Factors affecting seedling regeneration of woody species in a northern Australian tropical savanna

by

Samantha A. Setterfield

B.Sc.(Hons)  Monash University

School of Biological Sciences,
Northern Territory University

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Declarations

I hereby declare that the work herein, now submitted as a thesis for the degree of Doctor of Philosophy of the Northern Territory University, is the result of my own investigations, and all references to ideas and work of other researchers have been specifically acknowledged. I hereby certify that the work embodied in this thesis has not already been accepted in substance for any degree, and is not being currently submitted in candidature for any other degree.

S.A. Setterfield

Some chapters in this thesis have been written as scientific manuscripts. The following lists the co-authors and the status of the two manuscripts that have been accepted for publishing.

Chapter 2  Setterfield, S.A. and Williams, R.J. Patterns of Flowering and Seed Production in *Eucalyptus miniata* and *E. tetrodonta* in a Tropical Savanna Woodland, Northern Australia.


Chapter 3  Setterfield, S.A. The Impact of Experimental Fire Regimes on Seed Production in Two Tropical Eucalypt Species in Northern Australia.

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Abstract

Savanna vegetation covers approximately 40% of the surface of the tropics. Tropical savannas contain a large proportion of the world’s population and are experiencing increasing land use pressures, including vegetation clearance, grazing and the creation of pastures. A fundamental climatic characteristic of tropical savannas is rainfall seasonality, with annual alternation of rainy and dry seasons. Regular fire is also a characteristic feature of tropical savannas, and fire is a widely used management tool. Fire is considered to be an important determinant of savanna structure and growth, and has been demonstrated to have an important effect on plant population dynamics. The effective use fire as a management tool requires a thorough understanding of its ecological effects on the savanna plant community.

The tropical savannas of northern Australia cover approximately one-fifth of the continent. Land-use pressures are increasing in the region, and there is an increasing need to understand the regeneration ecology of savanna species so that sustainable land management practices (including vegetation rehabilitation) can be undertaken. This thesis examines factors affecting seedling regeneration of three common woody species in undisturbed and disturbed savanna in northern Australia. Fire is a predominant force in this region and particular attention is paid to the effects of fire on seedling regeneration.

Patterns of seed production and seed fall were investigated for the three species: *Eucalyptus miniata*, *Eucalyptus tetrodonta* and *Acacia oncinocarpa*. For all species, there were substantial temporal and spatial variation in seed production. Ovule production in these species occurred during the dry season, coinciding with a period of frequent (often annual) fire. Fire reduced seed production in all species by at least an order of magnitude compared to the unburnt trees, and the results indicated that both the fire intensity, and its timing in relation to phenological events, are important determinants of seed supply for regeneration.
Investigations on the post-dispersal fate of seed showed that seedling regeneration of *E. miniata* and *A. oncinocarpa* are limited by both seed supply and microsite availability. The experimental application of seed to sites in three fire regimes showed that burning reduced seedling emergence success compared to unburnt sites. This suggests that annual fire regimes (the predominant management regime in the region) can have a dramatic impact on regeneration, by both reducing seed supply and seedling emergence. The latter effect may be partly attributed to the loss of seeds to harvester ants, although investigations showed that the major limit to *E. miniata* establishment is caused by seed-bed conditions. Seed predation by ants appears to be a significant factor limiting recruitment in *E. miniata* by reducing the chance of seedling establishment from low (<10%) to virtually none.

A study of patterns of vegetation recolonisation on gravel pits in Kakadu National Park showed that despite the completion of physical rehabilitation to the pits, the re-establishment of overstorey vegetation, particularly Eucalypts, was poor. Like the undisturbed savanna, the re-establishment of woody vegetation on these severely disturbed areas is limited by both the availability of seed and the availability of suitable microsites. The primary supply of seed to the gravel pits in Kakadu is natural seedfall from the surrounding undisturbed vegetation. The work in thesis suggests that this supply will be low for several common woody species. Minor soil scarification substantially increased seedling emergence success, but the study suggests that seed supply must immediately follow the physical soil treatment. Therefore, due to the unreliability of an adequate seed supply from the vegetation surrounding the pits, seed must be artificially broadcast to ensure the re-establishment of woody vegetation. In addition, the rehabilitated site must be protected from fire for at least one year following seedling emergence to allow the seedlings to develop sufficient resources to survive burning.
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Chapter 1 Introduction

1.1 Tropical Savannas

Savannas are ecosystems characterised by a continuous layer of graminoids with a discontinuous layer of trees and/or shrubs occurring in the wet/dry tropical environment (Johnson and Tothill 1985; Frost and Robertson 1987; Solbrig et al. 1996). Savannas cover approximately 40% of the surface of the tropics, including large areas in Central and South America, Africa, India, southeast Asia and Australia (Cole 1986; Gerhardt and Hytteborn 1992) and occur over a wide range of climatic and edaphic conditions (Solbrig 1996). A fundamental climatic characteristic of tropical savannas is rainfall seasonality, although the duration of the dry season ranges from 3 to 9 months (Solbrig 1996). Frequent fire is predominant in tropical savannas worldwide as a consequence of the annual cycle of profuse herbaceous production during the wet season, followed by seasonal drought (Huntley and Walker 1982). Humans have been the main source of ignition for the past tens of thousands of years (Frost and Robertson 1987). Fire is considered to be one of the determinants of savanna structure and function, and frequent fire has played an important role in the development of many savannas from other vegetation types (Frost and Robertson 1987; Skarpe 1992; Andersen 1996).

Savannas contain a large and rapidly growing proportion of the world’s population (Werner et al. 1991). Most savannas are experiencing increasing land use pressures and have been exposed to severe large-scale changes through tree clearance, the creation of pastures, grazing and the widespread use of fire (Gerhardt and Hytteborn 1992).

1.2 Australia's Tropical Savannas

In Australia, tropical savannas cover a wide continental arc that extends across the coastal and sub-coastal lands of northern and eastern Australia (Figure 1.1, Mott et al. 1985).
Figure 1.1 The distribution of tropical tallgrass savannas in Australia
(from Mott et. al. 1985)
They have a graminoid understorey of variable floristic composition and an upper stratum dominated by *Eucalyptus* species (Mott *et al.* 1985). They typically occur on soils of low nutrient status that are weathered relics of earlier pedological processes (Mott *et al.* 1985; McKeon *et al.* 1991).

Unlike most savannas elsewhere, Australia's tropical savannas have not experienced intensive use by humans (Gillon 1983). Although they cover more than one-fifth of the Australian continent, they support only a sparse population of approximately 1% of Australia's population (~200,000 people; Lindsay 1996). Pastoralism is the most widespread landuse in Australia's tropical savannas. Other uses include traditional use by indigenous people, mining, military, tourism, agriculture and nature conservation (Tothill *et al.* 1985; Winter and Williams 1996). Land use pressures are increasing and land managers are faced with an increasing need to understand the ecological processes in savanna ecosystems, so that sustainable land management decisions can be made (Winter and Williams 1996). In addition, this knowledge is required to rehabilitate land that has already been degraded, particularly areas disturbed by mining and intense grazing (Hooper 1985; Winter 1991). Effective methods of land rehabilitation require a detailed understanding of community structure and function, as well as knowledge of the regeneration strategies of the vegetation communities (Ray and Brown 1994). To date, there have been few detailed investigations of the regeneration of savanna vegetation. The role of seed and seedlings in forest regeneration is poorly understood (Wilson *et al.* 1996).

1.2.1 The use of fire in land management

In Australia's tropical savannas, fire has been an intergral part of Aboriginal life for many thousands of years. Fire is currently used as a land management tool throughout the region by pastoralists (Andrew 1986), conservation park managers (Press 1988) and Aboriginies continuing traditional burning practices (Haynes 1985). Fire frequency is high, often annual, and tens of thousands of square kilometres of savanna are burnt each year.
during the dry season (Press 1988; Graetz et al. 1992). The characteristics of fire change throughout the year. Early in the dry season, fires are typically low in intensity and patchy (Williams 1995; Williams et al. 1995). As the dry season proceeds, the fuel loads cure and increase due to leaf litter inputs (Williams 1995), winds strengthen and atmospheric humidity declines (Gill et al. 1995). Fires lit late in the dry season are typically more intense and cover extensive areas (Williams et al. 1995). In the 1980’s, late dry season fires were more widespread than early dry season fires (Day 1985; Press 1988). Currently, the most common fire management strategy in the savannas of northern Australia is the burning of large areas of savanna early in the dry season to reduce the risk of intense late dry season fires (Andersen 1996).

Despite the extensive use of fire as a land management tool, the ecological effects of the various fire regimes on savanna vegetation in northern Australia are poorly known (Lonsdale and Braithwaite 1991). Studies have previously focused on changes in grass composition and productivity of pastoral lands (Tothill 1971; Andrew 1986), or on the structure and composition of woody vegetation (Bowman 1988; Lonsdale and Braithwaite 1991), rather than on ecological process, especially plant regeneration. Land managers are therefore having to make decisions about burning practices without adequate ecological information (Andersen 1996).

1.2.2 Regeneration of woody species in Australia’s tropical savannas

Like savannas throughout the world, vegetative regeneration is prominent in the tree stratum of Australia’s tropical savannas (Sarmiento and Monasterio 1983; Dunlop and Webb 1991). Vegetative regeneration commonly occurs from lignotubers (Carr et al. 1984), rhizomes (Lacey 1974), and root suckers (Carr 1972). As a consequence, a dominant structural feature of the savannas in this region are the vegetatively produced ‘woody sprouts’ in the ground layer (Fensham and Bowman 1992). These features may be a response to seasonal drought, frequent fire or low soil fertility (Lacey and Whelan 1976;
Wilson et al. 1996). In contrast to the conspicuous abundance of vegetative sprouts, seedling regeneration of tree species has been described as rare (Lacey 1974; Mott et al. 1985). The lack of seedlings could be due to low rates of seed production, high rates of seed predation, inappropriate conditions for germination and seedling establishment, or high rates of seedling mortality (Harper 1977). To date, there has been little work investigating factors that affect seed production, germination and the establishment of seedlings of savanna tree species (Wilson et al. 1996).

