology, in conjunction with direct monitoring of reproductive structures, proved to be a useful indicator of seasonality and magnitude of reproductive output. In contrast to other wind pollinated plants, *A. littoralis* and *A. torulosa* flower towards the end of the wet season, with a high rate of fruit maturation. There was little variation between years in the male flowering of *A. littoralis*, but substantial variation in *A. torulosa*. Most abortions of female reproductive structures in *A. littoralis* occurred at the inflorescence stage. In *A. torulosa*, abortions at the inflorescence stage may have been under-estimated, but more abortions occurred at the immature cone stage in this species than in *A. littoralis*, resulting in a lower dry-matter output per mature cone produced in the former species. A similar proportion of female reproductive structures reached maturity in *A. littoralis* and *A. torulosa*, although reproductive success of *A. torulosa* may have been over-estimated. Most mature cones are shed within one year of maturation, and two years of flowering, but up to one-third of initiated cones were retained for at least 18 months after reaching maturation. A two year cycle in seed production is suggested for both species and in male flower production in *A. torulosa*, but this needs further investigation.

Difficulty in determining the contribution of individual trees prevented calculation of relative male and female reproductive effort. However, as relative reproductive output of males and females varied between years, it is apparent that studies involving a single year of observation could give misleading results. Nevertheless, growth rates, mortality rates, sex ratio and reproductive litter-fall over two years all suggest equality of reproductive effort between male and female plants of both species at Kirrama.

The reproductive schedule of *A. littoralis*, in comparison to that of *A. torulosa*, is characteristic of a shorter-lived species investing a greater proportion of its resources in reproduction. Although the period of reproductive activity was longer, and relative reproductive investment greater, in *A. littoralis* than in *A. torulosa*, similarity of peak periods of shoot growth and reproductive output in the two species may influence their ability to co-exist in mixed stands.

CHAPTER 8

FIRE ECOLOGY

8.1 Introduction

The ability of a population to recover after fire will depend either on the persistence of regenerative ability at the site, through seeds or dormant buds, or the influx of seeds from elsewhere (Noble and Slatyer 1980). Therefore, the impact of fire on a population should be studied at all stages of the life cycle (Gill 1981b; Wellington and Noble 1985a).

Although seed availability often increases after a fire (Ashton 1979; O'Dowd and Gill 1984), as could be expected for *A. littoralis* and *A. torulosa* from the persistence of canopy stored seed (Chapter 4), conditions favourable to germination may not occur immediately after a fire (Cowling and Lamont 1985). Increases in seed availability after fire will be affected by the activity of post-dispersal seed predators (Andersen and Yen 1985; Ashton 1979; O'Dowd and Gill 1984; Wellington and Noble 1985b). It has been shown that reduced predation pressure results in more seed entering safe sites (O'Dowd and Gill 1984), and while it has been suggested that an ash-covered soil surface may contain more safe sites than unburnt or mildly burnt litter (Purdie 1977), no attempt has been made to determine the effect of fire on the availability of safe sites.

The heat generated by fire may either destroy seed or remove the cause of seed dormancy (Beadle 1940) and ash from fires may stimulate germination (Wellington 1981) or have little effect (Renbuss *et al.* 1973). While the temperature tolerance of *A. rigida* has been determined (Beadle 1940), there is no information available regarding the effects of fire on germination in *A. littoralis* and *A. torulosa*.

A. torulosa is reported to exhibit no recovery after slash and burn (Floyd 1966). The only other response to fire recorded for the two species is the ambivalent statement that both *A. littoralis* and *A. torulosa* are "fire tender", but produce vigorous new shoots after fire (Anon. 1984b p 45). No information has been published regarding their responses to fires of different intensity, or the effect of fire in relation to plant size.

In this chapter, the effect of fire on availability of safe sites, germination, and survivorship of juvenile and mature plants will be investigated.

8.2 Methods

8.2.1 Natural Seedling Establishment

During the population survey in July 1983, it was noted that several seedlings were associated with patches of charcoal (Chapter 7). Therefore, the substrate on which seedlings of *A. littoralis* and *A. torulosa* with cotyledons occurred was recorded at 19 sites in North Queensland.

8.2.2 Effect of Ash and Charcoal on Post-dispersal Seed Losses

The effect of charcoal or ash on predation of *A. littoralis* and *A torulosa* seed was monitored. The charcoal and ash used in this experiment was obtained from a forest with *A. torulosa*, *Eucalyptus resinifera* and *E. intermedia* active, immediately after a wildfire. However, this supply was supplemented in later trials by *Eucalyptus* wood, burnt in an open fire place. The charcoal was coarsely ground in a meat mincer to enable an even substrate to be produced.

A 9 x 9m plot was established in Kirrama State Forest under a closed canopy of *A. littoralis*, adjacent to the plot established to measure normal levels of seed losses (Chapter 4). The plot was treated in the same manner, i.e. divided into a grid of 100 numbered stations at one metre intervals, at which the vegetation was cleared, exposing 100 x 100 mm of bare ground. Each station was covered with 10 mm of charcoal. In the evening of the first day, a single seed of *A. littoralis* was placed in the centre of each of 50 randomly chosen stations, on top of the charcoal, and seed of *A. torulosa* was similarly placed at each of the remaining stations. Presence or absence of seed was monitored at 12 hourly intervals for 72 hours.

This experiment was repeated three times between 28/9/83 and 25/11/83, at four week intervals, simultaneously with the experimental trials described in Section 4.2.2, which was used as a control. The charcoal was replaced with fresh material the second time the experiment was undertaken, but the third time, seed was placed on the remaining month-old charcoal.

The above plot was extended on 18/1/84 to 14 x 9m to comprise a grid of 150 stations. All charcoal previously added was cleared from the stations, and one of three treatments applied to the exposed soil. These were (1) control (bare soil), (2) a bed of charcoal and (3) ash, applied as above, each treatment being randomly allocated to fifty stations. A single seed of *A. littoralis* only was placed in the centre, on top of each treatment on the evening of 18/1/84. Presence or absence of seed was monitored at 12 hourly intervals for 96 hours. This experiment was repeated from 5/7/84 for 72 hours. The effect of ash and charcoal on seed loss was tested using a chi-squared test for percentages (Siegel 1956 p 175).

8.2.3 Effect of Fire on Seed Stored in the Surface Litter

To test the effect of heating by fire on germination rate of *A. littoralis* and *A. torulosa* seed, germination trials were undertaken following the methods outlined in Chapter 5 (25°C, 14 hr daylength), using heat- treated seed. Seedlots were divided in two, half being used as a control. The remainder was scattered on trays of sand and covered with leaf litter which was then ignited. The litter was allowed to burn and self-extinguish after a few minutes, and the seed was then recovered. Much of the seed was destroyed by this mild burn. Only firm fat seed with minimal charring was selected for germination trials. Germination was monitored for 42 days.

Statistical analysis follows Chapter 5: an angular tranformation was performed on percent germination data active, t-tests were used to compare homoscedastic data sets and approximate t-tests for heteroscedastic data.

8.2.4 Effect of Ash and Charcoal on Seed Germination

The effect of ash and charcoal on germination of *A. littoralis* and *A. torulosa* seed was tested following the methods outlined in Chapter 5 (25°C, 14 hr daylength). In the experimental treatments, ash or charcoal replaced the filter paper and vermiculite, and was also kept saturated. Germination was monitored for 42 days. 100% germination was calculated separately for each species. Statistical analysis follows that outlined in Section 8.2.3.

8.2.5 Effect of Ash and Charcoal on Pot Seedlings

To test the response of seedlings to fire, 18 one year-old seedlings each of *A. littoralis* and *A. torulosa* were selected. These seedlings were grown in glasshouse conditions (approximate daily temperature range of 20 to 35°C) in 1.7 l pots of mixed topsoil taken from beneath stands of *A. littoralis* and *A. torulosa* at Kirrama State Forest. The seedlings were burnt with a "Soudogaz" liquid petroleum gas torch to produce 100% foliage scorch, then maintained under glasshouse conditions and subjected to one of two watering regimes: wet (watered to pot capacity three times per week) or dry (soil surface moistened three times per week). Recovery was monitored weekly for seven weeks, by measuring number of live shoots and length of longest shoot on surviving plants. An index of photosynthetic area was calculated as a product of longest shoot (L), and shoot number (S), before the burn, and afterwards at weekly intervals (Chapter 6). Recovery was assessed as follows:

$P.I._n = L_n \times S_n$ (Photosynthetic Index)

$R.I._n = P.I._n / P.I._i$ (Recovery Index)

where n = measurements taken at n weeks,

i = initial measurements,

L_i = initial plant height,

and L_n = longest photosynthetic shoot.

As the numbers of plants of each species surviving in each treatment were dissimilar, two way analysis of variance for unequal and disproportionate sample sizes (Steel and Torrie 1960 p 252) was used to determine the contribution of species and watering regime to the Photosynthetic Index and the Recovery Index at seven weeks, for those still surviving. Photosynthetic Index of live plants at seven weeks was tested for relationship to the Initial Biomass Index using regression analysis (Sokal and Rohlf 1969 p 419).

8.2.6 Effect of Fire on Field Populations

Recovery of populations of *A. littoralis* and *A. torulosa* was recorded within one to two months after unplanned fires. *A. littoralis* regeneration was evaluated at one site, Atherton 2 (Site 7), on 8/7/83, and *A. torulosa* regeneration at three sites: Paluma 3 (Site N_3) on the 7/3/82, Paluma 2 (Site N_2) on the 24/11/82, and Wild River (Site F) on the 20/7/83 (for location of sites see Table 3.1 and Fig 3.1). The response to 100% foliage scorch (which both reflects a relatively narrow range of fire intensities and is biologically comparable, representing full loss of photosynthetic ability with little damage to the vascular system (Gill 1981a)) was recorded. No information on fire intensity could be obtained for any of the fires.

Mode of recovery - none, basal lignotuber sprouting (after James 1984) or non-basal, epicormic sprouting - was assessed in relation to plant species, sex and diameter at 1.2 m (DBH).

8.3 Results

8.3.1 Natural Seedling Establishment

Almost all seedlings recorded in the field in July 1983 were growing in charcoal beds (Table 8.1). At most sites there was no sign of recent fire, and the charcoal may have been several years old, or from an isolated burn, such as a camp fire.

8.3.2 Effect of Ash and Charcoal on Post-dispersal Seed Losses

New charcoal, but not old charcoal, substantially reduced the rates of seed loss of both species (Figs. 8.1a,b,c). In the first new charcoal trial, the ratio of seed removed at 72 hrs from charcoal compared to the control was 53% for *A. littoralis* ($\chi^2 = 3.934$, d.f. 1, $P < 0.05$), and 27% for *A. torulosa* ($\chi^2 = 20.543$, d.f. 1, $P < 0.001$). In the second new charcoal trial, this ratio was 27% for *A. littoralis* ($\chi^2 = 23.645$, d.f. 1, $P < 0.001$), and 5% for *A. torulosa* ($\chi^2 = 51.492$, d.f. 1, $P < 0.001$). Higher losses in the first new charcoal trial coincided with higher rainfall (9.6 mm), than in the later new charcoal trial (0.2 mm). This may have resulted in some of the seed being buried within the charcoal beds. Higher loss rates may also have been caused by higher soil moisture or different seed predators being active. On the month-old charcoal, the ratio was 97% for *A. littoralis* ($\chi^2 = 0.053$, d.f. 1, $P > 0.05$), and 86% for *A. torulosa* ($\chi^2 = 2.098$, d.f. 1, $P > 0.05$).

Table 8.1 Occurrence of seedlings of *A. littoralis* and *A. torulosa* in relation to charcoal.

[a] Site numbers refer to numbers in Fig. 3.1.
[b] No sign of recent fire.
[c] Fire occurred within the last two months.

A. littoralis			*A. torulosa*		
Site Name (Site No.)[a]	Number of Seedlings		Site Name (Site No.)[a]	Number of Seedlings	
	Charcoal Bed	No Bed		Charcoal Bed	No Bed
Isabella[c] (1)	40	0	Boolbun 2[b] (A)	0	0
Wallaby[b] (2)	0	0	Gillies[b] (B)	0	0
Home Rule[b] (3)	0	0	Atherton 3[b] (C)	21	0
Boolbun 1[b] (4)	0	0	Wongabel 1[b] (D)	2	0
Julatten[b] (5)	0	1	Wongabel 2[b] (E)	0	0
Atherton 1[c] (6)	4	0	Wild River[c] (F)	2	0
Atherton 2[b] (7)	0	0	Cardstone[b] (G)	0	0
Holdcroft[b] (8)	1	0	Fox 2[b] (M)	1	0
Coolgara[b] (9)	2	1			
Sullivan[b] (12)	0	0			
Fox 1[b] (15)	0	0			
Total (11 Sites)	47	2	Total (8 Sites)	26	0

Both ash and charcoal reduced the rates of harvesting of seed of *A. littoralis* (Figs. 8.2a,b). In the first trial, losses at 72 hrs from the charcoal and ash were equivalent to 80.5% and 58.3% of that from the control ($\chi^2 = 9.211$, d.f. 2, $P < 0.01$). In the second trial, losses at 72 hrs from the charcoal and ash were equivalent to 4% and 7% of that from the control ($\chi^2 = 46.229$, d.f. 2, $P < 0.001$). Again, higher