1.3 Thesis Aims and Structure

1.3.1 Thesis Aims

In view of the paucity of knowledge on regeneration in woody species in the world’s tropical savannas, this thesis has two major aims:

1. **To investigate factors affecting seedling regeneration of woody species in northern Australia’s savannas.** This includes studies on factors affecting seed production, and the post-dispersal fate of seed. Due to the high frequency of fire in the region, these studies also focus on the effects of fire on seedling regeneration.

2. **To investigate patterns of, and limits to, regeneration on disturbed sites.** This information, and the knowledge gained on the regeneration in the natural savanna, are used to develop guidelines for revegetation of disturbed sites.

1.3.2 Thesis Scope and Structure

This thesis focuses on the most common savanna types in Northern Australia - that dominated by *Eucalyptus miniata* and *Eucalyptus tetrodonta*. These species are two of the most common and widespread eucalypts in the northern Australian savannas. The reproductive strategies of these species are poorly understood (Fensham 1990), and the
majority of studies on their reproduction has focussed on vegetative regeneration. Previous authors have suggested that seedling regeneration in these species is rare, possibly due to sporadic flowering and low seed production (Fensham 1990; Wilson 1991). However, these suggestions were based on casual observations rather than quantification. Chapter 2 therefore describes the reproductive phenology of *E. miniata* and *E. tetrodonta*, and quantifies the temporal and spatial variation in seed production in these species. This study was undertaken in an area of savanna that had been protected from fire for four years prior to its commencement. These species are known to flower during the dry season (Brock 1988). This coincides with the period of frequent fire in the savannas (Braithwaite and Estbers 1985). Chapter 3 therefore describes the effect of three fire management regimes on ovule development and seed production in the two species.

*Acacia* species are common in the understorey of *E. miniata/E. tetrodonta* forests, but little is known about regeneration of any of the *Acacia* species in this region. *Acacia oncinocarpa* is one of the most common *Acacia* species in the savanna understorey, and is currently used for revegetation of cleared sites. Like *E. miniata* and *E. tetrodonta*, ovule development occurs during the dry season for *Acacia oncinocarpa*, and therefore fire may also affect ovule development and patterns of seed production in this species. Pre-dispersal seed predators have been identified as a major cause of seed loss for many *Acacia* species (Auld 1983; New 1983; Auld 1986; Auld and Myerscough 1986). Chapter 4 discusses the annual variation in seed production of *Acacia oncinocarpa*, and quantifies the impact of seed predators and fire regimes on seed production.

Having quantified seed production and investigated some of the factors affecting the pre-dispersal fate of seed, Chapters 5 and 6 examine the factors affecting seedling emergence of *Eucalyptus miniata* and *Acacia oncinocarpa*. The principal limitations to seedling emergence are the availability of seed and the availability of suitable sites for germination and seedling establishment (Crawley 1990). Therefore, Chapter 5 determines
which of these factors limit seedling emergence of *E. miniata* or *A. oncinocarpa*. Fire history can have a substantial effect on seedling regeneration, by altering the seed-bed conditions by removing competition for resources (eg. moisture and nutrients), changing light quality, the soil structure and presence of seed predators (Purdie 1977; Wellington and Noble 1985; Lamont *et al.* 1993; Tyler 1995). Chapter 5 therefore also investigates the effect of fire regime on seedling emergence.

The amount of seed available for regeneration may be substantially reduced by post-dispersal seed predators (Crawley 1989). Ants are the dominant post-dispersal seed predator in Australia (Andersen 1991), and the composition and abundance of seed-harvester ants is influenced by fire regime (Andersen 1991). Chapter 6 directly tests the relationship between seed removal by ants and seedling emergence, and investigates the effect of burning on this relationship.

In Chapter 7, the knowledge gained on regeneration of the study species is used to suggest methods for the rehabilitation of disturbed savanna. This chapter focusses on rehabilitation of gravel pits. Within Kakadu National Park in northern Australia, over 500 gravel pits have been mined to obtain road-building materials. Revegetation on the majority of these pits has been poor, even though it is over 20 years since many of the pits were mined. Chapter 7 investigates physical and biological factors that affect the composition and cover of vegetation that re-establishes on these disturbed sites. The limitations to seedling establishment of *E. miniata* and *A. oncinocarpa*, having been investigated in uncleared savanna in Chapter 5, are further investigated on gravel pits in Chapter 7. The results from this chapter, and our understanding of seedling regeneration in the undisturbed savanna (Chapters 2 to 7), are used to develop guidelines for the revegetation of disturbed sites in northern Australia’s savannas.
1.4 Study Site Description

1.4.1 Study location

The phenological and fire impact studies were conducted at Kapalga Research Station (12°40'S 132°25'E) in Kakadu National Park in the ‘Top End’ region of northern Australia (Figure 1.2). Kapalga is bounded to the west by the West Alligator River, and to the east by the South Alligator River. The Arnhem Highway forms the southern boundary. The Research Station covers approximately 670 kilometres of floodplain and savanna ecosystems. It was set aside as a research station in 1976, and early work at the station focused on the wetland communities, and on the impact of buffalo on the ecology of the savanna and floodplain communities. In 1990, a fire experiment commenced on the southern half of Kapalga (Andersen et al. 1997). The work at Kapalaga was undertaken within the area of the fire experiment.

The studies of regeneration on gravel pits were conducted on pits adjacent to various roads in Kakadu National Park, within 50 kilometres of Kapalga. Detailed investigations on vegetation recruitment were undertaken on pits within Kapalga.

1.4.2 Climate

Kapalga Research Station is located in the northern Australian tropics, and the climate is characterised by a winter dry season and a summer wet season. Although there are little climatic data available for Kapalga, 18 years of data are available for the nearby township of Jabiru (12°40'S 132°53'E). These data are used to describe the climate of the region. The wet season typically occurs between November and April, and 85% of the mean annual rainfall occurs between December and March (Jabiru data; Bureau of Meterology). Taylor and Tulloch (1985) have demonstrated considerable inter-annual variability in the timing of the
Figure 1.2 Location of Kapalga Research Station in Kakadu National Park, Northern Australia
transition between the wet and the dry seasons, the length of the rainless periods during the wet season, and the total annual rainfall.

Temperatures are high all year, ranging from a mean monthly maximum of 31.3°C in June to 37.5°C in October (Jabiru data; Bureau of Meterology). Mean monthly minimum temperatures range from 19.3°C in June to 25.7°C in December (Jabiru data; Bureau of Meterology). Hours of daylight vary throughout the year by only 1.4 hours (Bureau of Meterology).

1.4.3 Geology and Soils

Kapalga consists of an upland plain between seasonally inundated floodplains, and its highest point is 92m above sea level (G.D. Cook unpublished data). The underlying rocks are Proterozoic sandstones, quartzites, siltstone and other sedimentary or weakly metamorphosed rocks (Russell-Smith et al. 1996). These are overlain by Late Tertiary sands, silts, clays and gravels (Williams 1969). The upland plain of Kapalga forms part of the Koolpinyah surface, which comprises the gently undulating lowland plains that stretch from Darwin to the Arnhem Land escarpment (Russell-Smith et al. 1996). The upland plain in the southern part of Kapalga is drained by about 20 small, intermittent streams, that generally flow between December and June.

The soils supporting the open-forest communities are typically deep, well-drained soils with a gradational texture profile ranging from 5 to 15% clay at the surface to 15 to 30% clay at depth (G.D. Cook unpublished data). These soils have been derived from laterisation of the substrata, and have been repeatedly weathered, eroded and redeposited and the leaching of soluble components has resulted in low fertility soils. Small ferruginous nodules occur in moderate to high amounts in the soil, with the amount commonly increasing with depth (G.D. Cook unpublished data). These soils have sufficient
moisture in the top one metre of the soil profile to support tree growth throughout the year (Wilson and Bowman 1994).

### 1.4.4 Vegetation

The work was undertaken in open forest dominated by tall eucalypts, most commonly *Eucalyptus miniata* and/or *Eucalyptus tetrodonta* (Wilson *et al.* 1990). These forests are widespread across the northern coastal parts of the ‘Top End’ region, and is the most common vegetation type on the upland area of Kapalga. Canopy subdominants include *Erythrophleum chlorostachys*, *Terminalia ferdinandiana*, *Acacia* spp., *Buchania obovata*, and *Xanthostemon paradoxus* (Williams and Douglas 1995). The ground layer is dominated by a mixture of annual and perennial tall (up to 3 m) grasses, particularly *Sorghum* spp. and *Heteropogon* spp (Williams and Douglas 1995). The substantial growth of the grasses in the wet seasons provide the majority of the fuel for dry season fires. Forbs are a common component of the ground layer in the wet season.

### 1.4.5 Experimental Layout

The Kapalga fire experiment was undertaken using a series of similar water catchments (Figure 1.3). Each catchment was 15-20 km$^2$ and local relief was typically less than 30 m. Seasonal stream flow occurs east-west into the floodplains associated with the South and West Alligator Rivers. Kapalga had been subjected to fires annually or biennially between 1976 and 1987, and then remained unburnt until the commencement of a fire experiment in 1990 (Andersen *et al.* 1997).

In this thesis, three fire treatments were used:

- 'Unburnt' no fires were lit, and wildfires were excluded (Figure 1.4)
- 'Early' burnt annually early in the dry season (May/June). This is the predominant management regime in conservation reserves in the region (Figure 1.5).
‘Late’ burnt annually late in the dry season (September). These fires may occur in the region as unplanned ‘wildfires’ (Figure 1.6).

The fire treatments were applied annually between 1990 and 1994. The Unburnt treatment was replicated 4 times, and the two burnt treatments were replicated three times. Subject to certain topographic and security constraints (such as proximity to the Arnhem Highway), treatments were assigned randomly to catchments (Andersen et al. 1997).
Figure 1.3  Location of study catchments within Kapalga Research Station. Letters denote the experimental fire regime of the catchments: \( U \) = Unburnt, \( E \) = Early dry season regime, and \( L \) = Late dry season regime. Numbers denote treatment replicates used in this study.
Figure 1.4  Savanna vegetation in an Unburnt catchment at Kapalga Research Station. Note the *Eucalyptus* dominated overstorey and midstorey containing *Acacia* species.
Figure 1.5  Savanna vegetation being burnt early in the dry season (May). Fire intensity and scorch height are low.
An area of savanna being burnt late in the dry season (September). Fire intensity and scorch height are typically higher than fires earlier in the season.
Chapter 2

Patterns of Flowering and Seed Production in
Eucalyptus miniata and E. tetrodonta in a Tropical
Savanna Woodland, Northern Australia.

2.1 Introduction

The genus *Eucalyptus* is the most conspicuous element of the Australian flora, dominating most of the forests and woodlands of the continent (Boland *et al.* 1992). Its widespread distribution ranges from the temperate wet sclerophyll forests of southern Tasmania to the tropical savanna woodland of Cape York (Boland *et al.* 1992). The reproductive biology of many *Eucalyptus* species in temperate regions of Australia has been thoroughly documented due to their ecological importance (e.g. Jacobs 1955; Ashton 1975; Ashton 1976; Wellington and Noble 1985; Yates *et al.* 1994; Yates *et al.* 1995) and to their value to the wood production industry (Cremer *et al.* 1978). By contrast, the reproductive strategies of eucalypts in the tropical regions of Australia are poorly understood (Fensham 1990). This paper focuses on two common and widespread eucalypts of the Australian tropical savannas: *Eucalyptus miniata* (Cunn. ex Schauer) and *E. tetrodonta* (F. Muell.).

Vegetative resprouting from underground organs is the most conspicuous form of regeneration in tropical *Eucalyptus* savanna species (Lacey and Whelan 1976; Fensham and Bowman 1992; Bowman and Panton 1993). Like most eucalypts in temperate Australia (Pryor 1976), *E. miniata* and *E. tetrodonta* have the capacity to regenerate from lignotubers (Lacey and Whelan 1976). *E. tetrodonta* can also regenerate from root sprouts (Lacey and Whelan 1976). By contrast, seedling regeneration has been described as rare for *E. miniata* and *E. tetrodonta* (Lacey 1974; Mott *et al.* 1985; Fensham and Bowman 1992). Although a common feature of savanna vegetation worldwide (Sarmiento and Monasterio 1983; Mott *et
al. 1985; Fatubarin 1987; Bazzaz and Ackerley 1992), this apparent scarcity of sexual reproduction differs from the regeneration strategies of many Eucalyptus species in temperate regions of Australia. Sexual regeneration of eucalypts in temperate forests is common, particularly after fire, when seed is released *en masse* from a canopy store (Florence 1982).

Previous authors have noted sporadic flowering in the savanna eucalypts (Wilson 1991) and a low proportion of *E. miniata* trees bearing seed-holding capsules (Fensham 1990). This has led to suggestions that seed production in *E. miniata* and *E. tetrodonta* is low and that a lack of seed supply may be a factor limiting seedling recruitment (Fensham 1990; Wilson 1991; Bowman 1993). The major aims of this study are therefore to describe the reproductive phenology of *E. miniata* and *E. tetrodonta* and quantify seed supply. Spatial and temporal variations in flowering and flowering success can be important factors influencing plant reproductive ecology (Carthew 1993). Therefore, in this study floral bud initiation and ovule survival of *E. miniata* and *E. tetrodonta* were quantified, and the spatial and temporal variations in these patterns described. This 3-year study was undertaken in sites protected from fire. Chapter 3 will assess the effect of fire regime on seed production.

2.2 Methods

2.2.1 Study Site

The study was undertaken at the CSIRO Kapalga Research Station in Kakadu National Park, Northern Territory, Australia (132°25'E, 12°40'S). The climate of the region is monsoonal (wet-dry tropical) characterised by high temperatures throughout the year and a highly seasonal rainfall. Average mean monthly maximum temperatures vary from 31°C in June and July to 36°C in January. Although rainfall totals and timing vary greatly between years (Taylor and Tulloch 1985), generally 85-95% of the 1400 mm annual rainfall falls between December and March.
Eucalyptus miniata and/or E. tetrodonta dominated open forests and woodlands (structural nomenclature after Specht 1981) are the most common savanna types in the wetter, sub-coastal regions of northern Australia (Dunlop and Webb 1991). These forests extend from the Kimberley Region of Western Australia to northern Queensland (Dunlop and Webb 1991) and occur on well-drained red or yellow sandy loam soils (Walker and Gillison 1982). The ground layer is dominated by annual or perennial grasses, commonly species of Sorghum and Heteropogon (Wilson et al. 1990).

2.2.2 Study Species

E. miniata and E. tetrodonta occur in the informal sub-genus Eudesmia (Pryor and Johnson 1971). Both species of Eucalyptus usually grow to 15-25 m in height but can grow to 30 m under optimum conditions (Boland et al. 1992). A distinctive feature of E. miniata is the very large, ribbed fruits (3-6 x 1.7-5 cm). E. tetrodonta fruits are smaller (1.3-2.2 x 1-1.4 cm) with 4 distinct sepals (Boland et al. 1992). The seeds of both species are very large by Eucalyptus standard. A description of 415 eucalypts by Boland et al. (1980) places E. miniata and E. tetrodonta in the top 5% of eucalypts based on the number of viable seed per 10 g.

2.2.3 Bud Initiation, Flower Intensity, Flowering Success and Seedfall

Surveys for fecund trees of E. miniata and E. tetrodonta were conducted between June and August in 1992, 1993 and 1994. Although the timing of floral bud initiation varied between years, the timing of buds becoming visible on all fecund trees in a stand occurred within 4 to 6 weeks. The surveys were undertaken when widespread flowering was apparent in each species. Trees that had not developed visible floral buds by this stage were classified as not fecund. The proportion of fecund trees was calculated by assessing 10 trees in each of 3 plots (c. 1 ha) in each of two catchments (10-20 km²). At each plot, trees were
selected by laying out a 100 m transect and assessing the tree (> 5 m tall) closest to 10 randomly selected points. The canopy of each tree was scanned using 10 x 20 binoculars from a distance of 10 metres. In addition, the ground beneath the canopy was searched for buds in case the bud load had already been aborted. Eucalyptus miniata and E. tetrodonta were assessed at different plots to ensure independence for ANOVA, and different plots were randomly chosen each year so that assessing temporal trends was not confounded by spatial auto-correlation.

Patterns of ovule production and survival were examined in 1992, 1993 and 1994 by counting the numbers of reproductive structures falling into cloth traps located beneath the canopy of fecund trees. For each species, seven trees were monitored in each of two catchments and different trees were randomly chosen for monitoring each year. A tree was considered suitable for monitoring if floral buds were present in the canopy, irrespective of density. Eight traps were randomly located under the canopy of each tree at the first sign of bud initiation. Traps consisted of 0.2 m² x 40 cm deep cloth cones suspended from three metal posts. Therefore, the total trap area beneath each tree was 1.6 m², which was considered to reflect an equivalent area of canopy above it. Sites for monitoring were selected on the basis that they offered easy access and were unburnt throughout the study. The two E. miniata monitoring sites were 5 km apart whereas the E. tetrodonta monitoring sites were 20 km apart.

Traps were emptied monthly and reproductive structures classified as: buds, opercula, flowers, immature capsules, mature capsules and seeds. Annual variation in flowering intensity was assessed by comparing the number of opercula which had fallen into the traps. Fruit set was estimated by subtracting the number of aborted flowers and immature capsules from the number of opercula (Ashton 1975). Flowering success was calculated as the percentage of flowers that successfully developed to fruit set. The results represent the number of reproductive units per m² of trap, therefore, it represents a relative measure of
reproductive success rather than an absolute measure (as would be represented by a unit measure of the ground surface). This indirect sampling methodology is less accurate than directly tagging reproductive structures and following their fate through time. However, the height of the tree canopies (>8 metres) precluded the use of direct tagging in this study. Seed fall was calculated from the number of seeds in the traps. Seed viability was determined by a germination test. Seeds were placed on moistened filter paper in a petri dish and placed in a controlled temperature cabinet at 25°C within a 12/12 hour light/dark photoperiod for 3 weeks. Seed that had not germinated after this time were squashed to determine if they contained ungerminated embryos.

2.2.4 Predation of Capsules

Red-tailed Black Cockatoos (*Calyptorhynchus magnificus*) are commonly observed feeding on *Eucalyptus* seed capsules, and are potentially important seed predators (Morton and Brennan 1991). Seed capsules that had been fed on by cockatoos were easily recognised. Damage was sometimes minor, with capsules intact but some beak marks on the outside, but generally the damage was extreme with the top of the capsule removed and the developing seed and ovules eaten. Although most of the damage occurred to capsules prior to seed maturity, some damage also took place after seed had matured. Unconsumed seed then fell into the traps. The number of cockatoo-damaged capsules that fell into traps was counted and this information was used to estimate both the proportion of capsules which failed to mature due to cockatoo predation, and the number of mature capsules damaged by cockatoos. The proportion of immature capsules lost to cockatoo predation was divided into 5 categories (0 losses, 1-10 %, 11-30 %, 31-50 % and greater than 50% of the capsule load).
2.2.5 Statistical Analysis

Assumptions of analyses of variance (ANOVA) were checked using Cochran's test for homogeneity of variances and assessing boxplots and residuals. Data were transformed where necessary using arcsin transformation for proportional data and natural log transformation for ordinal data. The proportion of trees flowering were compared within a three-way mixed model ANOVA, with factors: Species (fixed), Year (fixed) and Site (random).