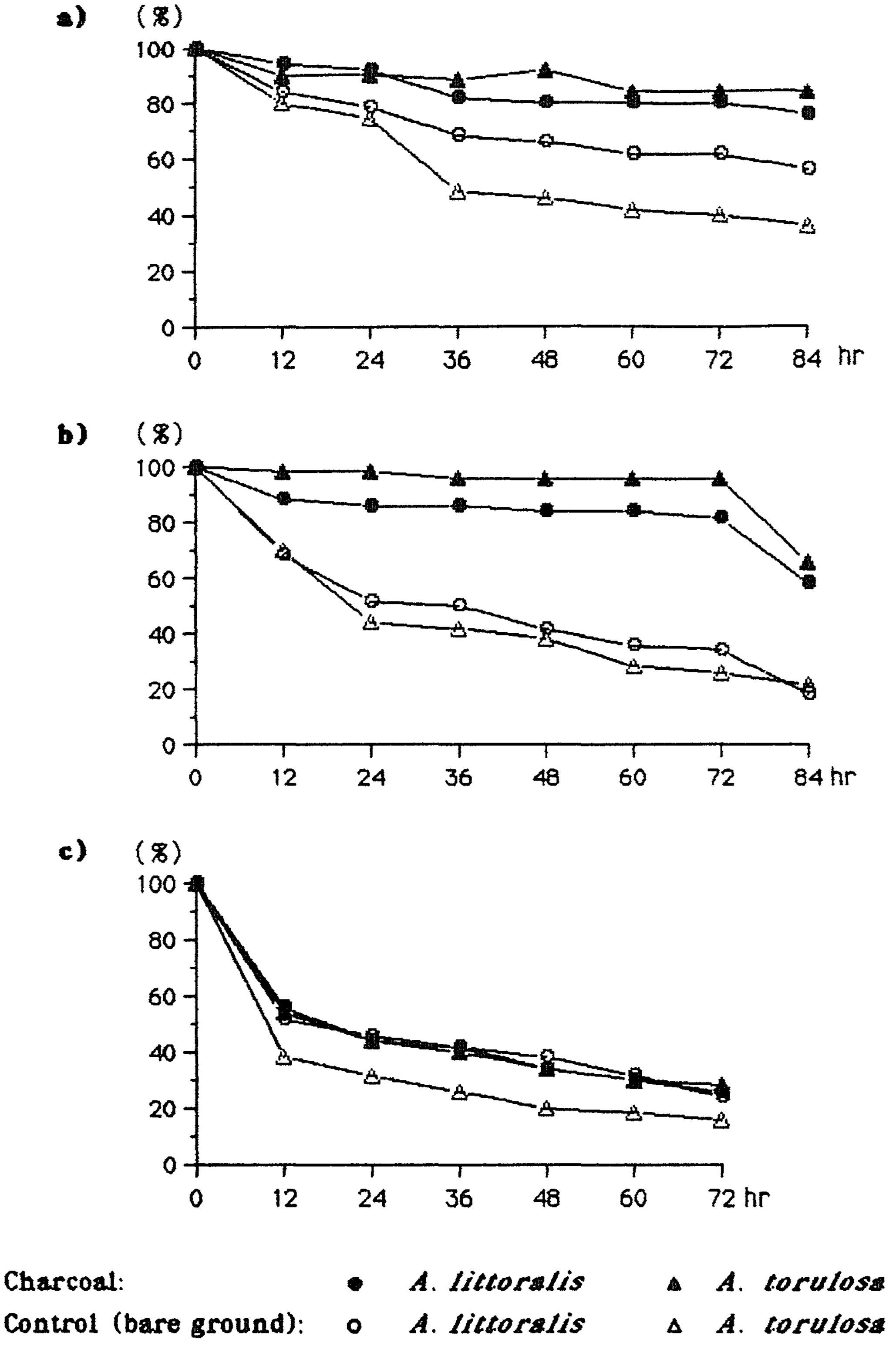
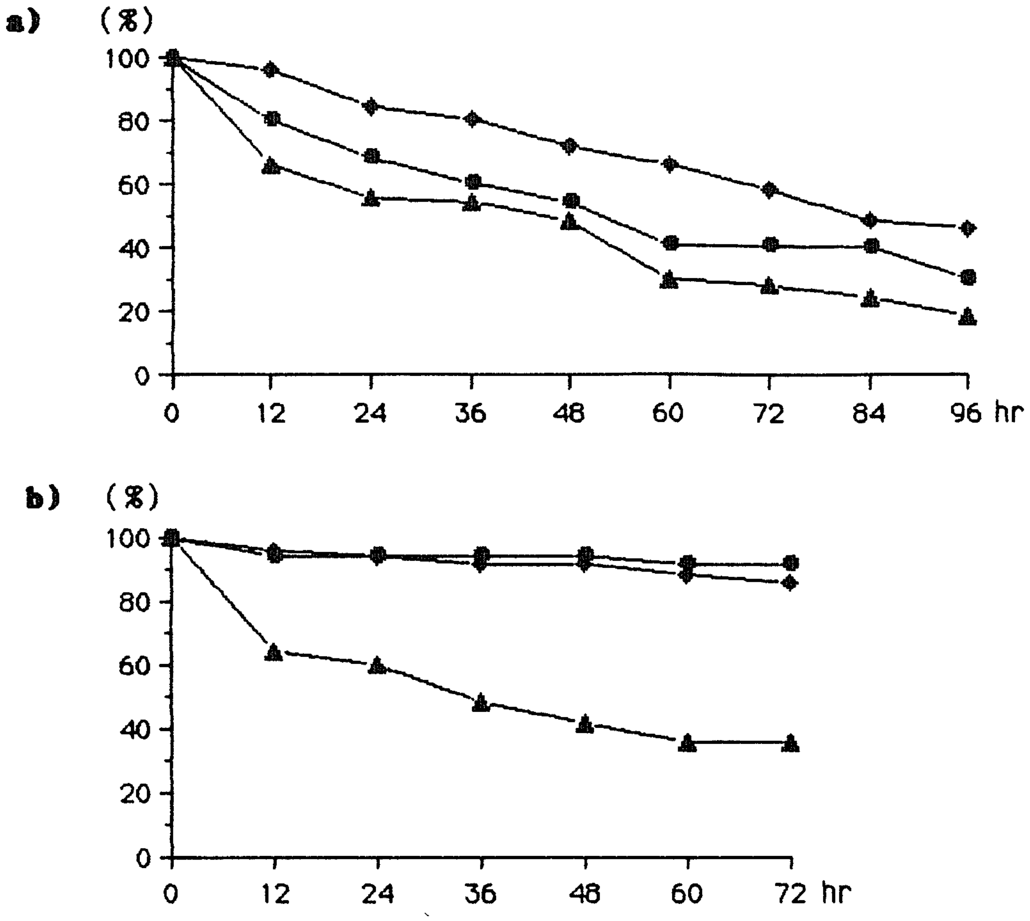


Fig. 8.1 Effect of charcoal on seed loss rates

a) Percent seed remaining on new charcoal and soil, trial 1, 28/9/83.
b) Percent seed remaining on new charcoal and soil, trial 2, 26/10/83.
c) Percent seed remaining on old charcoal and soil, trial 1, 25/11/83.



Substrate: ▲ Control, ● Charcoal, ◆ Ash.

Fig. 8.2 Effect of charcoal and ash on seed loss rates.

a) Percent *A. littoralis* seed remaining on charcoal, ash and soil, trial 1, 18/1/84.

b) Percent *A. littoralis* seed remaining on charcoal, ash and soil, trial 2, 5/7/84.

rainfall during the first trial (13.6 vs 0 mm) may have caused greater apparent seed loss, or seed may have been more vulnerable to predation due to higher soil moisture or differences in the seed predators which were active.

There was no evidence that seed harvested from the ash or charcoal was taken by ants. Rats were also an important vector of seed loss in this area (Chapter 4) and, on two occasions, rat foot-prints were observed in the ash beds from which seed had been removed.

8.3.3 Effect of Fire on Seeds in the Surface Litter

The burning treatment significantly reduced germination of *A. littoralis* seeds from 65.2 to 42.0% ($t_S = 4.347$, d.f. 6, $P < 0.01$), but the reduction for *A. torulosa*, from 69.1 to 50.0%, was not significant ($t_S = 1.975$, d.f. 6, $P > 0.05$). In both species, a slight increase in time to 50% germination was not significant (*A. littoralis*: control 5.9, burn 7.0, approx.-$t_S = 1.940$, d.f. 3, $P > 0.05$; *A. torulosa*: control 5.21, burn 7.06, $t_S = 1.760$, d.f. 6, $P > 0.05$).

8.3.4 Effect of Charcoal and Ash on Seed Germination

In both species, charcoal had no significant effect on percent germination (*A. littoralis* control 63.8, charcoal 62.8, $t_S = 0.154$, d.f. 6, $P > 0.05$; *A. torulosa* control 92.8, charcoal 85.5, $t_S = 1.048$, d.f. 6, $P > 0.05$) or time to 50% germination (*A. littoralis*: control 4.87 days, ash 5.16 days, $t_S = 1.391$, d.f. 6, $P > 0.05$; *A. torulosa*: control 4.47 days, charcoal 4.27 days, $t_S = 2.132$, d.f. 6, $P > 0.05$). In *A. littoralis*, ash significantly reduced percent germination from 63.8

to 43.6% (t_s - 3.301, d.f. 6, $P < 0.05$) and increased time to 50% germination from 4.87 to 21.4 days (approx. t_s - 5.073 d.f. 3, $P > 0.05$). As germination of *A. littoralis* on ash was continuing at day 42 (Fig. 8.3a), the effect of ash germination rate may have been more extreme than indicated above. However, percent germination may not be reduced in the long term. While percent germination in *A. torulosa* was not significantly affected by ash (Fig. 8.3b; control 92.8, ash 82.6, t_s - 1.509, d.f. 6, $P > 0.05$), time to 50% germination was significantly increased from 4.47 to 6.81 days (t_s - 8.028, d.f. 6, $P < 0.001$).

8.3.5 Effect of Fire on Pot Seedlings

In both *A. littoralis* and *A. torulosa*, resprouting occurred along the basal two-thirds of the stem, with over 80% of plants of either species exhibiting recovery within one week of damage. Although some plants had a slight basal swelling, resprouting was not concentrated around this swelling. Most plants of *A. littoralis* survived until seven weeks after the experimental burn (Wet treatment 8, Dry treatment 9), while only four *A. torulosa* plants survived in either treatment (Fig. 8.4). Although the mean size of *A. littoralis* plants, as measured by the Initial Biomass Index, was greater than for *A. torulosa* (6.679×10^4 vs 2.378×10^4, t_s - 4.358, d.f. 34, $P < 0.001$), there was no significant difference between the Initial Biomass Index of *A. torulosa* plants which survived and those that died (2.593 vs 2.206, t_s - 0.711, d.f. 16, $P > 0.05$). This suggests that plant survival was not related to initial size.

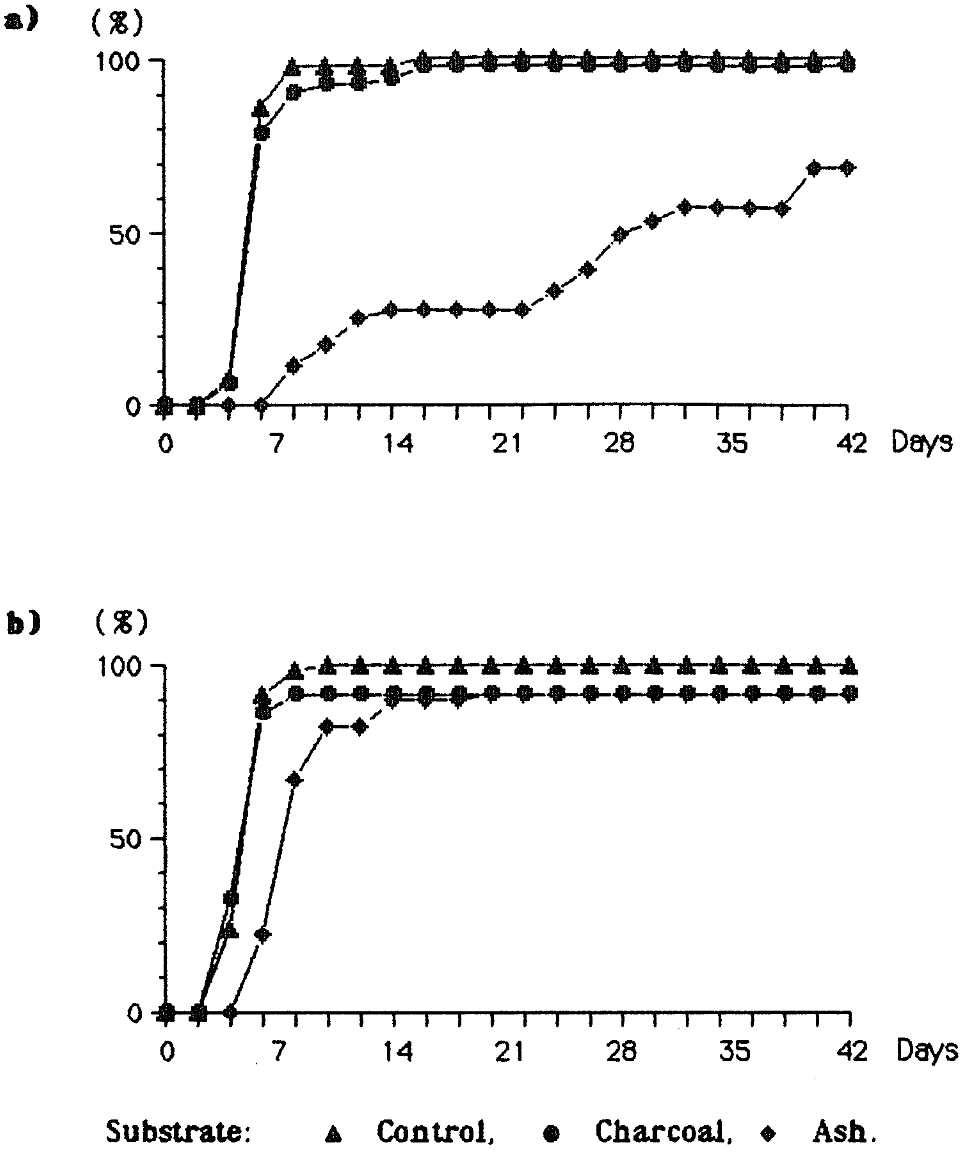


Fig. 8.3 **Percent germination versus time for seeds in control, charcoal and ash treatments.**

a) *A. littoralis* **b)** *A. torulosa*

100% germination = mean germination of control treatment at 42 days.

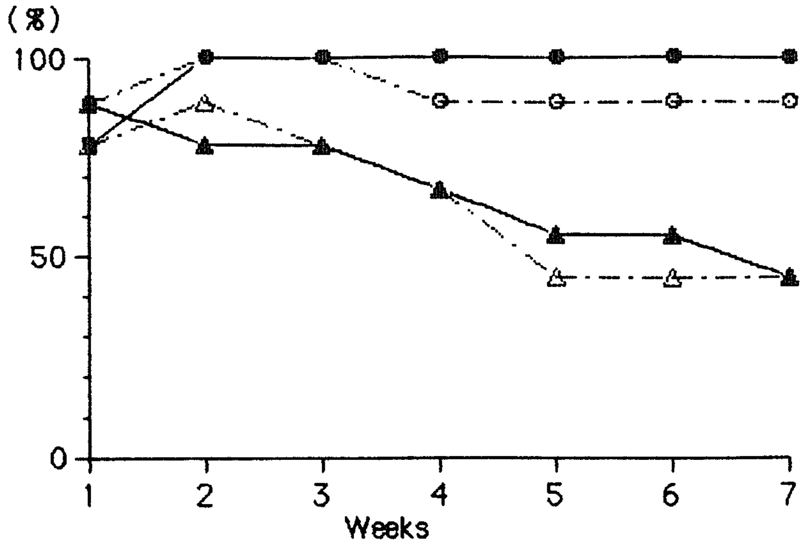


Fig. 8.4 **Percentage of plants with green shoots after 100% foliage scorch.**

Dry treatment: ● *A. littoralis*, ▲ *A. torulosa*,
Wet treatment: ○ *A. littoralis*, △ *A. torulosa*.