Annual variation in flowering intensity, fruit set and flowering success were assessed by a series of two-way ANOVAs, with factors Year (fixed) and Site (fixed). The replicate unit used in the analysis was a tree (ie. the sum of 8 traps). Species comparisons of these data were not made since only one common site was used for monitoring of both species. Multiple comparisons were done using Ryan's tests after ANOVA (Day and Quinn 1989). Whilst data were transformed to meet the assumptions of analyses, mean values presented are untransformed data.

2.3 Results

2.3.1 Variation in Bud Initiation, Flowering Intensity and Ovule Development

For both species, the proportion of fecund trees was highest in 1994 (93% and 80% for *E. miniata* and *E. tetrodonta* respectively) and lowest in 1993 (48% and 25% for *E. miniata* and *E. tetrodonta* respectively, Figure 2.1). The variation between years was significant for both species (Figure 2.1, $F_{2,2} = 27.3, P < 0.05$) and Ryan's test indicated that the difference between each year was significant. There was no significant difference between species (Figure 2.1). All interaction terms were insignificant.
Figure 2.1 The mean percentage of fecund trees per stand in 1992-1994 for

*E. miniata* (□) and *E. tetrodonta* (■). Error bars are ± 1 SE.
The reproductive cycles of *E. miniata* and *E. tetrodonta* were completed within 8 months of floral buds becoming visible on the trees (Figure 2.2, Figure 2.3). In *E. miniata*, floral buds appeared soon after the end of the wet season (April-May), and ovule development continued through the dry season, terminating with seed being shed between August and December. Peak seed fall occurred in September and October and therefore commenced 1 month prior to the first rains and continued into the period of consistent rains (Figure 2.2). For *E. tetrodonta*, bud initiation occurred in May and June, and peak seedfall occurred in October and November, coinciding with the first rains (Figure 2.3).

Flowering intensity varied significantly between years for both *E. miniata* and *E. tetrodonta* (Table 2.1), with, on average, more than double the number of flowers per area of canopy in 1994 than in the 2 previous years (Figure 2.4). Ryan's test showed that the flower intensity of both species was significantly greater in 1994 than the previous 2 years, but no difference could be detected between 1992 and 1993. A significant site effect occurred for *E. miniata* (Table 2.1). Flowering success was lower in 1993 than the other 2 years of the study but this difference was not significant for either species (Figure 2.5). However, fruit set per unit area of tree canopy varied significantly between years for both species (Figure 2.6, Table 2.1).

Ryan's test showed that for *E. miniata*, fruit set was significantly greater in 1994 (c. 26 fruit m\(^{-2}\)) than in 1993 (c. 4 fruit m\(^{-2}\)) and 1992 (c. 12 fruit m\(^{-2}\)), with no significant difference between 1992 and 1993. For *E. tetrodonta*, fruit set was also highest in 1994 (143 fruit m\(^{-2}\)) and significantly greater than in 1992 (65 fruit m\(^{-2}\)). Fruit set was significantly lower in 1993 (22 fruit m\(^{-2}\)) than both 1992 and 1994.
Figure 2.2  The reproductive phenology of *E.miniata* in 1992, 1993 and 1994.

Results for each species are from two sites: Site 1 (○) and Site 2 (■).

Error bars are ± 1 SE.
Figure 2.3  The reproductive phenology of *E.tetrodonta* in 1992, 1993 and 1994.

Results for each species are from two sites: Site 1 (○) and Site 2 (■).

Error bars are ±1 SE
Figure 2.4  Annual variation in flowering intensity for (a) *E. miniata* and (b) *E. tetrodonta*. Results are from two sites: Site 1 (□) Site 2 (■). Error bars are ± 1 SE.
Figure 2.5  The annual variation in the proportion of flowers that successfully developed to mature fruit for (a) *E. miniata* and (b) *E. tetrodonta*. Results are from two sites. Results are from two sites: Site 1 (□) and Site 2 (■). Error bars are ± 1 SE.
Figure 2.6  The annual variation in the density of fruit set for (a) *E. miniata* and (b) *E. tetrodonta*. Results are from two sites. Results are from two sites. Results are from two sites: Site 1 (□) and Site 2 (■). Error bars are +1 SE.
Table 2.1 Summary of significant results from two-way ANOVA on variation in (a) flowering intensity, (b) fruit set and (c) seedfall for *E. miniata* and *E. tetrodonta*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Source of</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Variation</td>
</tr>
<tr>
<td>(a) flowering intensity</td>
<td><em>E. miniata</em></td>
<td>Year</td>
<td>8.10</td>
<td>12.04</td>
</tr>
<tr>
<td></td>
<td><em>E. miniata</em></td>
<td>Site</td>
<td>4.87</td>
<td>7.26</td>
</tr>
<tr>
<td></td>
<td><em>E. tetrodonta</em></td>
<td>Year</td>
<td>424.24</td>
<td>6.15</td>
</tr>
<tr>
<td>(b) fruit set</td>
<td><em>E. miniata</em></td>
<td>Year</td>
<td>16.50</td>
<td>9.48</td>
</tr>
<tr>
<td></td>
<td><em>E. tetrodonta</em></td>
<td>Year</td>
<td>20.34</td>
<td>2.98</td>
</tr>
<tr>
<td>(c) Seedfall</td>
<td><em>E. miniata</em></td>
<td>Year</td>
<td>6.02</td>
<td>8.70</td>
</tr>
<tr>
<td></td>
<td><em>E. tetrodonta</em></td>
<td>Year</td>
<td>17.00</td>
<td>6.41</td>
</tr>
</tbody>
</table>
2.3.2 Variation in Seedfall

Seed fall occurred soon after capsule ripening. Traps were left under the trees until all capsules had fallen from the canopy. Capsule fall was typically completed by the early wet season. Therefore, there was no storage of seed in the canopy of these Eucalyptus species. The annual variation in seed fall reflected the pattern for fruit set (Figure 2.7). Average seedfall was 11, 4 and 19 seeds m$^{-2}$ of fecund canopy for E. miniata in 1992, 1993 and 1994 respectively and 27, 3 and 37 seeds m$^{-2}$ of fecund canopy for E. tetrodonta. The annual variation was significant for both species (Table 2.1) and Ryan's test showed that seedfall was significantly greater in 1994 than the previous 2 years for E. miniata and significantly greater in 1994 and 1992 than 1993 for E. tetrodonta.

Seed viability ranged between 50 and 88% for E. miniata and 72 and 100% for E. tetrodonta. There was no significant difference between sites or years for proportional seed viability.

2.3.3 Predation of Capsules by Cockatoos

The majority of trees monitored were affected to some degree by cockatoo predation of immature capsules (Figure 2.8, Figure 2.9). However, the intensity of the damage varied between years. For example, in 1994, most trees suffered either no loss or only minor losses (< 10%) of immature capsules to cockatoos. By comparison, in 1992 and 1993, fewer trees had minor losses of immature capsules to cockatoos, and a larger proportion of trees suffered from damage in the extreme category (> 50%).

The proportion of mature seed-holding capsules that displayed signs of cockatoo attack varied between 0 and 22% for E. miniata and 0 and 11% for E. tetrodonta, and the amount of damage was consistent between years. For both species, this rate of loss was less than 6% of total ovule production initiated per tree. This figure represents maximum loss since some of the seed probably fell from the capsules, and escaped predation.
Figure 2.7 The annual variation in seedfall per m⁻² of fecund canopy for (a) *E. miniata* and (b) *E. tetrodonta*. Results are from two sites. Results are from two sites: Site 1 (□) Site 2 (■). Error bars are ± 1 SE.
Figure 2.8 The proportion of *E. miniata* trees showing losses of immature capsules due to cockoo predation. The severity of losses of immature capsules is divided into five categories: 0 losses, 1-10 %, 11-30 %, 31-50 % and greater than 50% of the capsule load. Bars represent the mean of two sites (10 trees at each site) and error bars are ± 1 SE.
The proportion of *E. tetrodonta* trees showing losses of immature capsules due to cocktoo predation. The severity of losses of immature capsules is divided into five categories: 0 losses, 1-10 %, 11-30 %, 31-50 % and greater than 50% of the capsule load. Bars represent the mean of two sites (10 trees at each site) and error bars are +1 SE.
2.4 Discussion

2.4.1 Annual Variation in Fecundity

Both *E. miniata* and *E. tetradonta* showed substantial inter-annual variability in fecundity. Both species showed a similar pattern of annual variation at an individual and at a population level during the three year period of this study. For example, in 1994, there was a high rate of bud initiation per area of tree canopy and a high proportion of fecund trees per stand. By contrast, in 1993, the number of buds per area of tree canopy and the proportion of fecund trees per stand were very low. This pattern of temporal variation in flowering has been described for many eucalypts (Hillis and Brown 1978). Ashton (1975) suggested the pattern of variation was the result of individuals having their own cycle of bud production, with heavy flowering years occurring when there is a coincidence of phases between individuals. In this study, a good flowering year for both species occurred in 1 out of the 3 years. Further monitoring is necessary to determine the frequency of these events for *E. miniata* and *E. tetradonta*.

2.4.2 Developmental Phenology

A summary of the major reproductive events in *E. miniata* and *E. tetradonta*, pooling years and sites, is presented in Figure 2.10. The majority of ovule losses occurred prior to capsule development in both species (Figure 2.10). Bud losses were consistent between sites and between years for *E. miniata* (c. 25%). However, for *E. tetradonta*, average bud losses at one site doubled that at the other site (≥ 50% compared to < 20%) in 1992 and 1994 but were consistent between sites (c. 30%) in 1993, when few buds were initiated per canopy. This suggests that possible mechanisms for bud loss, such as insect attack and resource availability fluctuate spatially and temporally. Temporal variation in these factors has been previously noted for *E. baxteri* in an open woodland of temperate Australia (Andersen 1989).
Figure 2.10  Summary of the proportional losses of reproductive structures at various stages of development for (a) *E. miniata* and (b) *E. tetrodonta*. Bars represent mean values from ten trees at two sites over 3 years.
Eucalypts are pollinated by birds, small mammals (Ashton 1975) and insects (Pryor 1951), with wind having a limited role (Pryor 1976). Both E. miniata and E. tetrodonta produce high energy yields of nectar (Franklin 1994) and the richest avian nectivore community in Australia has been documented in a tropical E. miniata/E. tetrodonta dominated savanna (Franklin 1994). Birds appear to be important vectors for pollen in these savanna species.

There was little overlap between flowering times of E. miniata and E. tetrodonta, with the peak flowering of E. miniata finishing with the appearance of the first E. tetrodonta flowers (Figure 2.2). It has been proposed that plant species which depend on the same pollinators may minimise phenological overlap to reduce competition for pollinators, although this has rarely been demonstrated (Rathcke and Lacey 1985; van Schaik et al. 1993).

During this three year study, approximately 14% of E. miniata and 30% of E. tetrodonta flowers initiated survived to fruit set (Figure 2.10). This proportion was comparable to species of Eucalyptus from temperate regions of Australia (Ashton 1975; Andersen 1989; Yates et al. 1994) and species in other genera (Stephenson 1981; Whelan and Goldingay 1986; Vaughton 1990).

Red-tailed black cockatoo predation resulted in substantial losses of developing fruit from individual trees of E. miniata and E. tetrodonta, and in some cases, all developing fruit were destroyed. However, the impact of their damage to a stand varied between years. The proportional loss of immature capsules due to cockatoo damage was lowest during 1994. Although the majority of trees did lose some immature capsules to cockatoos (Figure 2.8), the proportion of immature fruit destroyed per tree was lower in 1994 than in the previous two years, probably due to the abundance of fruit in each canopy, and the high proportion of trees bearing fruit. For both E. miniata and E. tetrodonta, the loss of mature capsules to cockatoos each year was minor (<6% of initiated floral buds). Ashton (1975) noted that for
E. regnans, cockatoos are not very efficient seed eaters, spilling approximately 30% of seed from the mature capsules of E. regnans while feeding. Similarly, in this study, eaten capsules in seed nets were generally accompanied by seed but the amount of spilled seed was not quantified. Therefore, although cockatoos feeding on eucalypt capsules are a ubiquitous sight in the savannas in the late dry season, their impact is only likely to result in a significant reduction of seed production in years of poor flowering and fruit development.

2.4.3 Seed Fall

Eucalyptus miniata and E. tetrodonta are non-serotinous, with seed release occurring soon after ripening. This pattern of an annual cycle of seed production and release has been documented for Eucalyptus species from central Queensland woodlands (Burrows and Burrows 1992), but clearly contrasts with that of the reproductive cycle of most eucalypts in temperate regions of Australia. In some temperate species, flowering can occur two or more years after bud initiation, followed by development of fruit which takes approximately 1 year with seed then held in the canopy for up to 4 years (Cremer et al. 1978). The annual rate of seedfall for E. miniata (4-19 seeds m\(^{-2}\)) and E. tetrodonta (3-37 seeds m\(^{-2}\)) lies within the range reported for the intermittent release of seed from Eucalyptus species from temperate Australia (Ashton 1975; Andersen 1989; Yates et al. 1994), but is 'orders of magnitude' lower than the amount which occurs in temperate Eucalyptus forests when there is massive seed release following fire (O'Dowd and Gill 1984).

Peak seedfall occurred up to 1 month before the first wet season rains for E. miniata but coincided with these rains for E. tetrodonta. Eucalyptus seeds which fall before the wet season are likely to be harvested by ants (Andersen and Lonsdale 1990) and thus the survival of seeds falling during this period is probably low. Eucalypt seed which falls following the onset of regular rains would have a much higher probability of germination; a trial of shallowly burying seed in the savanna at the time of natural seedfall showed that viable seed of both Eucalyptus species germinated within one week after rain had moistened the first few centimetres of soil (Setterfield, unpub. data). These "build-
up" rains are very variable between years (Taylor and Tulloch 1985), intense but highly localised, with storm fronts normally only a few kms wide. It is likely that the timing and frequency of these rains in relation to seedfall determines seed germination and establishment success.

2.5 Conclusions

This study has demonstrated that seed production and seed supply of *E. miniata* and *E. tetrodonta* varies substantially between years and that this pattern of temporal variation is consistent between sites. Ovule survival from bud initiation to seed fall did not vary significantly between years. Therefore, years of low seed production are due primarily to low densities of floral bud initiation per tree canopy and low numbers of fecund trees per stand.

Neither *E. miniata* nor *E. tetrodonta* maintained a canopy seed-store. This contrasts markedly with temperate eucalypts that may store several years of seed production in the canopy. The storage of seed in the canopy counteracts the high variability of annual seed production and ensures that seed is available for *en masse* seed fall following the disturbance (Cremer et al. 1978). By contrast, seedfall in *E. miniata* and *E. tetrodonta* directly reflects the annual variation in seed production.

Seed supply is unlikely to be a major factor limiting the seedling recruitment of *E. miniata* or *E. tetrodonta* in areas of unburnt savanna. The establishment of large numbers of seedlings, however, would only occur in areas receiving consistent early wet season rains during years of average to high seed production. As these early wet season rains are often very localised, seedling establishment would be expected to reflect this patchiness. This is supported by observations in the literature of isolated swards of seedlings for both species (Fensham and Bowman 1992; Bowman and Panton 1993). Frequent burning - a feature of the Top End savannas - may also affect this pattern by altering seed production and seedling
establishment. To understand the major limitations to seedling regeneration, further consideration will be given in later chapters to the effects of burning on seed production and to factors affecting the seed germination and seedling establishment conditions, such as microsite availability and the small-scale distribution and timing of early rainfall events.
Chapter 3 The Impact of Experimental Fire Regimes on Seed Production in Two Tropical Eucalypt Species in Northern Australia.

3.1 Introduction

Savanna woodlands and open forests dominated by *Eucalyptus* species are the most common vegetation type in the wet-dry tropics of northern Australia (Dunlop and Webb 1991). Regular fires occur in tropical savannas throughout the world, and fire is an important determinant of savanna structure and function (Walker 1985; Frost and Robertson 1987). Approximately 70% of the savannas in the 'Top End' region of Australia are burnt each year, with many areas burnt annually (Braithwaite and Estbergs 1985; Press 1988). The majority of fires are now human-lit, by pastoralists (Andrew 1986), conservation park managers (Press 1988) and Aborigines continuing traditional burning practices (Haynes 1985).

Fire can have a major impact on the reproductive phenology of trees, especially on seed production through its effects on plant fecundity and ovule development. Floral bud initiation and flowering are stimulated by fire in some species (Daubenmire 1968; Rowley 1970; Gill and Ingwersen 1976; Coutinho 1990), but for others, fecundity may be either unaffected (Pemble et al. 1981; Coutinho 1990) or reduced by burning (Daubenmire 1968; Knapp 1984; Miyanishi and Kellman 1986; Glenn-Lewin et al. 1990). Ovule development can obviously be interrupted by the burning of flowers or flowering stems (Coutinho 1990; Howe 1994). Alternatively, ovules may be unaffected by burning depending on the characteristics of the fire, and the fruit (Mercer et al. 1994).

*Eucalyptus miniata* Cunn. ex Schauer and *Eucalyptus tetrodonta* F.Muell are the most common overstorey species in northern Australia. Peak flowering occurs at the beginning of the dry season (May/June) and ovule development is completed by the start of
the following wet season (December/January; Setterfield & Williams 1996). As most fires in the region are lit during the dry season (Braithwaite and Estbergs 1985; Press 1988) these species have a high probability of being burnt during their seed production cycle (Brock 1988). Bowman & Panton (1993) suggested that a possible cause of the apparent scarcity of seedling regeneration in *E. tetrodonta* could be due to the effect of fire on buds, flowers and immature fruit.

Seed production is likely to be influenced by both fire intensity and timing. As fire intensity increases, the likelihood of tissue death also increases (Mercer *et al.* 1994). Floral parts can be destroyed, and seed production in the years following the burn may be reduced if a species diverts nutrient or energy reserves to growth (Miyanishi and Kellman 1986). Fire intensity in Top End savannas increases as the dry season proceeds. Fires lit early in the dry season (April to June) are typically low in intensity and patchy (Williams 1995; Williams *et al.* 1995). As the dry season proceeds, fuel loads increase and cure (Williams *et al.* 1995), winds strengthen and atmospheric humidity declines (Gill *et al.* 1995). Consequently, fires that occur late in the dry season (July to November) are typically more intense, often scorching the canopy completely, and burning extensive areas (Braithwaite and Estbergs 1985; Williams *et al.* 1995).

Fire timing can affect flowering phenology (Coutinho 1990), flowering duration (Platt *et al.* 1988) and the intensity of flower and seed production (Trollope 1982; Glenn-Lewin *et al.* 1990). In the northern Australian savannas, the effects of fire timing may be difficult to isolate from the effects of fire intensity (Frost and Robertson 1987) since intensity increases during the dry season (Williams *et al.* 1995).

A landscape-scale fire experiment in northern Australia (Andersen and Braithwaite 1992) provided the opportunity to study the effect of three experimental fire regimes on fecundity, ovule development and seedfall in *E. miniata* and *E. tetrodonta*. The fire regimes studied were Unburnt (fire exclusion treatment), Early dry season burns (annual, generally
low intensity fires lit in May/June), and Late dry season burns (annual, generally high intensity fires lit in September).