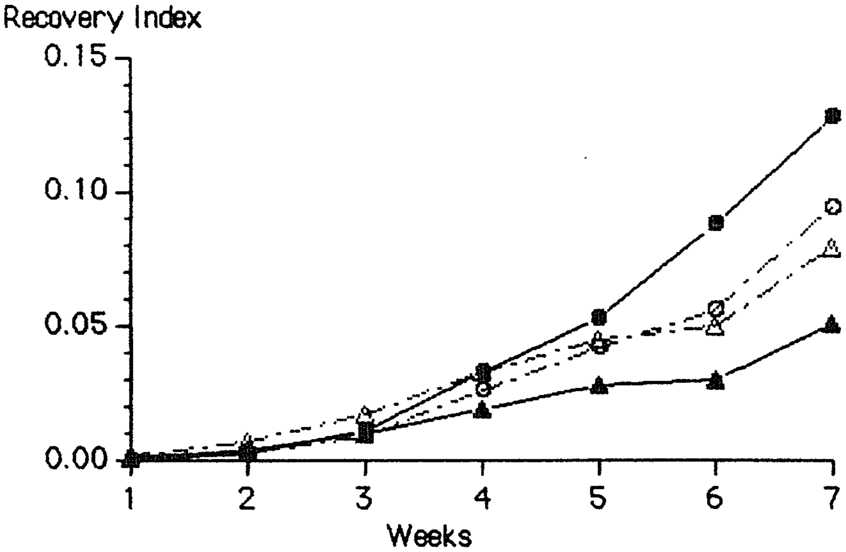


Fig. 8.5 **Recovery index after 100% foliage scorch.**
Only plants surviving to 7 weeks included.
Dry treatment: ● *A. littoralis*, ▲ *A. torulosa*,
Wet treatment: ○ *A. littoralis*, △ *A. torulosa*.

Mean Photosynthetic Indices at seven weeks differed between species ($F_S = 6.855$, d.f. 1,21, $P < 0.05$), but not between watering regimes ($F_S = 1.506$, d.f. 1,21, $P > 0.05$). The Photosynthetic Index at seven weeks was found to be significantly related to the Initial Photosynthetic Index, only in *A. littoralis*. This relationship was expressed by the following equation (for symbol definitions see Section 8.2.5):

$$P.I._7 = (0.0961 \times P.I._1) + 244.701$$

$$(F_S = 13.562,\ d.f.\ 1,15,\ P < 0.01)$$

Although *A littoralis* seedlings appeared to recover at a faster rate than those of *A. torulosa* (Fig. 8.5), the Recovery Index of plants of the two species up to seven weeks were not significantly different ($F_S = 1.8013$, d.f. 1,21, $P > 0.05$), nor did the two watering regimes used significantly affect the Recovery Index ($F_S = 0.2014$, d.f. 1,21, $P > 0.05$).

8.3.6 Effect of Fire on Field Populations

Over half the individuals of *A. littoralis* which had experienced 100% foliage scorch at Atherton 2, showed no sign of recovery (Fig. 8.6a). The remainder exhibited resprouting, with a marked transition from lignotuber to epicormic sprouting between 3 and 6 cm DBH. Mode of sprouting therefore appeared to be a function of size (and possibly capacity of bark to insulate the stem), rather than of sexual maturity, as recovery of reproductively active female trees was similar to that of plants for which sex could not be determined.

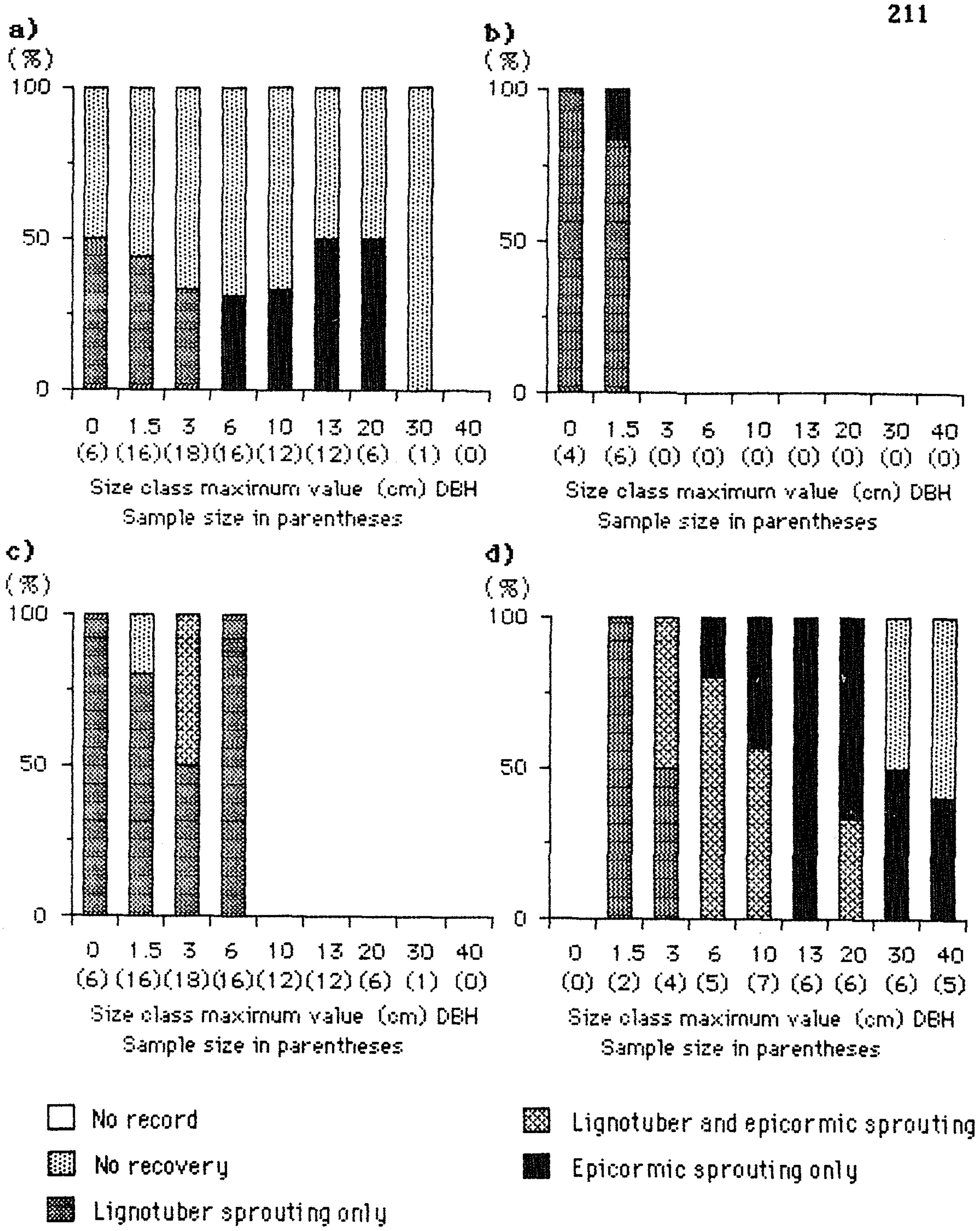


Fig. 8.6 Response of field populations to 100% foliage scorch.

a) *A. littoralis*, Atherton 2, 8/7/83.
b) *A. torulosa*, Paluma 3, 7/3/82.
c) *A. torulosa*, Wild River, 20/7/83.
d) *A. torulosa*, Paluma 2, 24/11/82.

Recovery rates of *A. torulosa* after all fires were extremely high, with most mortality occurring in the smallest and largest size classes (Fig 8.6b,c,d). Lignotuber sprouting was the most common form of recovery for individuals of up to 5 cm DBH. The transition zone, was less distinct than in *A. littoralis*, with both lignotuber and epicormic sprouting occurring in individuals between 1.5 and 20cm DBH.

However, epicormic sprouting was the dominant form of recovery in individuals greater than 10cm DBH. Again, the recovery of reproductively active females was similar to that of plants which could not be sexed. At Paluma 3, all recovering *A. torulosa* had evidence of previous lignotuber sprouting.

In both species, where less than 100% foliage scorch had occurred, lignotuber sprouting was uncommon, unless damage to the base of the plant had occurred.

8.4 Discussion

8.4.1 Effect of Fire on Seed Survivorship, Germination and Seedling Recruitment

The observation made here that seedlings may be associated with the charred remains of burnt-out logs, has previously been stated by Pryor (1963). While previous investigations into the cause of such germination distribution have concentrated on many factors affecting germination success and seedling survivorship (Hermann and Chilcote 1965; Renbuss *et al.* 1973), the studies here suggest that protection from predators may also be involved, with ash and charcoal reducing the rate of seed harvesting, and thus providing "safe sites" (after Harper 1977).

Reduced harvesting rates may be due to the powdery nature of ash and the finer charcoal particles (Russell *et al.* 1967). While *Rhytidoponera* sp. C was reluctant to venture from soil or charcoal on to ash, the smaller *Pheidole* spp. would not venture on to either ash or charcoal (S.T. Garnett pers. comm.). Ants of this genus, important seed predators at Kirrama (Chapter 4), may have been more sensitive to the fine particle sizes of ash and charcoal than the larger *Rhytidoponera* sp. C. When workers of *Pheidole* spp. were observed on charcoal under a microscope (S.T. Garnett pers. comm.), particles could be seen adhering to their legs, causing difficulty in walking. Within five minutes, the ants desiccated and died. As *Pheidole* spp. are responsible for seed predation in many Australian vegetation communities (Andersen 1982; Majer 1985; Majer and Lamont 1985; O'Dowd and Gill 1985; Russell *et al.* 1967), it is expected that the deterrent effect of ash and charcoal will have widespread implications for seed survival in the field. The extent of protection will depend on the species identity of the major seed predators. The possibility that rats, rather than ants, were responsible for seed losses from the charcoal and ash may have resulted in the effect of these substrates on seed predation by ants being under-estimated.

Further reduction in seed predation may be caused by absorption of attractive odours by the large internal surface area of charcoal (Smisek and Cerny 1970). Ants, which appear to detect seed by smell (Cremer 1966), would be therefore less likely to find seed in fresh charcoal beds. Moreover, once a group of seeds was discovered on a charcoal bed, as occurs when indehisced cones fall, ants would be unable to establish a pheromone trail to exploit the resource systematically. Therefore, all seed predation would require visual recognition of individual seeds.

As rain splash results in some seeds becoming buried in the friable ash and charcoal beds, the probability of seed predation would be further reduced. Seed predation rates at Kirrama are generally greatest during wet weather, when rapid burial would be most advantageous (Chapter 4). However, it is unclear whether burial in charcoal and ash beds, predation or a combination of both was responsible for greater apparent seed loss during wet weather in the experiments described in this chapter.

The temporary nature of ash beds could make them less significant to seedling recruitment, as field observations suggest. The lack of effect of month-old charcoal on seed loss rates may be due to the washing out of the finer particles or saturation of the charcoal molecules (Smisek and Cerny 1970). However, the protection by new charcoal may persist long enough for the seed to become buried, as was the effect of rain splash. Once buried, inherent seed longevity will then become important in determining germination success. Species with smaller seed are likely to be afforded even greater protection, as they offer a smaller visual cue to the ants and will be more readily buried by rain splash.

Although ant foraging may increase after fire (Andersen and Yen 1985; O'Dowd and Gill 1984), the probability of an individual seed being removed may decrease due to massive release of canopy stored seed (Ashton 1979; O'Dowd and Gill 1984). However, as conditions favourable to germination rarely occur immediately after fire (Cowling and Lamont

1985; O'Dowd and Gill 1984), a large proportion of seed will be exposed to seed predation and pathogens in the intervening period. Purdie (1977) suggested there could be more safe sites on the ash-covered soil surface following intense fire, as she observed greater germination rates in severely burnt, dry sclerophyll forest than in similar vegetation that had experienced a mild burn. The present work suggests charcoal and ash beds do indeed provide safe sites, and are thus involved in the flush of germination which occurs in recently burnt vegetation.

Factors identified as improving germination and survivorship in ash or charcoal beds include increased soil insolation (Hermann and Chilcote 1965), removal by fire of the source of allelopathic substances (Christensen and Muller 1975) and litter which presents a physical barrier between emerging radicles and the soil (Purdie 1977), reduction of competition for resources by pre-existing plants (Wellington 1984), soil sterilization (Renbuss *et al.* 1973), and stimulation of germination by ash or charred wood (Keeley *et al.* 1985; Wellington 1981). Changes in nutrient status can be either beneficial or detrimental to early seedling growth (Humphreys 1968; Pryor 1963; Raison 1980).

As optimum temperature for germination of both *A. littoralis* and *A. torulosa* is about 25°C (Chapter 5), insolation effects of charcoal beds (Hermann and Chilcote 1965) may be of benefit during the cooler months of the year. However, during the summer when moisture availability is highest, insolation could be detrimental, raising temperatures above optimum levels. This may explain why the survey in this chapter, undertaken in July, found few seedlings away from charcoal beds, while natural seedling germination at Kirrama in the late wet season, with maximum temperatures between 26 and 32°C was not associated with charcoal beds. The effect of soil sterilization, reducing seed losses to fungal attack, and promoting plant health (Renbuss *et al.* 1973) may be offset by as yet unknown effects on symbiotic actinomycetes and mycorrhizal fungi (Warcup 1981).

As germination of *A. littoralis* and *A. torulosa* does not appear to be adversely affected by allelopathic substances in the field, and litter provides a more favourable microclimate than bare ground for germination (Chapter 5), removal of the litter layer may reduce successful germination. However, the removal of thick mats of cladodes and replacement by grasses (Chapter 5), accompanied by a reduction in the moisture consumption of existing vegetation (Wellington 1984), may provide a microclimate more conducive to seedling survival. However, the low flammability of cladodes (Dickinson and Kirkpatrick 1985) and the low fuel porosity of dense mats of litter (Chandler *et al.* 1983) makes it unlikely that fire would often effect such a vegetation change.

In *A. littoralis*, any acceleration in germination through insolation could be offset by reduction in germination rate by seed burial (Chapter 5) or ash. However, as seeds in such situations are more likely to escape predation, and rainfall in the fire season is unlikely to be sufficient to sustain seedling growth, this may be a mechanism which ensures maximum seedling survivorship (Chapter 5). This contrasts with the stimulation of germination of *Eucalyptus incrassata* by ash, in the semi-arid zone of Victoria (Wellington 1981), and of various suffrutescent and annual species in the Californian chaparral (Keeley *et al.* 1985), both environments where heavy rainfall events may be rare. The less pronounced delay in germination of *A. torulosa* by ash, may reflect the greater likelihood of soil moisture levels remaining high after initial rainfall (Chapter 5).

The direct effect of fire on seed in the surface litter will depend on the temperatures reached and the moisture content of the substrate. *A. rigida* can tolerate temperatures up to 110°C for four hours in dry conditions, but only up to 70°C for five minutes in wet conditions (Beadle 1940). Although the temperature tolerance range is presently unknown for *A. littoralis* or *A. torulosa*, germination results here suggest that *A. torulosa* may be able to tolerate higher temperatures. However, it is likely that high temperatures involved in the production of charcoal (up to about 1000°C) will destroy seed already present on the surface soil (Beadle 1940) and that most seed germinating after fire will have been released from the canopy subsequent to the burn.