3.2 Methods

3.2.1 Study site and burning regimes

The study was undertaken within the CSIRO Kapalga Research Station in Kakadu National Park, Northern Territory, Australia (132°25'E, 12°40'S). The most common vegetation types on well-drained soils at Kapalga Research Station are *E. miniata* and/or *E. tetrodonta* dominated open forests with an understory dominated by a mixture of annual and perennial grasses, commonly species of *Sorghum* and *Heteropogon* (Wilson et al. 1990). The climate is monsoonal (wet-dry tropical), characterised by high temperatures throughout the year and a highly seasonal rainfall.

Kapalga had been subjected to fires annually or biennially until 1987, and then remained unburnt until the commencement of a fire experiment in 1990. For this experiment, the study area was subdivided into a number of 15-20 km² catchments, each based on seasonal creeklines, and an experimental fire regime was applied to each catchment (Figure 1.3). The catchments were separated by firebreaks. The fires were lit along the length of the fire breaks surrounding the catchments by vehicle-based ground crews. This study considered three fire treatments applied for four years between 1990 and 1994: (i) 'Unburnt' (ii) 'Early' - burnt annually early in the dry season (May/June), and (iii) 'Late' - burnt annually late in the dry season (September). Three replicate catchments of each fire regime were studied (Figure 1.3). In the year of this study (1994), the Early burns were lit between 7-9 June, and the Late burns were lit between 19-22 September.

For each replicate catchment the Byram fire-line intensity (heat yield of fuel x fuel load x rate of forward spread, Byram 1959), the char height (the height of blackened leaves - used as a surrogate for flame height) and the scorch height (the height of leaves killed by radiant heat) of the fires in 1994 were recorded (Moore et al. 1995; Williams et al. 1995).
The rate of fire spread was determined by measuring the time taken for the fire to move across 100 metres. All fire measurements were made within a one hectare, relatively uniform area within each compartment. These data are presented in Table 3.1. The mean overall intensity of the Late regime (7500 kW m\(^{-1}\)) was double that of the early regime (3070 kW m\(^{-1}\)). The mean char height (3.2 m) and scorch height (20 m) in the late regime also doubled those of the early regime (char ht = 1.3 m, scorch ht = 12.5 m).

3.2.2 Study species

*Eucalyptus miniata* and *E. tetrodonta* are the two most common overstorey species in wetter, sub-coastal regions of northern Australia. Both species usually grow to 15-25 metres in height but can grow to 30 m under optimum conditions (Boland *et al.* 1992). They usually grow to 18-22 metres on sites in this study. Both can regenerate from seed or vegetatively, from underground organs (Lacey and Whelan 1976). A distinctive feature of *E. miniata* are the very large, ribbed fruits (3-6 x 1.7-5 cm). *E. tetrodonta* fruits are smaller (1.3-2.2 x 1-1.4 cm) with 4 distinct sepals (Boland *et al.* 1992). The seeds of both species are very large. Wilson (1991) determined that the average seed weights for *E. miniata* and *E. tetrodonta* were 3.00 and 2.84 \(10^{-3}\) grams respectively. A description of 415 eucalypts by Boland *et al.* (1980) places *E. miniata* and *E. tetrodonta* in the top 5% of eucalypts based on the number of viable seed per 10 g.

The reproductive phenology of both *E. miniata* and *E. tetrodonta* was described in Chapter 2, and is summarised in Figure 3.1. Floral buds appear soon after the end of the wet season and ovule development and seed fall are completed within the eight month dry season. Seed release occurs upon ripening in both species (Chapter 2; Setterfield and Williams 1996). Bud initiation and subsequent stages of development occur approximately
Table 3.1  Intensity, Char and Scorch heights in 1994 (Data of Williams *et al* 1995 and R.J. Williams, unpub.).

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<th>EARLY FIRES</th>
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<td>E1</td>
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<td>Intensity (kW m(^{-1}))</td>
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<td>Char height (m)</td>
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<td>Scorch ht (m)</td>
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The reproductive phenology of *E. miniata* (●) and *E. tetrodonta* (○) from Chapter 2, and timing of the Early and Late fire regimes. The Early regime has fires lit annually during the early dry season (early June), and the Late Regime has fires lit annually during the late dry season (late September).
2-4 weeks later in *E. tetrodonta* than *E. miniata*, so that the stage of development of reproductive structures with respect to the timing of a fire varies between the two species.

In this study, the Early fires occurred while *E. tetrodonta* was in bud, but after *E. miniata* had commenced flowering. The late season fires occurred while immature capsules were present on both species, although these were closer to maturity in *E. miniata* than *E. tetrodonta* (Figure 3.1).

### 3.2.3 Floral Bud Production

For both species, the proportion of fecund individuals was determined in all nine experimental catchments between 20 May and 7 June 1994 (prior to burning in all catchments). For this study, an individual was defined as fecund if floral buds were visible in the tree canopy. Data were collected at three sites within each catchment for both species. At each site, the proportion of fecund trees was determined by assessing 10 randomly selected individuals. *E. miniata* and *E. tetrodonta* were assessed at different sites within each replicate catchment. Data were compared with a three-way ANOVA, with factors “Species” (fixed), “Fire” (fixed) and “Catchment” (random and nested in Fire). Multiple comparisons were done using Ryan’s tests after ANOVA (Day and Quinn 1989).

Visual assessment of the density of floral buds in the tree canopy was undertaken during the above surveys. For each tree, bud density was scored according to a four point scale: 0 = no buds present within the canopy; 1 = <20% suitable leaf axils contained buds; 2 = 20 - 80 % suitable leaf axils contained buds; and 3 = > 80 % suitable leaf axils contained buds.

For this analysis, the individual tree was the replicate and the data were compared with a four-way ANOVA, with factors “Species” (fixed), “Fire” (fixed) and “Catchment” (random and nested in Fire) and “Site” (random and nested in Catchment and Species). Significant spatial effects occurred in bud density across the catchments within fire treatments and across sites within catchments, but they are not described further in this
chapter. Multiple comparisons were done using Ryan’s tests after ANOVA (Day and Quinn 1989).

3.2.4 Ovule success

Ovule survival - from bud initiation to seedfall - was monitored in five fecund trees of both *E. miniata* and *E. tetrodonta* in each replicate catchment of the three fire regimes (ie. 45 trees of each species in total). The trees were randomly located within each catchment. Four 0.5 m² diameter x 40 cm cloth traps were randomly located under the canopy of each tree at the first sign of bud initiation, and the contents were collected in the last week of each month. Traps were left under the tree canopy until all the reproductive structures had fallen. The trap area beneath each tree totaled 2m².

Reproductive structures were classified as buds, opercula, flowers, immature capsules, mature capsules or seed. Seed viability was determined with a germination test as described in the previous chapter (Section 2.2.3). Seed was placed on moistened filter paper in a petri-dish and placed in a control temperature cabinet at 25°C within 12/12 hour light photoperiod for three weeks.

The basket contents were used to calculate:

(i) the proportion of buds which successfully matured to capsules. The number of mature capsules was calculated by subtracting the number of aborted flowers and immature capsules from the number of opercula (Ashton 1975).

(ii) the proportional losses of structures at each of the three stages of development: bud, flower and immature capsule.

(iii) capsule density and seedfall

Experimental treatments were replicated three times, but a wildfire burned one of the control (Unburnt) catchments part way through the study. Because of this loss, the factors “Fire” and “Catchment” were no longer orthogonal, so species were analysed separately by two factor means model ANOVA (Milliken and Johnson 1984) using specific contrasts to
test the hypotheses of interest (these were Fire (fixed) and Catchment (random and nested in Fire). Post-hoc pooling of the Catchment and Residual Sums of Squares was done if the Catchment factor was non-significant at P=0.25 (Winer 1971). Multiple comparisons were done using Tukey’s-Kramer tests after ANOVA (Day and Quinn 1989). Whilst data were transformed to meet the assumptions of analyses, mean values presented are untransformed data.

3.3 Results

3.3.1 Floral Bud Production

The Late regime significantly reduced the proportion of fecund trees/stand compared to the Unburnt regime, whereas the Early regime showed no significant effect (Figure 3.2, $F_{2,6} = 7.47, P < 0.05$, Ryan’s test; Unburnt = Early > Late). For *E. miniata*, the proportion of fecund trees in the Unburnt (~90%) and the Early (~80%) regimes was double that in the Late regime (~40%). The difference was even more extreme for *E. tetrodonta*, with less than 20% of fecund trees/stand in the Late regime compared to the Unburnt (~80%) and the Early (~75%) regimes. There were no significant differences between catchments within fire regimes, or between species.

For both species, the Late regime significantly reduced bud density whereas the Early regime showed no significant effect (Figure 3.3, $F_{2,6} = 14.80, P < 0.01$, Ryan’s test; Unburnt = Early > Late).

3.3.2 Ovule success

Bud to Capsule development

Losses of buds, flowers and immature capsules were highest in the Early regime for both species. For *E. miniata*, the proportional loss of buds was ~50% in the Early regime, compared to ~25% and ~35% for the Unburnt and the Late regimes respectively. This difference between regimes was significant ($F_{2,37}=4.98, P<0.05$). Similarly, for *E.
tetrodonta, the rate of bud abortion for the Early burn regime (~40%) was approximately double that of the Unburnt and Late burn regimes, although the difference between regimes was not significant.

Flower losses were higher in the Early burn regime (80% for *E. miniata* and 40% for *E. tetrodonta*) than either the Unburnt (61% for *E. miniata* and 28% for *E. tetrodonta*) and Late burn regimes (33% for *E. miniata* and 27% for *E. tetrodonta*). However, the difference between regimes was not significant. Flower losses were higher for *E. miniata* than *E. tetrodonta*; this is probably due to the presence of flowers on *E. miniata* at the time of the fires, whereas *E. tetrodonta* had not commenced flowering.

Losses of immature capsules from *E. miniata* varied significantly between regimes ($F_{3,37}=3.88, P<0.05$) with the rate of ~45% in the Early and Late regimes double that of the Unburnt regime (15%). Losses of immature capsule from *E. tetrodonta* was greater in the Early regime (~60%) than both the Late (~40%) and Unburnt regimes (~25%), although differences between regimes were not significant ($F_{2,3}=ns$).

The high proportion of bud, flower and immature capsule lost in the Early burn regime resulted in a major reduction in bud-to-capsule success compared with the other regimes (Figure 3.4). The difference between regimes was significant for both *E. miniata* ($F_{2,3}=9.38, P<0.001$), and *E. tetrodonta* ($F_{2,3}=6.03, P<0.001$). Bud success was approximately 2 to 3 times greater in the Unburnt and Late burn regimes compared to the Early burn regime. There was no significant difference between the Unburnt and Late regimes, and both of these regimes had significantly higher rates of success than the Early burn regime.

**Density of mature capsules and seedfall**

The density of mature capsules was significantly affected by fire regime (Figure 3.5). For *E. miniata*, capsule density was highest in the Unburnt regime (~90 caps/m² of trap area) compared with the Late regime (~20 caps/m²) and the Early regime (6 caps/m²). Density
**Figure 3.2** The mean proportion of fecund trees per stand in 1994 for *E. miniata* and *E. tetrodonta*. Means are from 3 sites within 3 replicate catchments of the fire regimes: Unburnt ( □ ), Early ( ■ ), and Late ( ■■ ). Error bars are +1 SE. Different letters (a,b) above bars denote significantly different means (\( P<0.05 \)).
Figure 3.3 The mean rating of floral bud density for (a) *E. miniata* and (b) *E. tetrodonta*. Ratings of bud density are on a four point scale: 0 = no buds present within the canopy; 1 = $<20\%$ suitable leaf axils contain buds; 2 = 20 - 80 % suitable leaf axils contain buds; and 3 = $>80\%$ suitable leaf axils contain buds. N = 3 sites within 3 catchments. Error bars are $\pm$1 SE. Different letters (a,b) above bars denote significantly different means ($P<0.05$)
Figure 3.4 The success of ovule development from bud initiation to seedset for *E. miniata* and *E. tetrodonta* in three fire regimes: Unburnt (□), Early (■), and Late (■). Error bars are ±1 SE.
Figure 3.5  The density of mature capsules/m² of trap area for *E. miniata* and *E. tetrodonta* in three fire regimes: Unburnt (□), Early (■), and Late (■).

Error bars are +1 SE
varied significantly between regimes ($F_{2,37}=12.47$, $P<0.001$ Tukey-Kramer test; Unburnt>Late=Early). Similarly, for *E. tetrodonta* capsule density in the Unburnt regime (~250 caps/m$^2$ of trap area) was significantly greater than the density in the two burnt regimes (~100 caps/m$^2$; $F_{2,37}=4.04$, $P<0.05$, Tukey-Kramer test; Unburnt>Late=Early).

For *E. miniata*, the density of seedfall followed the pattern of capsule density (Figure 3.6), with a significant difference between regimes ($F_{2,5}=7.1$, $P<0.05$; Tukey-Kramer test; Unburnt>Late=Early). A significant difference also occurred between catchments ($F_{2,5}=3.2$, $P<0.05$). Seed viability was approximately 94% in the Unburnt regime and approximately 75% in both the Early and Late regimes.

For *E. tetrodonta*, the density of seedfall differed from the pattern of capsule density with the lowest amount of seedfall collected in the Late regime (Figure 3.6). The difference between regimes was significant ($F_{2,5}=12.39$, $P<0.05$, Tukey-Kramer test; Unburnt>Early>Late). Relatively few seeds fell in the Late regime and those that were collected had a low viability (~55%). Seed from the Unburnt and Early regimes had a viability of approximately 90%.

### 3.4 Discussion

#### 3.4.1 Floral Bud Production

Plants partition resources among various functions including growth, maintenance and reproduction (Bazzaz and Ackerley 1992). In periods of limited resources, plant fecundity may be expected to decline (Miyanishi and Kellman 1986). For *E. miniata* and *E. tetrodonta*, fecundity in the Unburnt regime was high with respect to both the proportion of trees in bud (80-95%, Figure 3.2) and the density of buds per area of canopy (Figure 3.3). By comparison, tree fecundity was very low in the Late burn regime. The high intensity Late fires frequently scorch the *Eucalyptus* canopies and the canopy area had been severely reduced after 4 years of annual burning (R.J. Williams, unpub. data). Massive leaf fall occurred after the intense late dry season fires (Setterfield unpub. data) and trees expend
Figure 3.6  The number of seed/ m$^2$ of trap area for *E. miniata* and *E. tetrodonta* in three fire regimes: Unburnt (□), Early (■), and Late (■). Error bars are +1 SE.
considerable resources each year in forming new leaves. Plant resources that might otherwise be available for reproduction are probably allocated to canopy maintenance (Reekie and Bazzaz 1987; Bazzaz and Ackerley 1992), thereby limiting fecundity in these species.

Canopy scorch is less complete in the low intensity Early burn regime (Setterfield unpub. data). Therefore, fewer resources are expended by trees on canopy maintenance compared to the Late burn regime, and this is reflected in the higher proportion of fecund trees per stand (Figure 3.2) and the higher floral bud densities (Figure 3.3).

Fire regime therefore appears to be an important determinant of fecundity in *E. miniata* and *E. tetrodonta*. The effect on fecundity was apparent after four years of annual high intensity fires. Additional research is required to determine number of annual fires that induce these effects and how many fire-free years would be needed to return the eucalypts to full reproductive vigor.

### 3.4.2 Ovule success

The Early regime caused a major reduction in ovule success—from bud initiation to seed set—in both *E. miniata* and *E. tetrodonta* (Figure 3.4). Despite the low intensity and patchy nature of the Early fires, a large proportion of ovules were lost as buds, flowers and immature capsules. Tissue death by direct scorching from the fires is an obvious mechanism leading to the losses of reproductive structures. Indeed, heat damage to reproductive structures was clearly evident on the 20% of the monitored trees that suffered severe canopy scorching. On these trees, the buds and flowers were charred and stamens burnt. However, the rate of ovule abortion was also high on trees that did not suffer from canopy scorch. For example, 90% of ovules were aborted in catchment E3 despite an average scorch height of only 14 m (ie, at the base of the canopy, Table 3.1) and the lack of any visible damage to buds, flowers or the canopy (pers. obs). Other studies have shown that fires that do not scorch the crown of eucalypts may still alter the reproductive cycle by stimulation of an
abscission layer at the base of the pedicel (Cremer 1965; Christensen 1970). Cremer (1965) noted that this response may take two forms: visible damage to the base of the tree (termed "girdling"), or no visible trunk damage. The latter form occurred in this study since the low intensity Early fires did not damage the trunks of the monitored trees. Although this phenomenon has been documented for both tropical and temperate eucalypts and at various reproductive stages, the underlying mechanisms resulting in the abscission layer formation remains obscure (Cremer 1965).

The effect of the Late regime on ovule success differed between species with a greater impact on *E. tetrodonta*. Although both species had relatively high proportions of bud-to-capsule success, *E. tetrodonta* showed extremely low seed fall (Figure 3.6) and viability. This suggests that the intense heat of the Late fires had caused the death of the majority of the immature ovules of *E. tetrodonta* without an obvious effect on the fruit. These fruit continued to be held in the canopy, then dehisced and fell to the ground at the beginning of the wet season, which is the typical time for the fruit to be torn from the canopy by rain (Setterfield and Williams 1996). This resulted in an overestimation of bud to capsule success for *E. tetrodonta*. By comparison, the greater seed fall (Figure 3.6) and the high seed viability of *E. miniata* suggests that the Late regime was not detrimental to ovule success for this species.

The higher susceptibility of *E. tetrodonta* ovules to the Late fires compared to *E. miniata* ovules could be due to the difference in fruit size between the two species. The radius of eucalypt fruit has a critical bearing on their internal temperatures developed during fire (Mercer *et al.* 1994). The larger fruit of *E. miniata* (radius 0.7 - 1.3 cm) would take a longer time than that of *E. tetrodonta* (radius 0.5 - 0.7 cm) to reach temperatures lethal to the enclosed ovules. Another difference between the species was the advanced stage of development of *E. miniata* fruit compared to *E. tetrodonta*. In eucalypts, ovule development is accompanied by an increase in the size and woodiness of fruits (Boland *et al.* 1980) and a decline in the moisture content of the capsule walls so that there is a decline in their
conductivity to heat (Boland et al. 1980; Ashton 1986). The woody nature of eucalypt fruit (Gill 1981) protects the enclosed ovules from the heat of fires (Gill 1975). At the time of the Late burns, the drier, more developed fruit of *E. miniata* would provide more protection to the enclosed ovules than the *E. tetrodonta* fruit.

The proportion of *E. miniata* floral buds that successfully developed to mature capsules was substantially lower in the low intensity Early regime (7%) compared to the higher intensity Late regime (18%). The possible interactions between the time of the burn and fire intensity make this result difficult to interpret, but a possible explanation is that the fires lit early in the dry season coincided with a period of high vulnerability during the reproductive phenology of this species. This suggests that fire timing may be an important determinant of seed production in tropical *Eucalyptus* species.