8.4.2 Effect of Fire on Plant Survivorship

The greater root : shoot ratio in *A. littoralis* compared to *A. torulosa* (Chapter 6) may be the cause of the greater capacity of year-old seedlings of this species to survive burning. However, an apparent reversal of resprouting ability in older individuals of the two species, suggests that other factors may be involved., such as the development of a lignotuber in *A. torulosa* (Chapter 6, 7; Boland *et al.* 1984). Although the watering regime used in this chapter did not affect the rate of recovery of pot seedlings or probability of survival, moisture availability is likely to be important in the field.

The survival of a plant through a fire depends on the escape of a complete interconnected unit of root, shoot and vascular system (Gill 1975). Protection of this unit is largely dependent on bark thickness and its resistance to ignition (Gill and Ashton 1968; Vines 1968). As *A. torulosa* bark is usually thick and corky, while that of *A. littoralis* often thinner and more compact (pers. obs.), variation in bark thickness may be the cause of lower survivorship of *A. littoralis*. While Gill (1981a) recommended the use of 100% crown scorch as a measure to indicate equivalent levels of biological damage in different species, and the tissue of members of the Casuarinaceae would be expected to have a thermal tolerance similar to that of other families (Rosenberg *et al.* 1971), the low flammability of their foliage (Dickinson and Kirkpatrick 1985) may mean that a wide range of internal cell damage may occur before external damage more severe than 100% crown scorch is apparent. Thus, 100% crown scorch may represent a broad range of biological damage in this family.

Although pre-fire plant size was identified as an important factor affecting rate of recovery only in *A. littoralis*, the small sample size caused by low survival in *A. torulosa* may have obscured the relationship in this species. Findings by Noble (1984) in *Eucalyptus* spp. suggest that size and plant condition before a fire may be the most important factor affecting recovery. Thus, it appears that any competitive advantage achieved before a fire will be maintained afterwards. Moreover, plants which resprout in the crown will have an advantage over plants which resprout only from the base, as the maintenance of their biomass will ensure access to a large resource pool. So plants greater than 3 cm DBH, which generally resprout in the crown, are likely to enhance their advantage over smaller plants.

The ability of a plant to recover after repeated fires will depend on the availability of stored photosynthates needed for regrowth, and the replacement of damaged protective bark, and is therefore related to the time between fires and season of burn (Bamber and Humphreys 1965; Cremer 1973; MacArthur 1973). At present, absence of data on the accession of photosynthates and rates of bark recovery in *A. littoralis* and *A. torulosa* make it impossible to approximate the fire interval which could be tolerated.

8.4.3 Effect of Fire Regime on the Life-cycles of *A. littoralis* and *A. torulosa*.

Although this study has demonstrated that *A. littoralis* and *A. torulosa* can resprout after fire damage, and that germination of their seed is favoured by beds of charcoal and ash, it should not be assumed that fire will promote, or is necessary for, their establishment. Elsewhere in this thesis, it has been shown that successful germination occurs under favourable climatic conditions in the absence of fire (Chapter 5). As fire regimes vary in intensity, frequency, season, extent and type, and many other factors influence the composition of the vegetation (Gill 1975, Hill and Read 1984), it would be unrealistic to attempt to predict regimes that would promote either *A. littoralis* or *A. torulosa*, at the expense of each other, or other species. However, it is possible to discuss the processes involved in the maintenance of existing communities in North Queensland from the information made available in this thesis.

Most fires occur in North Queensland towards the end of the dry season, fire risk being highest from September to December, depending on the timing of the onset of summer rains, and the greatest extent of area burnt in November (Luke and MacArthur 1978). Fires in the open woodlands of North Queensland are essentially grass fires, with the general absence of a highly combustible shrub layer to transfer fire to the canopy, although canopy damage or death may occur (Luke and Macarthur 1978; Stocker 1980). Up to 65% of the fuel is grass, which cures each dry season and reaches peak flammability in four years after fire (Luke and MacArthur 1978; Walker 1981). Average interval between fires has been estimated to be one to two years (Walker 1981). As fires are frequent and restricted to the grass layer, they are generally of low intensity. The communities containing *A. littoralis* and *A. torulosa* are often intentionally burnt, either to prevent severe wildfires which might threaten adjoining rainforests, or to encourage the palatable "green pick" desired by cattle. Casuarina forests at the Kirrama study site were burnt every three to five years (J. Snell pers. comm.). However, non-uniform fuel loads and pockets of mesic shrub species prevents complete burn in some areas, particularly under *A. torulosa* (J. Snell pers. comm.). Therefore, a typical fire regime in the habitats of *A. littoralis* and *A. torulosa* is one of patchy, low intensity, late dry season fires, at three to five year intervals, in which partial to complete canopy scorch or, occasionally, plant death may occur. Many plants will recover after fire, those escaping severe damage will be favoured by the reduction in competition from plants more severely affected. Where existing plants are killed or severely damaged, smaller plants or new seedlings may be recruited to the canopy. In the absence of canopy gaps, *A. torulosa* seedlings may join the pool of suppressed juveniles which is a feature of closed *A. torulosa* communities, while *A. littoralis* seedlings do not appear to be recruited under such conditions (Chapter 7).

Under most circumstances, it would be expected that seed enclosed in cones in the canopy would survive the fire and be released shortly afterwards. Canopy stores of mature seed reach a maximum in the late dry season, before maturation of cones from the most recent flowering season and abscission of remaining mature cones from the previous season (Chapter 4). While this pattern of seed maturation and release ensures high seed fall through the wet season, it also results in high availability of canopy stored seed during the period of greatest fire hazard. Wet season rains sufficient to stimulate germination may occur from October to May, although in some years they may not occur at all (Chapter 5). Therefore conditions favourable for germination may occur at any time in the seven months following a fire.

Where fire has been of relatively high intensity, the post-fire environment is likely to be more favourable for seed survival and recruitment. The soil will be sterilized from pathogenic bacteria and fungi (Renbuss *et al.* 1973), competition will be reduced (Ashton and MacCauley 1972; Wellington 1984) and an abundance of charcoal and ash, after cooling, will provide protection from seed-eating ants.

Once conditions favourable for germination occur, seed of *A. torulosa*, and that of *A. littoralis* not buried or in contact with ash, will germinate rapidly (Chapter 5). Should conditions for seedling survival not persist, there will be a pool of *A. littoralis* seed carried over to the next period favourable for germination, while the seed bank of *A. torulosa* will be depleted (Chapter 5). Where conditions prohibit germination for some time after the fire, seed falling on exposed soil may be exhausted by continued ant harvesting or pathogenic attack (Chapter 4). Where all canopy seed reserves have been released after the fire, it will be at least a year before seed is again added to the soil seed bank, although some immature cones may have sufficient moisture content to escape desiccation by fire, in which case their seed will begin to mature in the late wet season, and may be released during the ensuing year. The more precocious reproductive maturity of *A. littoralis* (Chapter 7), may mean that it will recover its full reproductive potential sooner after a fire.

While plants of *A. littoralis* and *A. torulosa* are likely to be affected similarly to other species by the alteration of conditions in the post-fire environment, such as changes in abundance of herbivore numbers (Cremer and Mount 1965; Christensen and Kimber 1975; Whelan and Main 1979), soil sterilization (Renbuss *et al.* 1973), changes in nutrient availability (Humphreys 1968; Raison 1980), changes in soil permeability (deBano and Rice 1973), reduction of competitive pressures (Ashton and MacCauley 1972; Wellington 1984) and predisposition of fire-damaged individuals to insect attack (Hadlington and Gardner 1959), they may be adversely affected by the elimination of mycorrhizal fungi (Anderson and Ladiges 1982) or that of *Frankia* spp.

Fire, or its absence, appears to cause the local extinction of *A. torulosa* only under conditions of high moisture availability. *Eucalyptus pellita*, is promoted by fire in moist environments (Hopkins and Graham 1984), and this may be at the expense of *A. torulosa* (Stocker 1980). Where *E. pellita* forest has escaped fire for several generations, it has been replaced by both *A. torulosa* and rainforest species (Stocker 1980). Once dense stands of *A. torulosa* have formed, grass growth is suppressed by a thick mat of relatively non-flammable cladodes, which retard fire and allow the recruitment of the rainforest species (pers. obs.). These rainforest species may subsequently develop to the exclusion of *A. torulosa*. In moist environments, therefore, *A. torulosa* forest will be promoted by an intermediate fire frequency. Under conditions of lower moisture availability, however, there is no evidence of replacement of either *A. littoralis* or *A. torulosa* in North Queensland, despite regular burning of much of their habitat. While *A. littoralis* has been reported to replace *Eucalyptus ovata* in the absence of fire in Victoria (Withers and Ashton 1978), the dominance of *E. ovata* after fire is facilitated by the temporary release from moisture competition (Withers 1978a,b, 1979a,b). It might therefore be concluded that in a drier environment, *A. littoralis* would maintain its dominance after fire and not be replaced by eucalypts. Both these examples suggest that these *Allocasuarina* spp. may be disadvantaged by fire at the wetter end of their distributions, but provide no evidence that they will be replaced by eucalypts in drier environments. Thus, it seems unlikely that, within that part of their current North Queensland distributions too dry for rainforest, fire alone could result in their replacement by other tree species.

8.5 Summary

Both ash and charcoal provide seeds with protection from seed-eating ants. Possible reasons for this include the powdery nature of ash and the finer charcoal particles, absorption by charcoal of attractive odours and ease of burial. Other effects of ash and charcoal may be beneficial or detrimental to seeds of *A. littoralis* and *A. torulosa*. Insolation effects of charcoal beds may enhance germination during the cooler months of the year, but raise temperatures above optimal levels in the warmer wet season. In *A. littoralis* protracted germination by ash or burial may increase survival of seed through short-lived periods of moisture availability which would be likely to follow dry season fires. The effects of ash on germination rate are less pronounced in *A. torulosa,* which occurs where moisture availability is more continuous and delay in germination would be of little benefit. High temperatures would be likely to destroy seed already present on the surface soil, and *A. littoralis* may be more vulnerable than *A. torulosa.*

The greater resprouting ability of year-old plants of *A. littoralis* than of *A. torulosa* may be due to the greater root : shoot ratio in the former species, while the development of a lignotuber (and possibly thicker bark), in *A. torulosa* gives older individuals of this species a greater fire resistance. However, populations of both species regenerate after fire, by both resprouting and seed germination, and it seems likely that most of the present North Queensland distributions of these species would be maintained, if fire frequency alone is altered slightly.

CHAPTER 9

DISCUSSION

9.1 Introduction

In this chapter, the ecology and life histories of *A. littoralis* and *A. torulosa* are summarized to enable identification of factors influencing the distributions of these species in North Queensland. Implications of the ecology of *A. littoralis* and *A. torulosa* for forestry programs and palaeoenvironmental reconstructions are then discussed.

9.2 Ecological Factors affecting the Distribution of *A. littoralis* and *A. torulosa* in North Queensland.

9.2.1 Differences between *A. littoralis* and *A. torulosa*.

The characteristics of *A. littoralis* and *A. torulosa* are described in Table 9.1. The major differences observed between the two species suggest that *A. littoralis* has a greater fitness in environments of low or seasonal moisture availability and high incident radiation, while *A. torulosa* requires more constant moisture availability and protection from high incident radiation. Differences between the species likely to be of particular significance in determining their distributions and interactions under these contrasting conditions, include germination rate (Chapter 5), shoot : root ratio, transpiration rate and cladode architecture (Chapter 6). Differences in life history characteristics are also likely to be of importance (Chapter 7), and are discussed separately in Section 9.3.

Table 9.1 A summary of the characteristics of *A. littoralis* and *A. torulosa* described in this thesis.

^{a}Superscript indicates chapter from which data was obtained.
P *** < 0.001, ** < 0.01, * < 0.05, n.s. not significant,
- not tested.

Characteristic^a	Species			P
	A. littoralis		*A. torulosa*	
1. Seeds^4				
a) seeds/cone	39.3	≈	38.4	-
b) seed-fall $m^{-2} d^{-1}$	11.95	>	0.85	-
c) seed landing > 3m from female tree ($m^{-2} d^{-1}$)	0.05	>	0.00	-
d) seed weight (mg)	1.73	<	5.24	-
e) surface area : weight	2.79	<	4.72	-
2. Seed-loss in 72 hrs^4				
a) Canopy A.l. (%)	72.3	>	71.0	*
b) Canopy A.t. (%)	64.9	>	52.5	*
3. Seed-bank^4				
a) seed m^{-2}	4.44	<	17.76	***
b) seed-fall equivalent (d)	2.57	<	38.61	-
4. Germination^5				
a) Percent viability	11-73		54-79	-
b) Median germination time for Kirrama provenances				
i) 15°C 14 hrs dark	24.9		14.4	-
ii) 15°C 14 hrs light	15.4		12.9	-
iii) 25°C 14 hrs dark	6.4		4.4	-
iv) 25°C 14 hrs light	4.5		4.6	-
v) 35°C 14 hrs dark	5.0		4.9	-
vi) 35°C 14 hrs light	4.2		4.7	-
c) Viability				
i) increases then decreases with cone maturity	yes		yes	-
ii) affected by storage temp (0-32°C)	no		no	-
iii) affected by storage humidity (25-75%)	no		no	-
iv) reduced by wetting then drying	no		yes	-

Characteristic	Species			P
	A. littoralis		*A. torulosa*	
d) Percent germination				
i) affected by temp (15-35%)	no		no	-
ii) affected by light	no		no	-
e) Germination time increased by				
i) low temperature	yes		yes	-
ii) dark	many provenances		no	-
ii) wetting and drying	yes		yes	-
f) Germination in free water	yes		yes	-
5. <u>Field Germination</u>[5]				
a) Season observed	Jan-April		Jan-April	-
b) Distribution of natural germinants				
i) Observed groupings	scattered (groups of <3)		under fecund females (groups of up to 100)	-
ii) Mean distance from trunk of nearest potential maternal parent	2.0	<	2.6	**
iii) Under canopy of parent species	48%	<	100%	
iv) Under canopy of potential maternal parent	35%	<	100%	
v) In a canopy gap	52%	>	0%	
c) Percent germination within parent stands				
i) closed, litter	23%		21%	
ii) closed, no litter	13%		1%	
iii) open, litter	47%		34%	
iv) open, no litter	32%		15%	
6. <u>Plant Parameters</u>[6]				
a) Average cladode length	$0.085xH + 8.52$	<	$0.182xH + 8.885$	***
b) Cladode angle	erect		horizontal to pendulous	
c) Total shoot length (H = height, S = shoot no.)	$0.628x(SxH)^{0.842}$		$0.618x(SxH)^{0.887}$	***
d) Anthocyanin production in response to full sunlight	no		yes	

Characteristic	Species			P
	A. littoralis		*A. torulosa*	
7. Transpiration[6]				
a) rate				
i) (g dm^{-2} d^{-1})	1.077xM - 5.66	>	0.787xM - 5.24	***
ii) (g g^{-1} d^{-1})	0.776xM - 3.96	>	0.617xM - 4.08	***
b) M when transpiration = 0	5.1-5.3	<	6.6	***
c) Transpiration when M = 35% (field capacity)				
i) (g dm^{-2} d^{-1})	32.0	>	22.3	***
ii) (g g^{-1} d^{-1})	23.2	>	17.5	***
(M = soil moisture (%))				
8. Survivorship after 6 months under controlled conditions (%)[6]				
moisture regime sunlight (%)				
a) wet 30	100.0 (100.0)		100.0 (100.0)	n.s.
b) dry 30	86.1 (100.0)		75.0 (81.8)	n.s.
c) control 100	73.7 (93.3)		35.7 (65.0)	*
d) control 10	100.0 (100.0)		95.1 (95.1)	n.s.
e) control 1	97.5 (97.5)		97.5 (97.5)	n.s.
(Figures in brackets exclude pots in which both plants died)				
9. Shoot weight after 6 months under controlled conditions (g)[6]				
a) wet 30	2.39	≈	2.22	n.s.
b) dry 30	1.73	≈	1.60	n.s.
c) control 10				
i) with A.l.	0.77	>	0.69	*
ii) with A.t.	1.16	>	0.82	*
d) control 1	0.90	≈	0.98	n.s.
10. Root weight (g)[6]				
a) wet 30	1.29	>	0.92	**
b) dry 30	0.92	>	0.72	*
c) control 10				
i) with A.l.	0.36	>	0.22	***
ii) with A.t.	0.55	>	0.28	***
d) control 1	0.29	>	0.19	*
11. Shoot/ Plant weight[6]				
a) wet 30	0.64	<	0.72	***
b) dry 30	0.65	≈	0.68	n.s.
c) control 10	0.69	<	0.76	***
d) control 1	0.78	<	0.84	***

Characteristic	Species			P
	A. littoralis		*A. torulosa*	
12. Plant weight (g)[6]				
a) wet 30	3.60	≈	3.14	n.s.
b) dry 30	2.67	≈	2.31	n.s.
c) control 10				
i) with A.l.	1.12	>	0.91	**
ii) with A.t.	1.73	>	1.10	**
d) control 1	1.19	≈	1.17	n.s.
13. Relative total weight[6]	(with A.t.)		(with A.l.)	
a) wet 30	0.53	≈	0.47	n.s.
b) dry 30	0.55	≈	0.45	n.s.
c) control 10	0.66	>	0.34	***
d) control 1	0.47	≈	0.54	n.s.
14. Field survivorship				
a) seedlings (over a 1 year period)[5]				
i) under open sub-canopy	36.6%	>	15.7%	***
ii) under closed sub-canopy	2.6%	≈	4.4%	n.s.
b) established plants (over a 2 year period)[7]				
i) 0 - 4 cm DBH	996.9%	≈	93.7%	-
i) 4 - 8 cm DBH	100.0%	≈	100.0%	-
iii) > 8 cm DBH	94.6%	≈	96.3%	-
15. Relative growth rate[7]				
a) maximum	$0.0034 + \frac{0.2629}{DBH_i}$		$0.0111 + \frac{0.1717}{DBH_i}$	***
b)	Faster up to 11.84 cm DBH		Faster over 11.84 cm DBH	***
c) RGR affected by				
i) reproductive maturity	?		no	-
ii) sex	no		no	-
16. Size[7]				
a) Kirrama	Larger up to 40 yrs		Larger over 40 yrs	-
b) North Queensland				
i) > 16 cm DBH	10.5%		25.0%	-
ii) mean DBH	4.6 - 15.0 (9.6)		5.9 - 32.5 (15.6)	-
17. Predicted longevity at Kirrama[7]	≈ 30 yrs	<	≈ 50 yrs	***

Characteristic	Species			P
	A. littoralis		*A. torulosa*	
18. <u>Sex Ratio</u>[7]				
a) Kirrama	1 : 1.84	≈	1 : 1.09	n.s.
b) North Queensland	1 : 1.36	≈	1 : 1.67	n.s.
c) Change in sex ratio[7]				
i) with site factors	no		no	-
ii) with size-class	no		no	-
d) Significant male bias				
i) pooled ratio	yes		yes	-
ii) summed ratio	no		yes	-
19. <u>Vegetative litter-fall</u>[7]				
a) $(g\ m^{-2}\ d^{-1})$	0.42	<	0.83	-
b) major period	Sep / Oct		Sep / Oct	-
c) $year_1/year_2$	90.9%	<	123.0%	-
20. <u>Reproductive litter-fall</u>[7]				
a) $(g\ m^{-2}\ d^{-1})$	0.10	<	0.15	-
b) /total litter-fall	23.8%	>	18.1%	-
c) $year_1/year_2$	50.9%	≤	56.0%	-
d) female : male	0.50 : 0.50	≈	0.53 : 0.47	-
e) major period	Nov to May		Mar to Jun	-
21. <u>Male reproductive schedule</u>[7]				
a) size at first flowering	≈ 0 - 4 cm DBH	<	≈ 8 - 12 cm DBH	-
b) flowering recorded	all year		Feb to Jul	-
c) main period	Dec to Jun		Mar to Jun	-
22. <u>Female reproductive schedule</u>[7]				
a) size at first flowering	≈ 0 - 4 cm DBH	<	≈ 8 - 12 cm DBH	-
b) flowering recorded	all year		Feb to Jul	-
c) main period	Dec to Jun		Mar to Jun	-
d) maximum cones/tree	≈ 1000	>	≈ 300	-
e) estimated max. seeds/tree	39,300	>	11,520	-
f) size at max. load	≈ 8 cm DBH	<	≈ 13 cm DBH	-
g) reproductive structures reaching maturity:				
i) by weight	96.0%	<	79.0%	-
ii) by number	16.3%	≈	18.5%	-

Characteristic	Species		P
	A. littoralis	*A. torulosa*	
23. Fire effects on seed longevity[8]			
a) Seedlings found more frequently in charcoal beds (July 1983)	yes	yes	-
b) Seed losses to predators reduced by			
i) fresh charcoal	yes	yes	-
ii) month old charcoal	no	no	-
iii) fresh ash	yes	not tested	-
24. Fire effects on germination[8]			
a) Percent germination reduced by			
i) burning litter over seed	yes	no	-
ii) addition of ash	yes	no	-
b) germination time reduced by			
i) burning litter over seed	no	no	-
ii) addition of ash	yes	yes	-
25. Fire effects on plants in pots[8]			
a) Recovery of burnt plants surviving at 7 weeks (%)			
i) Wet treatment	88.9	44.4	n.s
ii) Dry treatment	100.0	44.4	n.s
b) Initial recovery followed by plant death	no	yes	-
c) Growth after fire affected by watering regime	yes	yes	-
26. Fire effects on plants in field[8]			
a) Sizes of individuals with lignotuber sprouting (cm DBH)	0-10$^+$	0-60$^+$	-
b) Sizes of individuals with epicormic sprouting (cm DBH)	20-60$^+$	20-120$^+$	-
27. Climatic description of distribution[3]			
a) Annual rainfall (mm)	1,000-2,000	1,000-2,000	-
b) Mean temperature (°C)	19-25	19-25	-

Faster germination rate in the dark will result in earlier germination of *A. torulosa* than *A. littoralis*, for seeds which have become incorporated in the seed-bank and covered by litter or soil. The advantage of earlier germination in *A. torulosa* will be accentuated by the larger seed-bank of this species. Thus, when germination-stimulating rain events are followed by conditions favourable to seedling growth, *A. torulosa* seedlings will both outnumber those of *A. littoralis* and establish more rapidly. Therefore, establishment of *A. torulosa* seedlings will be favoured in environments where moisture availability is initially continuous.

Conversely, short-lived conditions of moisture availability result in the germination of a greater proportion of the seed-bank of *A. torulosa*, which will be likely to deplete the seed-bank of this species. Hence, when moisture levels decline and the newly-germinated seedlings die, the slower response of *A. littoralis* seed to conditions favourable to germination, as well as the retention of 100% viability through a wetting and drying cycle, will mean that a larger proportion of the seed-bank of this species will be retained, and be available for germination during subsequent periods of moisture availability. Thus, under conditions of intermittent moisture availability, a larger proportion of *A. littoralis* seeds that have escaped predation should successfully establish.

Under conditions of high moisture availability and low light, *A. torulosa* allocates a greater proportion of its resources to shoot growth than does *A. littoralis*. This allows the accumulation of a greater amount of photosynthates, which are then stored in a basal lignotuber (Chapter 7; Boland *et al.* 1984). Development of the lignotuber would in turn allow persistence of *A. torulosa* beneath the canopy where light levels are low and the frequency of stem damage from falling branches and leaf litter high. Conversely, the greater investment in root growth by *A. littoralis* under conditions of high moisture availability would confer on it the ability to survive when moisture level declined. Therefore it is proposed that there will be greater recruitment of *A. littoralis* under conditions of intermittent moisture availablity, and of *A. torulosa* under conditions of low light.

The development of a distinct lignotuber in *A. torulosa* may endow this species will a superior ability to resprout after fire (Chapter 8). This was suggested by a lower recovery of *A. littoralis* plants after wildfire, although the relative ability of natural populations to recover from fire needs further investigation. However, both species do resprout after fire, and before the lignotuber of *A. torulosa* has developed, *A. littoralis* appears to have a greater recovery ability.

Ability of *A. littoralis* to maintain a higher transpiration rate than *A. torulosa* (Chapter 6), would also be of advantage to *A. littoralis* in conditions of low moisture availability and would have further survival value in poorly drained soils which are periodically waterlogged by heavy rains. This could explain the occurrence of *A. littoralis* on seasonally waterlogged coastal plains. The absence of *A. torulosa* from the plains may also be caused by the sensitivity of this species to the high levels of insolation characteristic of such environments. This sensitivity appeared to be partly a result of cladode architecture. The initially horizontal cladodes of *A. torulosa* intercept more light than the erect cladodes of *A. littoralis*, an advantage under low light levels, but are likely to suffer high foliage temperatures in full sunlight (Hadfield 1975). Cladode angle in *A. torulosa*, would also result in rapid drainage, an advantage where persistent mist and rain was likely to result in fungal attack of foliage. The erect cladodes of *A. littoralis*, however, would be beneficial where moisture availability was limiting, directing moisture supply to the base of the plant, and evading high insolation levels. The higher transpiration rate of *A. littoralis* would also be more effective at reducing cladode temperature.

The above characteristics suggest that *A. littoralis* will be more successful on sites of lower or more intermittent moisture availability, where the vegetation is more open, than would *A. torulosa*. However, both species occur on sites receiving an annual rainfall of between 1,000 and 2,000 mm (Chapter 3). Therefore, it appears that drainage patterns and seasonality of rainfall may be more important than annual rainfall in determining which of the two species will be successful at a particular site.

Elsewhere, it has been suggested that *A. littoralis* grows on sites of lower soil fertility than does *A. torulosa* (Anon. 1984b). Although not tested directly in this thesis, similar performance of seedlings of the two species in pot trials, regardless of soil conditions, does not support the proposition of differential tolerance of nutrient availability (Chapter 6). Further investigation of soil tolerance is required. As, in North Queensland, the gradient from high rainfall zones to low rainfall zones is generally accompanied by a decline in soil fertility (Hubble and Isbell 1983), the apparent occurrence of *A. torulosa* on better soils may be a artefact of this species being favoured by more mesic conditions.

9.2.2 Establishment and Maintenance of the Distributions of *A. littoralis* and *A. torulosa*.

A. littoralis and *A. torulosa* frequently occur in adjacent but unmixed stands. The establishment of these stands may be a slow process and was not observed directly during the course of this thesis. However, the differences between the two species described above suggest the following pattern of vegetation development.

Few newly-germinated seeds of either species survive beneath the canopy, because of the reduction in moisture availability by existing vegetation and the physical damage caused by litter-fall (Chapter 5). In open vegetation or a large canopy gap, where moisture availability is low or seasonal, and seedlings receive high incident solar radiation, survivorship of *A. littoralis* would be greater than that of *A. torulosa*. If such conditions are maintained, then *A. littoralis* seedlings would become established, while those of *A. torulosa* would be eliminated.

Under a closed canopy or in a small canopy gap which was soon closed by the encroaching crowns of pre-existing species, where moisture was not severely limited and seedlings did survive the first year, the lignotuber, high shoot investment and horizontal cladodes would assist survivorship of *A. torulosa* seedlings over those of *A. littoralis*. Once *A. torulosa* seedlings have become established, they may remain as a regeneration pool, until the canopy is once again broken.

Hence the major recruitment of *A. torulosa* seedlings would appear to be through germination beneath a closed canopy, or in small canopy gaps, while those of *A. littoralis* are likely to be on the margins of a stand, or in larger canopy gaps. This conforms with the observations of natural germination in the field in North Queensland (Chapter 7). Although it seems to contradict the findings of Withers and Ashton (1977), who describe *A. littoralis* in southern Victoria as germinating in small canopy gaps, the lower stature of the vegetation at their site resulted in higher light infiltration into such gaps than was the case at Kirrama.

The boundary between *A. littoralis* and *A. torulosa* thus appears to be maintained by moisture availability and the light environment as modified by the vegetation. The abruptness of the boundaries between contiguous stands of the two species suggests that changes in drainage or soil moisture retention may be sufficient to cause the replacement of one species by the other, although other factors not investigated in this thesis, such as antagonism between associated actinomycetes, may also be involved.

The boundaries may also represent a front of invasion of one species into the other. *A. littoralis* seeds may germinate in a mesic habitat which had recently become open, such as due to fire or clearing, assisted by its greater seed dispersal (Chapter 4) and tolerance of high light levels. As *A. littoralis* became established, and its canopy provided protection from sunlight, *A. torulosa* seedlings may then be able to invade, and the gradual replacement with the longer-lived *A. torulosa* would occur. The reverse situation might occur if the density of existing stands of *A. torulosa* reached a level which imposed severe moisture stress. *A. littoralis* seeds reaching canopy gaps of sufficient size could then germinate and grow, producing a source for further seed invasion. However, if *A. littoralis* is more dependent on canopy gaps for establishment, then it appears likely that sharp boundaries between the two species will be more common when *A. torulosa* is replacing populations of *A. littoralis*. Even where the current distributions represent an equilibrium situation, several moist growing seasons may result in the encroachment of *A. torulosa* into stands of *A. littoralis*. This process may then be reversed by drier conditions. Restricted seed dispersal would generally limit the rate of such encroachment (Chapter 4).

In conclusion, although many factors may be involved in the control of the distributions of *A. littoralis* and *A. torulosa* in North Queensland, moisture availability appears to be dominant. Both species are restricted to areas with an annual rainfall of 1,000 to 2,000 mm, with *A. littoralis* predominating where site factors result in fluctuating moisture availability through the growing season, and being replaced by *A. torulosa* where more favourable soil moisture levels permit the development of a closed canopy. It is likely that boundaries between the two species, although apparently abrupt, are in a state of constant flux, and while they may respresent invasion of *A. littoralis* by *A. torulosa*, the final position of the boundary will be determined by moisture availability.

9.3 Life History Characteristics

Various attempts have been made to characterize plant life history traits most suited to particular enviroments. Initial attempts were based on an extension to the model of r- and K-selection of MacArthur and Wilson (1967) (Gadgil and Solbrig 1972; Pianka 1970). This model has more recently been brought into question. Grime (1974, 1977, 1979) developed a two dimensional model similar to r-and K-selection, in which competition, disturbance and stress were believed to have different effects on life history characteristics. These models will be examined to assess their ability to predict the life history characteristics of *A. littoralis* and *A. torulosa*.

9.3.1 r- and K-selection

Models of life history characteristics based on the theory of r- and K-selection (MacArthur and Wilson 1967) predict that an r-selected species will have a shorter life-span, shorter juvenile period and greater reproductive effort, and produce a larger number of smaller seeds than a K-selected species (Gadgil and Solbrig 1972; Pianka 1970). The reasoning behind this theory is that investment in non-reproductive activities will enhance a species' fitness when its population is controlled by density-dependent mortality characteristic of crowded environments, whereas increased reproductive output will increase fitness under density-independent mortality characteristic of uncrowded environments (Gadgil and Solbrig 1972).

Hence, *A. littoralis* with greater reproductive effort, earlier reproductive maturity and shorter life-span than *A. torulosa*, would be closer to the r end of the postulated r-K gradient of life history characteristics. However, such an interpretation of r- and K-selection has received much criticism (Boyce 1984; Harper 1977; Parry 1981; Schaffer 1974b). High reproductive effort is not necessarily associated with a high fecundity (Parry 1981; Stearns 1984), nor does higher fecundity always result in a greater abilty to leave descendents (Harper 1977). Therefore, it cannot be assumed that higher reproductive effort is equivalent to r-selection. Furthermore, life history characteristics may be influenced by many factors other than density-dependent and density-independent mortality, such as seasonality, habitat stability, predation, stress and the need for dispersal (Parry 1981 and references therein). Were it possible to determine the likely effect of density-dependent mortality versus density-independent mortality, it would not necessarally follow that species possessing such characteristics did so because of r- or K-selection.

Although competition, predation, parasitism, pathology and pollination are all affected by density (Antonovics and Levin 1980; Dobson and Hudson 1986), each will have a different influence on life history characteristics (Boyce 1984; Whitehead 1983). As r- and K-selection are traditionally considered in terms of competition, the effects of competition will be considered here. If a crowded environment is defined as one in which there is high intraspecific competition for resources, then crowding must be measured by the resource for which there is most intraspecific competition. In the previous section it was shown that *A. littoralis* is adapted to environments of low moisture availability, where light is not limiting, while *A. torulosa* is adapted to environments of low light availability, where moisture is not limiting. This can be restated in the following way: *A. littoralis* is adapted to survival in environments which are crowded in terms of moisture availability, and *A. torulosa* is adapted to survival in environments which are crowded in terms of light availability. Therefore, individuals within populations of *A. littoralis* will be most likely to suffer density-dependent mortality caused by moisture stress, while those within *A. torulosa* populations are most likely to suffer density-dependent mortality caused by stress induced by shading. It is only to the human eye that a closed-forest apears more crowded than an open woodland. The demonstration of competition for moisture between neighbours in desert shrublands (Ehrleringer 1984; Fonteyn and Mahall 1981) indicates that density-dependent mortality can occur in an apparently open environment.

Therefore, it may be constructive to examine more closely the effects of availability of light and moisture on life history characteristics. Plants that grow in environments limited by light must be able to either tolerate low light levels or avoid shading by rapid growth to the canopy (Abrahamson and Gadgil 1973). Among *Solidago* spp., Abrahamson and Gadgil (1973) found that species of *Solidago* in light-limited environments had greater investment in shoot biomass, if this enabled the plant to reach the canopy, and that species from wet meadow or forest environments, in which shading occurred, had a higher reproductive effort than those of disturbed, dry environments, where shading did not occur because of low plant density. However, as they assumed that higher reproductive effort in the dry environment was a result of r-selection, and low reproductive effort in the wet and hardwood environments a result of K-selection, they did not examine the reproductive patterns characteristic of light-limited and moisture-limited environments. From their observations it is possible to conclude that while plants of a moist environment are likely to experience competition for light, and thus increase their stature at the expense of reproductive output, those of dry environments, in which there is little competition for light, are more able to maximize reproductive effort. Thus the larger maximum size reached by *A. torulosa* is likely to be a result of its occurrence in a more shaded environment than *A. littoralis*.

Several studies have demonstrated an inter-relationship between life history traits, with size being positively correlated with length of juvenile period and life-span, and negatively correlated with reproductive effort (Blueweiss *et al.* 1978; Harper and White 1971; Schaffer 1974a; Stearns 1983, 1984; Strauss and Ledig 1985; Western and Ssemakula 1982). Selective forces operating on one of these traits will have a parallel effect on the associated traits. This has been demonstrated for selective forces influencing size (Stearns 1984).

If shading selects for a larger stature, it is therefore also likely to select for later reproductive maturity, smaller reproductive effort and a longer life-span. Thus the life history characteristics of *A. torulosa* and *A. littoralis* are simply in agreement with those which would be expected in shaded and unshaded habitats, respectively. However, it cannot be assumed that such a model will be universal for comparison between plants in shaded versus non-shaded environments, as plants may have different responses to moisture stress and competition for light, which may be morphological, anatomical or physiological (Blackman and Wilson 1951a,b; Gadgil and Solbrig 1972; Levitt 1980; Nilsen *et al.* 1984; Withers 1979a).

A major criticism of the r- and K- selection model of life history traits is that it does not differentiate between mortality imposed on different stages of the life cycle. Schaffer (1974b), following Murphy (1969), calculated that environmentally induced variation in the proportion of offspring reaching maturity favours a reduction in reproductive effort, whereas variations in post-breedling survival among adults favour greater investment in breeding. Barclay and Gregory (1982) interpret this more narrowly, by stating that mortality imposed on one life stage will reduce the length of this life-stage in relation to the other.

If differential adult and juvenile mortality are responsible for the differences in life history, then *A. littoralis*, with a higher reproductive effort, would be expected to have a higher ratio between reproductive success (proportion of offspring reaching maturity) and post-breeding adult survival. If this theory is correct, then the probability of offspring reaching maturity should be higher in *A. littoralis* than in *A. torulosa*, as two years' mortality data at Kirrama showed that adults of the two species have similar survival rates (Chapter 7). No differences were detected in the proportion of female inflorescences producing cones (Chapter 7) and while more seed escaped predation in *A. torulosa*, more seedlings successfully germinated and survived to the end of the first year in *A. littoralis* (Table 9.2). The nett effect is that *A. littoralis* does indeed appear to have lower juvenile mortality to the end of the seedling phase (Table 9.2). As no mortality was detected in plants between 4 and 8 cm, the extended juvenile phase in *A. torulosa* may not detract further from juvenile survivorship probabilities.

Table 9.2 Probability of survivorship of different life stages in *A. littoralis* and *A. torulosa*.

Stage	*A. littoralis*		*A. torulosa*	
	Survivorship probability	Cumulative	Survivorship probability	Cumulative
Seed[a] (3 days)	27.7	27.7	47.5	47.5
Germination[b]	47.7	13.21	21.0	9.98
Seedling[b] (1 year)	36.6	4.84	4.4	0.44
Juvenile (2 years)	96.9	4.69	93.7	0.41

[a] Under canopy of parent

[b] In environment of optimal survivorship: *A. littoralis* open *A. littoralis* canopy, *A. torulosa* closed *A. torulosa* canopy.

Thus, the high reproductive effort of *A. littoralis* is associated with low juvenile mortality and, conversely, the low reproductive effort of *A. torulosa* with high juvenile mortality. However, as reproductive effort affects post-breedling survival (Harper 1977), which, in turn, affects seedling establishment, age-specific mortality can only be considered to be another of the inter-related life history traits.

The model of r- and K-selection has also been extended in an attempt to explain seed dispersal characteristics. Gadgil (1971) proposed that rapid population growth is maximized by low dispersal rates, and that greater dispersal should enhance escape from density-dependent mortality. In this model, greater seed dispersal distances achieved by *A. littoralis* would be K-selected in comparison to *A. torulosa*. Therefore, the interpretation of r- and K-selection for life history characteristics conflicts with that for dispersal.

In wind-dispersed species, dispersal has two possible roles: escape and colonization (Howe and Smallwood 1982). Escape may be from an environment influenced by the parent (Werner 1976), from density-dependent seed or seedling predation or pathogenic attack (Antonovics and Levin 1980; Janzen 1970; Platt 1976), or from intraspecific competition (Connell 1971). Greater seed predation and seed-fall under *A. littoralis* than under *A. torulosa* suggests that the seed predators are sensitive to seed availability (Chapter 4). Thus the greater dispersal of *A. littoralis* may reduce the effects of density-dependent seed predation. This is supported by the fact that although most *A. littoralis* seed fell beneath the canopy of potential female parent plants (Chapter 4), more seed germination was observed outside the canopy (Chapter 5). Seedlings of *A. littoralis* are less likely to establish under a canopy than in a canopy gap or open vegetation (Section 9.2). Therefore, dispersal may also increase the probability of seedling recruitment, by increasing the probability of seeds landing in an open environment.

The significantly lower predation of *A. torulosa* than *A. littoralis* seed, combined with the greater probability of seedlings establishing under a canopy than in the open (Section 9.2), is likely to result in a shorter optimal dispersal distance for *A. torulosa* seeds. This may explain why *A. torulosa* seeds not only have evolved a smaller surface area to weight ratio than *A. littoralis* seeds, but that few seeds are released from the cones before the cones are abscissed.

The low percentage of seedlings surviving the first year in any environment suggests that intraspecific competition among cohorts may not be a significant source of mortalities. Although survivorship may be greater in years with a longer, more intense wet season, it appears that the exploitation of moisture by established plants, of any species, may be a more important source of mortality.

While seed predation and distribution of environments suitable for seedling establishment may influence the optimal dispersal distance, nutritional reserves in the seed needed for seedling establishment also affect dispersal characteristics, by altering seed weight. Reserves in a seed include carbohydrates which are needed until photosynthesis of the seedling can produce enough to sustain plant growth (Bewley and Black 1978). As self-sufficient levels of photosynthesis are likely to be reached sooner in a species of open environments, seed reserves are likely to be greater in species of shaded environments (Baker 1972; Salisbury 1942), a pattern suggested by the relative seed size of *A. littoralis* and *A. torulosa*. Thus, the need for greater seed reserves in *A. torulosa*, resulting in this species having heavier seed, is likely to influence the dispersal abilities of the two species.

Analysis of the population dynamics of *A. littoralis* and *A. torulosa* therefore supports the conclusions of Parry (1981) and Boyce (1984), that there is no convincing universal correlation between life history characteristics and density-dependent versus density-independent mortality.

9.3.2 C-, S- and R-selection

Arguing that all factors influencing a plant's distribution are related to either stress or disturbance, Grime (1974, 1977, 1979) suggested that competitive ability would be selected for where both were low (C-selection), that stress tolerance would be selected for by high stress levels (S-selection) and that the selective processes of disturbance could be described as R-selection. When both stress and distubance are high, plant growth is impossible (Grime 1977). He went on to predict a range of traits which would be characteristic of plants occurring in each of the three environments, which he described as competitive, stress-tolerant and ruderal strategies. Extreme expression of his ruderal strategy is restricted to herbaceous species with short life-cycles (Grime 1977). The strategies of woody trees and shrubs range between being C-selected and S-selected. However, one tree genotype may be more R-selected than another. The model is analagous to r- and K-selection when viewed in relation to plant succession from uncrowded to crowded environments, with the dominant selective forces shifting from R- through C- to S- selection (Grime 1977).

Life history characteristics of *A. littoralis* and *A. torulosa* are allocated here to the C-, S- and R- categories of Grime (Table 9.3). Although consignment to a category is subjective and the overlap between them broad, both species are close to the C-selected category, *A. littoralis* being more R-selected and *A. torulosa* being more S-selected. Therefore, for the comparison between the two species, analysis using Grime's model does not alter the relative positions of the two species in relation to the r-K gradient.

There are, however, flaws in Grime's model, beyond those caused by the application of r-and K-selection to the interpretation of life history characteristics. These are related to the definition of a stressful environment, the separation between competition and the stress it imposes, and the point at which stress can be considered a disturbance.

Table 9.3 Life history characteristics of the strategies proposed by Grime (1977) and their occurrence in *A. littoralis* (L) and *A. torulosa* (T).

Strategy:	Ruderal	Competitive	Stress-tolerant
Longevity of established phase:	Short.	Long or relatively long. L,T	Long to very long. L,T
Leaf phenology:	Short period of leaf production in period of high potential productivity.	Well-defined peaks of leaf production coinciding with period(s) of maximum potential productivity. L,T	Evergreens with weakly-defined patterns of leaf production. (L,T)
Phenology of flowering:	Flowers produced early in the life history. L	Flowers produced after (or more rarely before periods of maximum potential productivity. L,T	No general relationship between time of flowering and season.
Frequency of flowering:	High frequency of flowering. L	Established plants usually flower each year. L,T	Intermittent flowering over a long life history. T
Proportion of annual production devoted to seeds:	Large.	Small. L > T	Small. L > T
Perennation:	Dormant seeds.	Dormant buds and seeds. L,T	Stress-tolerant leaves and roots. L,T ?
Regenerative strategies:			
-Numerous small widely dispersed seeds or spores	yes	yes	yes
-Seasonal regeneration in vegetation gaps	yes L,T	yes L,T	no
-Persistent seed bank	yes T	yes T	no L
-Persistent seedling bank	no L	no L	yes T
-Vegetative expansion	no L.T	yes	yes

Grime describes a stressful environment as one in which the stress is not only continuous, but as a consequence one in which "there is little scope for characteristics of morphology or phenology to provide mechanisms for avoiding stress" (Grime 1979 p 124), so that only stress-tolerant plants can survive and reproduce. However, he goes on to list morphological characteristics found in plants of such environments which are clearly adaptations to stress (Grime 1979). Moreover, stress tolerant plants are those capable of surviving stress until more favorable conditions return; only stress-avoiders can complete the life-cycle in a stressful environment (Levitt 1980). Thus no species could persist in Grime's stressful environment, if, by definition, it lacks the adaptations to avoid stress. This contradiction may be contributed to by the inconsitent use of stress terminology in the literature. While Levitt (1980) differentiates stress tolerators and stress avoiders, other authors have used the term stress tolerance to include Levitt's stress avoidance category (Jones *et al.* 1981).

Grime (1977) suggests there is no evidence that plants from stressful environments can ever outyield species adapted to competition, regardless of the level of resource availability. It is therefore unclear under what conditions S-selected species can replace C-selected species. In fact, not only has a disordinal (Lubin 1961) interaction between competitive succes and level of environmental stress been demonstrated (Fowler 1982, Chapter 6), but it is also now evident that competition can have a significant effect on plant survivorship in severe environments (Ehrleringer 1984; Fonteyn and Mahall 1981). While Grime recognizes that the majority of environments experience the influence of competition, stress and disturbance, his presentation gives the impression that the over-riding importance of one of the three will often be clear.

Grime defines stress as "the external constraints which limit the rate of dry-matter production of all or part of the vegetation" (Grime 1977 p 1175), and disturbance as "the mechanisms which limit the plant biomass by causing its destruction (Grime 1977 p 1182). Thus, while moisture availability levels limiting to growth are recognized as stress, slightly lower levels resulting in tissue death are called disturbance. While there is merit in differentiating between growth retardation and tissue death, most plants affected by moisture stress will experience at least some tissue loss, making distinction between stress and disturbance unclear.

Because of its imprecise predictions, which do not differ markedly from those of the life history model based on r- and K-selection, and further conceptual shortcomings, Grime's model contributes nothing to the understanding of *A. littoralis* and *A. torulosa*.

9.3.3 Conclusions

Both the above models fail to predict the association between life history characteristics and environment found in *A. littoralis* and *A. torulosa* in North Queensland. Neither recognises that particular environmental factors can have individual selective effects on life history characteristics. The equation of a crowded environment with one in which light is limiting has led to false conclusions regarding r- and K-selection: that the life history characteristics of light-limited communities are correlated with density-dependent population regulation, and those of non-light limited communities are associated with density-independent population regulation. It has been shown here that low reproductive effort may be associated with light-limited environments as a secondary effect of selection for greater stature, rather than as a direct result of crowding. Life history characteristics are influenced by many selective forces, including crowding, seasonality, habitat stability, dispersal requirements, predation, resource availability and stress (Parry 1981), and although it may be possible to demonstrate the effect of a single factor on a life history parameter, the reverse may not be true. While it may be productive to categorize the life history characteristics associated with particular environmental factors, the factors should be examined individually, without attempting to group them into effects of competition, stress or disturbance.

The suites of life history characteristics possesed by *A. littoralis* and *A. torulosa* are those increasingly found to be associated with each other (i.e. *A. littoralis*: small size with high reproductive effort, short juvenile period and life-span and high reproductive success, and *A. tourlosa*: large size with low reproductive effort, long juvenile period and life-span and low reproductive success), and may not be attributed directly to any one selective force. However, they are consistent with the life history characteristics expected in species adapted to high and low light intensities. The dispersal charcteristics of *A. littoralis* and *A. torulosa* are best explained by the ability of the species to regenerate and establish beneath the canopy of the parent.

9.4 Implications for Forestry Programs

Characteristics which have led to the increasing importance of Casuarinaceae species in tropical revegetation programs include fast growth rates, ease of propagation, the contribution of their symbiotic actinomycetes to soil nitrogen status, and suitability for utlization in stabilization of eroding soils, or as fodder in times of drought (Anon. 1984b). *A. littoralis* and *A. torulosa* share many of these characteristics, and although *Allocasuarina* spp. appear to have slower growth rates than the *Casuarina* species currently favoured in such programs (J.W. Turnbull pers. comm.), they may be more suitable in fire prone environments (Chapter 8). The information gathered in this thesis should assist the optimum utilization of these species.

9.4.1 Rainfall limits

A. littoralis and *A. torulosa* would be suitable for planting in tropical environments with a minimum rainfall of 1,000 mm. The upper rainfall limit of their natural distributions are probably determined by competitive exclusion by more mesic species. Therefore, although distribution of both species is generally about 2,000 mm, except on rocky outcrops, it is likely that either species would grow well under higher rainfall on well drained soils. *A. littoralis,* with its higher transpiration rate may tolerate more poorly drained soils than would *A. torulosa* as evinced by its occurrence on the floodplains of the Herbert, Tully and Murray Rivers (Tracey 1982), although it has been reported as unsuitable where annual rainfall reaches 5,000 mm (Anon. 1984b).

While the rainfall estimates for *A. torulosa* of Boland *et al.* (1984) are in agreement with those found here, other authors have described lower rainfall limits for both species (Anon. 1984b; Doran and Hall 1983). A lower rainfall limit of 300-500 mm has been described for *A. littoralis* (Anon. 1984; Doran and Hall 1983) and of 400-600 mm for *A. torulosa* (Doran and Hall 1983). Although no references distinguish between rainfall limits of tropical and temperate populations, and these species may occur at lower rainfall levels in the temperate or subtropical parts of their distributions, there is no evidence that they could survive under such conditions in the tropics, unless grown under irrigation. Furthermore, comparison of the distributions of the species (Doran and Hall 1983), with rainfall maps of Australia (Anon. 1984c), suggests that *A. littoralis* is unlikely to flourish under rainfall levels of less than 500 mm per year, or *A. torulosa* under 650 mm per year, even in the southern parts of their ranges. The higher rainfall requirements of these species should be taken into account when they are considered for tropical revegetation programs.

9.4.2 Growth Rates

The growth rates of *A. littoralis* and *A. torulosa* at Kirrama measured in this thesis are not applicable to individuals from provenances, or to artificial environments, where there is little or no interference from other species, and where spacing reduces intraspecific interference. Faster initial growth rate of *A. littoralis* than of *A. torulosa* may not occur in all situations or between all provenances, but has also been observed in Townsville (19°19' S 146°43' E) and Victoria (32°29' S 144°17' E), where individuals of a variety of provenances have been planted (pers. obs.). In Townsville, *A. torulosa* appeared to suffer because of the high temperatures and incident solar radiation, whilst in Victoria, its growth was retarded by frost damage. In both cases, the foliage of this species showed signs of anthocyanin production in response to stress.

North Queensland provenances of *A. littoralis* appear to have a faster growth rate than those from the lower rainfall populations in the south of their range. Whether this higher growth rate would be sustained in non-tropical environments has yet to be determined. The initially faster growth rates of *A. littoralis* makes it a more suitable species for revegetation programs where rapid, short term firewood production or land stabilization is required. As *A. torulosa* has the best quality timber of all members of the family (Anon. 1984b), this species should be considered where timber quality rather than fast growth is a consideration. The absence of many mixed stands of *A. littoralis* and *A. torulosa* in the field gives little indication of the suitability of the species for mixed planting. However, mixed plantings may combine the aims of short-term and long-term production, with *A. littoralis* being removed in the early thinnings. Whether such a combination is successful would partly depend on the nitrogen fixing actinomycetes. It has yet to be established how host-specific these organisms are. If host specificity is demonstrated, then interference between the strains or species associated with *A. littoralis* and *A. torulosa* should be investigated.

Only a small proportion of seedlings grown in soil from beneath *A. littoralis* and *A. torulosa* showed signs of nodulation, with a higher incidence of nodulation in *A. torulosa* (Chapter 6). This contrasts with the relatively high nodulation success recorded in Victoria for *A. littoralis* seedlings planted in soils from sites where nodules had been found (Lawrie 1982). If high nodulation rates are considered desirable, an active nodulation program may be necessary. However, attempts to artificially nodulate *A. littoralis* have met with little or no success (Coyne 1983).

Nodulation did not significantly affect seedling growth rate or appear to confer the individual with a superior interspecific or intraspecific competitive ability (Chapter 6). The effects of nodulation may become more evident with increasing plant age. However, as no nutrient analyses were undertaken, it is not known whether the lack of effect resulted from a high nitrogen level in the soil,

9.4.3 Fire

Both *A. littoralis* and *A. torulosa* would be suitable for planting in areas where fire is a hazard, or where it is desirable to burn the understorey vegetation. Most trees should recover from low intensity burning, where damage can be restricted to 100% canopy scorch (Chapter 8). Some individuals which experience more severe damage may also recover by basal sprouting. However, too frequent burning may inhibit establishment of seedlings.

9.4.4 Seed Losses

Most reafforestation programs using casuarinas are established from transplanted seedlings rather than seed (Midgely *et al.* 1983). However, in other forestry programs, seeding is frequently employed as a more cost-effective method of propagation (Grose 1960). However, losses to ants and other predators can be substantial (Grose 1960; Smith and Aldous 1947) and expensive pelleting of seed with insecticides has had restricted success in improving germination success (Russell *et al.* 1967). Seeding in association with charcoal or ash, however, should substantially reduce seed predation (Chapter 8). While ash delays germination in *A. littoralis* charcoal does not inhibit germination in either *A. littoralis* or *A. torulosa* (Chapter 8). Therefore, charcoal would be a more suitable agent to reduce seed losses. This charcoal may be produced by burning the site. However, where this is not desirable, a mixture of charcoal and seed may be successful, but needs further investigation. High germination success along burnt windrows has been attributed to increased soil fertility and decreases in antagonistic soil micro-organisms (Pryor 1963; Renbuss *et al.* 1978). However, it now appears that seed falling in an ash or charcoal bed, such as those associated with windrows, will be more likely to escape seed predation.

It appears that the activity of charcoal may be related to its ability to absorb odours, and thus prevent the ants from detecting the seed, while that of ash may be more related to the effect of its powdery structure on ant mobility. Further investigations into the influence of charcoal on the ability of ants to detect seeds are currently underway. Whether charcoal could be used to protect large quantites of seed from losses to ants, such as from cones placed in the sun to open (Kondas 1983), is also worthy of investigation.

9.5 Implications for Palaeoenvironmental Reconstructions

The present North Queensland distributions of *A. littoralis* and *A. torulosa* (Chapter 3), suggest that these species require a minimum annual rainfall of about 1000 mm, and, except on rocky outcrops, will be replaced by more mesic species above 2000 mm. The only location where either species was found on basalt, Mt Fox, has an estimated rainfall of about 1100 mm (BIOCLIM prediction, H.A. Nix pers. comm.). Thus the annual rainfall estimates of 500 to 750 mm for the basaltic Atherton Tableland in the vicinity of Lynch's Crater during the phase of highest Casuarinaceae representation (38,000 to 9000 yrs B.P.; Kershaw 1985) are too low to support either *A. torulosa* or *A. littoralis*. However, estimated rainfall levels of about 1000 to 1500 mm from 165,000 to 126,000 yrs B.P. and from 78,000 to 38,000 yrs B.P., when Casuarinaceae representation was also high (Kershaw 1985, 1986), are within the range required to support these species.

It has been suggested that the vegetation in the vicinity of the crater during these glacial maxima was grassland or sparse open woodland (Kershaw 1983) and, that under such conditions, high Casuarinaceae representation could be derived from areas of higher rainfall some distance away (A.P. Kershaw 1983). Pollen sizes suggest that *A. torulosa* was the dominant species contributing to the pollen spectra during these glacial maxima (A.P. Kershaw pers. comm.). If, during the last glacial, casuarinas were growing in the higher rainfall zones, which are restricted to the ranges and coastal plains to the east of Lynch's Crater, rainforests would have covered very little of the present continental area (Kershaw 1985).

If either species were present at Lynch's Crater during the latter part of the last glacial, Kershaw's rainfall predictions would be underestimates. Rainfall required to support these species at the site would thus be in the order of 20 to 60% lower than present day levels, rather than the 80% proposed by Kershaw (1985, 1986). Alternatively, casuarinas may have been able to survive lower rainfall levels at the site because of depressed temperatures or changes in rainfall seasonality. However, a change in rainfall seasonality seems unlikely as *A. torulosa* is currently restricted to areas of summer rainfall maximum (Doran and Hall 1983).

Therefore, until more information is gathered on vagility of Casuarinaceae pollen, and progress is made towards identification of Casuarinaceae pollen at the specific level, the area from which the pollen was derived and thus vegetation distributions within the region cannot be determined.

Kershaw (1986) concludes that increased fire frequency due to Aboriginal burning was responsible for the replacement of Araucarian rainforests by Casuarinaceae and *Eucalyptus* spp. at about 38,000 yrs B.P. Studies here confirm that *A. littoralis* and *A. torulosa*, although not dependent on burning, can indeed exist in a fire-prone environment. It is therefore possible that environments favourable to the coniferous species replaced in the vegetation change could have been opened up to casuarinas as well as the fire tolerant *Eucalyptus* spp. This interpretation is again limited by an inability to identify Casuarinaceae and *Eucalyptus* pollen to specific level.

CHAPTER 10

FUTURE DIRECTIONS FOR RESEARCH

While this thesis has identified many of the factors affecting populations of *A. littoralis* and *A. torulosa* in North Queensland, and determined some of those which differentiate the niches of the two species, many areas were identified where further research would be of benefit. Studies not attempted in this thesis, such as investigations into the influence of soils, microbiota and pathogens on plant growth and reproduction, an examination of genetic variation within the two species and a thorough bioclimatic analysis, would complement the present study.

Between an average annual rainfall of 1,000 and 2,000 mm, variation in moisture availability influences which of the two species will prevail. While germination characteristics, seedling architecture and transpiration rates are involved, a more detailed study of the water relations of the two species, such as that undertaken by Withers (1978a,b, 1979a,b) for *A. littoralis* and *Eucalyptus ovata*, is needed. Moreover, field examination of soils supporting *A. littoralis* and *A. torulosa* may allow firmer conclusions to be made regarding moisture and nutrient availability. Studies of lignotuber development and the influence of light levels on photosynthesis may elucidate the apparently greater ability of *A. torulosa* over *A. littoralis* to regenerate under a closed canopy.

In some situations, the invasion and domination by *A. torulosa* of *A. littoralis* stands, and by rainforest species of *A. torulosa* stands was indicated. However, such processes were not directly witnessed in this thesis. The long-term study of boundaries between *A. littoralis* and *A. torulosa* or *A. torulosa* and rainforest would help to determine whether such colonization occurs and the processes involved. This could be augmented by artificial seeding of sites which have experienced recent disturbance.

The apparent inconsistency between germination characteristics which should ensure the persistence of *A. littoralis* seed through periods of irregular moisture availability and the small size of the seed bank of this species compared to that of *A. torulosa* may be explained by more detailed examination of the distribution of seed banks of the two species. Studies should also be undertaken to identify the relative importance of different pre- and post-dispersal seed predators.

The effects of charcoal and ash on seed losses to predators which have broad implications for forestry, deserve further investigation. Examination of the mechanisms by which ants detect seed, the ability of charcoal to absorb odours, and deterrent effects of ash and charcoal on seed predators, is currently underway. Artificial seeding trials, using various proportions of seed to charcoal or ash will also be undertaken.

To separate the effects of physical factors and the influence of neighbours on the reproductive schedules of *A. littoralis* and *A. torulosa*, a plantation of several provenances of each species has been established in the grounds of James Cook University. Onset of sexual maturity, sex ratio, reproductive output and growth rates will be monitored. Reproductive cycles will be assessed by long-term measurement of reproductive effort of the two species in this plantation, but field studies will be needed to determine the amplitude of natural cycles.

To determine the implications for revegetation programs of the resprouting ability of *A. littoralis* and *A. torulosa*, studies of the response to fire of a wide range of Casuarinaceae species, including those traditionally employed in such programs, should be undertaken, along with measurements of relative growth rates before and after burning.

Progress in the interpretation of the abundance of Casuarinaceae in North Queensland pollen sequence awaits refinement of pollen identification for the family. Due to the narrow range of interspecific morphological variation within the family (Kershaw 1970), techniques such as discriminant analysis (Birks and Peglar 1980) may need to be employed. Once identification problems are overcome, studies of pollen rain within different vegetation communities may help to determine the likely source of pollen in the Lynch's Crater sequence. Fine resolution pollen analysis in conjunction with time series analysis (Green 1981) may then help to shed light on the long term population dynamics of *A. littoralis* and *A. torulosa* in North Queensland.

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APPENDIX 1

LIST OF PLANTS OCCURRING AT THE KIRRAMA STUDY SITE

Quadrats were numbered from East to West: A to J
and from North to South: 1 to 4.

Species are grouped in this list according to the tallest vegetation stratum in which they were found within the study site. Presence within each stratum is designated by the following letter:

C	Canopy	(20 - 30m)
S	Sub-canopy	(3 - 20 m)
L	Shrub Layer	(Woody species, other than vines, < 3 m)
V	Vines and Scramblers	(Woody species)
G	Ground Layer	(Herbaceous species)

Plants were identified by G.M. Crowley, B.R. Jackes, B.P.M. Hyland, G.A. Duff and the staff at Brisbane Herbarium.

SPECIES	QUADRAT			
	A1	A2	A3	A4
CANOPY (C)				
Eucalyptus tereticornis Sm.	C			
Eucalyptus intermedia R.T. Baker		S	C	C
Eucalyptus grandis W. Hill ex Maiden				
SUB-CANOPY (S)				
Allocasuarina littoralis (Salisb.) L. Johnson	S	SL		S
Allocasuarina torulosa (Ait.) L. Johnson				
Eucalyptus torelliana F. Muell.	S	S		S
Timonius timon (Spreng.) Merr.	S	S	S	S
Euroschinus falcata Hook. f.	S	S		
Glochidion spp. J.R. & G. Forst.	L		SL	SL
Litsea leefeana (F. Muell.) Merr.		S		
Banksia integrifolia L. f.			S	
Acacia aulacocarpa A. Cunn. ex Benth.			S	S
Guioa acutifolia Radlk. in Sitzb.				
Alphitonia whitei Braid				
Neolitsea dealbata (R. Br.) Merr.				
Alstonia muellerana Domin				
Polyscias australianum (F. Muell.) Philipson				
Mischocarpus lachnocarpus (F. Muell.) Radlk.				
Polyscias elegens (C. Moore & F. Muell.) Harms				
SHRUB (L)				
Callicarpa pendunculata R. Br.	L	L	L	L
Rhodomyrtus trineura F. Muell. ex Benth.	L			
Duboisia myoporoides R. Br.		L		L
Eucalyptus spp. L'Herit		L		L
Ficus congesta Roxb.		L		
Ficus septica Burm. f.				L
Rhamnella vitensis vel. aff. (Benth.) A.C Smith				L
Psychotria loniceroides Sieber ex DC.				
Rhodamnia sessiliflora Benth.				
Breynia cernua (Poir.) Muell. Arg.				
Pittosporum revolutum Aiton f. ex Dryander				
Tarenna dallachiana (F. Muell.) S. Moore				
Symplocos sp. Jacq.				
Alphitonia petrei Braid & C.T. White				
Planchonella chartacea (F. Muell. in Benth.) H.J. Lam				
Ficus fraseri Miq.				
Mackinlaya macrosciadia (F. Muell.) F. Muell.				
Melastoma affine D. Don				
Dendrocnide moroides (Wedd.) Chew				
Scolopia braunii (Klotzch) Sleumer				
Trema aspera (Brogn.) Bl.				
Rapanea sp. Aublet.				

SPECIES	QUADRAT											
	B1	B2	B3	B4	C1	C2	C3	C4	D1	D2	D3	D4
CANOPY (C)												
E. tereticornis		C			C							
E. intermedia		S	C	C	S	S	S	C		C	L	C
E. grandis												
SUB-CANOPY (S)												
A. littoralis	S	SL	S	S	SL	L	SL	S	SL	SL	SL	SL
A. torulosa												
E. torelliana		L	L		L							
T. timon		S	S		S	S	S	S	L	S	S	S
E. falcata								S				
Glochidion spp.	S	S	S	S	L	L	S	SL		L	L	L
L. leefeana												
B. integrifolia		S	S			S						
A. aulacocarpa			S			L	S		S	L	L	
G. acutifolia	L							L				
A. whitei			S									
N. dealbata			L	L								
A. muellerana						L		S				
P. australianum							S		L			
M. lachnocarpus								L				
P. elegens												
SHRUB (L)												
C. pendunculata	L	L				L	L	L				L
R. trineura												
D. myoporoides						L	L	L				
Eucalyptus spp.	L			L							L	L
F. congesta												
F. septica							L					
R. vitensis vel. aff.												
P. loniceroides	L											
R. sessiliflora			L									
B. cernua						L	L					
P. revolutum								L				
T. dallachiana									L	L		
Symplocos sp.											L	
A. petrei												
P. chartacea												
F. fraseri												
M. macrosciadia												
M. affine												
D. moroides												
S. braunii												
T. aspera												
Rapanea sp.												

SPECIES	QUADRAT E1	E2	E3	E4	F1	F2	F3	F4	G1	G2	G3	G4
CANOPY (C)												
E. tereticornis	C			S			C	C				
E. intermedia	S	C		L		C	L	C				C
E. grandis												
SUB-CANOPY (S)												
A. littoralis	SL	SL	S	SL	SL	SL	SL	SL	L		S	S
A. torulosa					SL	SL	SL	L	SL	SL	SL	SL
E. torelliana			L	L		L						
T. timon		S	S	S	L	L	L	SL	SL	L	SL	L
E. falcata		L		L		L		S	L	SL	S	S
Glochidion spp.	S		L	S		L	S	SL	L		SL	SL
L. leefeana												
B. integrifolia	L	S		S		L	L		S	S		SL
A. aulacocarpa	L		S	S	S	S			S	S	S	
G. acutifolia			L	L		L			L	L	L	L
A. whitei												
N. dealbata											L	
A. muellerana										L		L
P. australianum		L				L				S	S	
M. lachnocarpus										L	L	
P. elegens												
SHRUB (L)												
C. pendunculata			L			L	L		L			L
R. trineura		L										
D. myoporoides												
Eucalyptus spp.					L		L	L	L			
F. congesta										L		
F. septica				L		L	L					L
R. vitensis vel. aff.												
P. loniceroides												
R. sessiliflora			L			L					L	
B. cernua				L		L			L			
P. revolutum												
T. dallachiana												
Symplocos sp.												
A. petrei					L							
P. chartacea							L					
F. fraseri									L			
M. macrosciadia									L			
M. affine									L			L
D. moroides										L		
S. braunii											L	
T. aspera												
Rapanea sp.												

SPECIES	QUADRAT H1	H2	H3	H4	I1	I2	I3	I4	J1	J2	J3	J4
CANOPY (C)												
E. tereticornis				S		CS					C	
E. intermedia		C			CS	C	C		S			L
E. grandis								C				
SUB-CANOPY (S)												
A. littoralis												
A. torulosa	SL	SL	SL	SL	SL	SL	SL	S	SL	SL	SL	SL
E. torelliana												
T. timon	SL	SL	S	SL	SL	L	SL	S	S	L		SL
E. falcata	L	S	S							S	L	
Glochidion spp.		L	L	S	L		SL	L	S	S	L	L
L. leefeana							L				L	L
B. integrifolia			L	L			L					
A. aulacocarpa	L	S	SL	L		L		L			L	S
G. acutifolia	L	L	SL	L	L	L	SL				SL	SL
A. whitei											S	
N. dealbata		S	L			L	L				L	
A. muellerana			S									
P. australianum			S									
M. lachnocarpus			L				L				S	
P. elegens										S		
SHRUB (L)												
C. pendunculata	L	L	L	L	L	L	L	L		L	L	L
R. trineura	L	L	L	L			L			L	L	
D. myoporoides												L
Eucalyptus spp.				L								
F. congesta							L				L	
F. septica		L										
R. vitensis vel. aff.												
P. loniceroides						L	L					
R. sessiliflora												
B. cernua												
P. revolutum												
T. dallachiana												
Symplocos sp.												
A. petrei												
P. chartacea												
F. fraseri									L	L		
M. macrosciadia												
M. affine												L
D. moroides												
S. braunii	L											
T. aspera		L				L						
Rapanea sp.										L		

SPECIES	QUADRAT			
	A1	A2	A3	A4
VINES AND SCRAMBLERS (V)				
Parsonsia straminea (R. Br.) F. Muell.				
Cissus antarctica Vent.				
Hibbertia scandens Gilg				
Maesa dependens F. Muell.				
GROUND COVER (G)				
LILIATAE				
Sorghum laxiflorum F. M. Bailey	G	G	G	G
Themeda australis (R. Br.) Stapf.	G	G	G	G
Imperata cylindrica (L.) Beauv.	G	G	G	G
Paspalidum scrobiculatum L.				
Panicum effusum R. Br.				
Oplimenus imbecillus (R. Br.) Roemer & Schultes				
Eragrostis spartinoides Steudel				
Panicum mitchellii Benth.				
Digitaria orbata Hughes				
Dianella cærulea Sims	G	G	G	
Lomandra longifolia Labill.				
Scleria brownii Kunth.				
Xanthorrhoea johnsonii A. Lee				
Gahnia aspera (R. Br.) Spreng.				
MAGNOLIATAE				
Rubus hillii F. Muell.	G		G	
Hydrocotyle vulgaris Ewart			G	
Emelia sonchifolia (L.) DC.				
Pycnospora lutescens (Poir.) Schindl.				
Oxalis sp. L.				
Glycine clandestina J. Wendl.				
Hybanthus enneaspermus (L.) F. Muell.				
PTERIDOPHYTA				
Cheilanthes tenuifolia (Burm. f.) Sw.				

SPECIES	QUADRAT											
	B1	B2	B3	B4	C1	C2	C3	C4	D1	D2	D3	D4
VINES AND SCRAMBLERS (V)												
P. straminea			V									
C. antarctica								V				
H. scandens												
M. dependens												
GROUND COVER (G)												
LILIATAE												
S. laxiflorum	G	G	G	G		G		G	G		G	G
T. australis	G	G	G	G	G	G	G	G	G	G	G	G
I. cylindrica	G	G	G	G	G	G	G	G	G	G	G	G
P. scrobiculatum	G											
P. effusum						G						
O. imbecillus												
E. spartinoides												
P. mitchellii												
D. orbata												
D. cærulea		G	G					G				
L. longifolia	G		G	G			G					
S. brownii						G						
X. johnsonii												
G. aspera									G	G	G	G
MAGNOLIATAE												
R. hillii												
H. vulgaris												
E. sonchifolia		G										
P. lutescens					G			G				
Oxalis sp.								G		G		
G. clandestina												
H. enneaspermus												
PTERIDOPHYTA												
C. tenuifolia												

SPECIES	QUADRAT E1	E2	E3	E4	F1	F2	F3	F4	G1	G2	G3	G4
VINES AND SCRAMBLERS (V)												
P. straminea												
C. antarctica												
H. scandens		V										
M. dependens											V	
GROUND COVER (G) LILIATAE												
S. laxiflorum	G		G	G		G	G	G	G	G		G
T. australis	G	G	G	G	G	G	G	G	G	G	G	G
I. cylindrica		G	G	G	G	G	G	G	G	G	G	G
P. scrobiculatum												
P. effusum												
O. imbecillus				G		G						
E. spartinoides					G						G	
P. mitchellii												
D. orbata												
D. cærulea							G					
L. longifolia						G	G	G	G	G		
S. brownii												G
X. johnsonii					G							
G. aspera	G	G	G	G	G			G				
MAGNOLIATAE												
R. hillii									G	G		
H. vulgaris	G											
E. sonchifolia		G										
P. lutescens							G					
Oxalis sp.												
G. clandestina								G				G
H. enneaspermus												
PTERIDOPHYTA												
C. tenuifolia	G											

SPECIES	QUADRAT											
	H1	H2	H3	H4	I1	I2	I3	I4	J1	J2	J3	J4
VINES AND SCRAMBLERS (V)												
P. straminea												
C. antarctica	V											
H. scandens												
M. dependens	V	V	V				V				V	V
GROUND COVER (G)												
LILIATAE												
S. laxiflorum			G				G	G	G		G	
T. australis	G			G	G	G	G	G	G	G		G
I. cylindrica	G	G	G	G	G	G	G	G	G	G	G	G
P. scrobiculatum												
P. effusum				G	G			G	G		G	
O. imbecillus	G		G						G			
E. spartinoides	G			G					G			
P. mitchellii			G		G				G			
D. orbata	G	G			G					G	G	
D. cærulea	G											
L. longifolia		G										
S. brownii								G		G	G	
X. johnsonii	G						G					
G. aspera												
MAGNOLIATAE												
R. hillii											S	
H. vulgaris												
E. sonchifolia									G			
P. lutescens												
Oxalis sp.												
G. clandestina												
H. enneaspermus	G	G		G								
PTERIDOPHYTA												
C. tenuifolia												

APPENDIX 2

LIST OF ANTS COLLECTED AT THE KIRRAMA STUDY SITE

Collected by S.T. Garnett, between 26/11/83 and 2/4/84.
Identified by A.N. Andersen and S.T. Garnett.
Note: This is not a comprehensive collection.

Status:

+ Present, not known to eat seed,
E Present, probable seed eater (A.N. Andersen pers. comm.),
K Seen eating seed at Kirrama (pers. obs., S.T. Garnett pers. comm.),
C Seen collecting seed at Kirrama (pers. obs.; S.T. Garnett pers. comm.).

	Sub-canopy species	
Ant Species	*A. littoralis*	*A. torulosa*
Ponerinae		
Anochetus sp.	+	
Bothroponera sp.		+
Cerapachys sp.		+
Hypoponera sp.		+
Leptogenys sp.	+	
Odontomachus sp.		+
R. "*metallica*"	E	E
R. victoriae	E	E
Rhytidoponera sp.	C E	C E
Mymicinae		
Crematogaster sp.		+
Meranoplus sp.		E
Monomorium sp.		+
Oligomyrmex sp.	+	
Pheidole sp. A	E K	E K
Pheidole sp. B	E K	E K

	Sub-canopy species	
Ant Species	*A. littoralis*	*A. torulosa*
Pheidole sp. C	C E	
Pheidole sp. D		E
Pheidole sp. E		E
Pheidole sp. F	E	
Pheidole sp. G	E	
Tetramorium sp.		
Dolichoderinae		
Iridomyrmex "*glaber*"	+	
Iridomyrmex" *foetans*"		+
Iridomyrmex "*nitidus*"	+	
Iridomyrmex sp.		+
Formicinae		
Camponotus "*nigroaneus*"	+	
Camponotus "*claripes*"	+	
Camponotus "*discors*"		+
Melophorus "*hirsutus*"	E	
Notoncus "*enormis*"	+	
Paratrechina sp.	E	E
Polyrachis sp.	+	+