3.4.3 *Consequences for seedling regeneration*

This study suggests that both fire intensity and fire timing are important determinants of seed supply. High intensity fires reduced fecundity of the tropical eucalypts. Low intensity fire can substantially reduce ovule success, probably due to the effect of timing in relation to ovule development. Seedfall per hectare for each regime has been calculated for 1994 using average tree densities for each regime (R.J. Williams, unpub. data) and the results are presented in Table 3.2. Seed inputs to the regeneration process were substantially reduced, by at least an order of magnitude by annual fires lit either early or late in the dry season, for both *E. miniata* and *E. tetrodonta*. For *E. miniata*, seedfall was over 180,000 seeds/ha in the Unburnt regime compared with approximately 15,000 seeds ha⁻¹ and 18,000 seeds ha⁻¹ for the Early and Late regimes respectively. For *E. tetrodonta*, seedfall of approximately 200,000 seeds ha⁻¹ was reduced to approximately 30,000 seeds ha⁻¹ and 450 seeds ha⁻¹ in the Early and Late regimes respectively. The study was undertaken in a year of high seed production (Setterfield and Williams 1996), and the effect of fire may be even more significant for seed supply in years of poorer production.
Seedling regeneration has been described as rare for *E. miniata* and *E. tetrodonta* (Lacey 1974; Fensham 1992). This study suggests that the extensive use of fire in the tropical savannas may reduce seed availability and have a significant impact on seedling regeneration. However, more information is required on the limitations to seedling regeneration in these species, in particular, to determine the effects of fire regimes on seed germination and seedling establishment. Increased seed germination and seedling establishment on burnt compared to unburnt seedbeds has been demonstrated for some species of *Eucalyptus* (Abbott 1984) but does not occur in others (Wellington and Noble 1985). The detrimental effects of annual burning on the seed production of *E. miniata* and *E. tetrodonta* may be counteracted by the beneficial effects of fire on seedbed preparation. This study has focused on seed supply; and further studies are required on the effects of fire on seedling establishment to fully understand the impact of fire regimes on seedling regeneration.
Table 3.2 Impacts of the Unburnt, Early and Late regimes on (i) proportion of fecund trees/hectare (ii) bud density per tree (iii) ovule success, ie, the proportion of buds that successfully mature to seed set and (iv) seedfall per hectare. Seedfall/hectare was calculated by multiplying the average seedfall/tree by the average no. fecund trees/hectare. Seedfall for each tree was calculated by multiplying the number of seed per trap area by the total trap area (or canopy area) of that tree. The average number of fecund trees was calculated by multiplying the proportion of fecund trees/ha by the average number of trees/ha. The average number of trees/ha was calculated from 3 x 0.1 ha plots in three catchments of each regime (RJ Williams, unpub. data).

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<th>Late Fire</th>
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<tr>
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Chapter 4  Seed production of the tropical savanna shrub
_Acacia oncinocarpa_ Benth. in northern Australia: 
effects of fire and pre-dispersal predation.

4.1 Introduction

The genus _Acacia_ occurs throughout the tropical region of the world, and extends into temperate areas, particularly in Australia and Africa (New 1984). _Acacia_ species are an important source of nitrogen in forest ecosystems (Beadle 1968) and play an important role in soil conservation (Boland _et al._ 1992). Acacias have a broad range of uses for humans, including as a source of food, forage for stock, and timber (El-Lakany 1987; Orr and Hiddins 1987; Kushalapa 1991). Despite their ecological and economic importance, the reproductive ecology of only a small number of _Acacia_ species has been studied in detail (New 1983; Sedgley 1987), and these studies generally focus on species which are potentially economically important (New 1984).

_Acacia_ species are a common understorey plant in the tropical savannas of northern Australia, and over 20 species occur in the savanna of the Top End region. They reproduce sexually, and some species can also regenerate from root suckers (Lacey and Whelan 1976). Following pollination, seed production may be limited by resource availability, or by external factors such as fire or seed predation (Stephenson 1981). Like many plants in the northern Australian savannas, most of the _Acacia_ species flower and produce seed in the dry season (April to September, Brock 1990), which coincides with a period of frequent, often annual fires (Braithwaite and Estbergs 1985; Press 1988). The vast majority of these fires are deliberately lit by humans, as part of a land management strategy. Fire kills ovules and seeds in many species (Coutinho 1990; Howe 1994), although the effect of burning depends on the characteristics of the fire, and the fruit (Mercer _et al._ 1994). Although it has not been previously studied, fire is potentially an important cause of ovule mortality in _Acacia_
species in the north Australian savannas. Therefore, the use of fire by land managers in this region may be having a significant impact on the regeneration dynamics of this genus.

Pre-dispersal seed predation has also been demonstrated as a significant cause of ovule mortality in many plant species (Janzen 1969; Louda 1982; Louda 1982; Andersen 1989), including species of *Acacia* (Auld 1983; New 1983; Auld 1986; Auld and Myerscough 1986). Ovule losses to insect predators vary greatly, both within and between *Acacia* species (Janzen 1969; Auld 1983). Previous studies on *Acacia* species have concentrated on insects as seed predators (Auld 1983; New 1983; Auld 1986; Ernst *et al.* 1989). In America, Africa and Asia, the larvae of bruchid beetles are the major *Acacia* seed predator (Donahaye *et al.* 1966; Janzen 1969; Centre and Johnson 1976; Janzen 1980; Hauser 1994), but they have not been recorded from *Acacia* seed in Australia (New 1983). The main seed predators in Australia are weevils (Van der Berg 1980; New 1983; Auld and Myerscough 1986). Others include species of the orders Hemiptera and Lepidtera (Auld 1983; New 1983). A number of wasp species have been reared from *Acacia* pods, but their feeding habits are unclear (New 1984).

Seeds and ovules also provide a nutritious food supply for vertebrates (Janzen 1971; McKee 1978; Joseph 1986) and the proportion lost to vertebrate predators can be substantial (Janzen 1971; Janzen 1981). Although there have been various reports of birds feeding on *Acacia* seeds (Preece 1970; Pedley 1978; Forde 1986), there is little quantitative information on the losses of *Acacia* seed to avian predators. In Australia’s tropical savannas, Sulfur-crested Cockatoos (*Cacatua galerita*), Little Corellas (*Cacatua sanguinea*) and Red-winged Parrots (*Aprosmictus erythropterus*) are commonly seen feeding on immature *Acacia* seed (Pers. obs.). Avian predators may therefore represent a potentially important cause of ovule mortality.

This study focuses on *Acacia oncinocarpa* Benth., a common understorey shrub in the northern Australia savannas. This species commonly occurs on exposed and disturbed areas, and it has been widely used by rehabilitation managers to revegetate degraded sites.
The reproductive biology of this important species is currently unknown. This study aims to (1) describe the temporal pattern of seed production of *A. oncinocarpa*, (2) determine the levels of pre-dispersal seed predation, and (3) quantify the effects of fire on seed production.

4.2 Methods

4.2.1 Study site

The study was undertaken within the CSIRO Kapalga Research Station in Kakadu National Park, Northern Territory, Australia (132°25'E, 12°40'S). The most common vegetation types at Kapalga are *Eucalyptus miniata* (Cunn. ex Schauer) and/or *Eucalyptus tetrodonta* (F.Muell) dominated open forests with an understorey dominated by a mixture of annual and perennial grasses (Wilson *et al.* 1990). Canopy subdominants commonly include *Acacia* spp., *Erythrophleum chlorostachys*, *Buchanania obovata* and *Terminalia ferdinandiana*. The climate is monsoonal (wet-dry tropical) characterised by high temperatures throughout the year and a highly seasonal rainfall. Although rainfall totals and timing vary greatly between years (Taylor and Tulloch 1985), generally 85-95% of the 1400 mm annual rainfall falls between December and March.

The study area had been subjected to fires annually or biennially until 1986, and was then left unburnt until the commencement of a landscape-scale fire experiment in 1990 (Andersen and Braithwaite 1992). For this fire experiment, the study area was subdivided into a number of 15-20 km² catchments, each based on seasonal creeklines, and separated by firebreaks. One of a set of experimental, prescribed fire regimes was applied to each catchment (Figure 1.3). The two regimes examined in this study were (i) 'Unburnt', since 1988, and (ii) 'Early' - burnt annually early in the dry season (May/June) between 1990 and 1994. This is a common management regime employed by a range of land use agencies in the region. Extensive areas of the savannas are burnt early in the dry season to reduce the risk of more intense fires that occur later in the dry season. Stands of *A. oncinocarpa* were
searched for but not found within catchments subjected to burns lit annually late in the dry season (September).

4.2.2 The study species

*A. oncinocarpa* Benth. is a small spreading shrub (2-4 m high) which is common in open forests, woodlands and shrublands of Northern Australia. Its distribution extends across the Northern Territory and into the Kimberley Ranges in Western Australia. It is common on exposed and disturbed areas, and on shallow lateritic soils or sandy loams and sandstones on hills and ridges (Dunlop et al. 1995). At Kapalga, the shrubs mostly grew in stands, although scattered individuals also occurred.

*A. oncinocarpa* flowers early in the dry season (March - June) and ovule development occurs during the dry season. The flowers are pale yellow, cylindrical spikes (5-8 cm long), in clusters of 1-5 in leaf axils. Fruits mature late in the dry season (July - October). The fruit are flattish, woody pods, 5-10 cm x 0.1-1 cm with seeds (4-6 mm x 2-3.5 cm) arranged longitudinally or diagonally in the pods (Dunlop et al. 1995).

4.2.3 Annual variation in seed production

Seed production was measured in Unburnt catchments in 1992, 1993 and 1994. In each year, seed production was measured on ten randomly chosen trees from two *A. oncinocarpa* stands within each of two randomly selected Unburnt catchments (ie. n=20 / catchment; see U1 and U2 in Figure 1.3). The height and diameter at breast height (dbh) of each tree was measured. The number of pods on each tree was counted. The method of counting varied depending on the size of the crop. If the number of pods on the tree was low (<300), then the pods were counted directly on the tree. However, if the crop of seed-pods was large, the majority of pods were cut from the tree (leaving at least 100 pods on the tree), and transported back to the lab. Pod counting took place when the seed-pods were close to maturity (the immature seed could be distinguished within the pods), but prior to predation
by birds. Consequently, collections were made between mid-August and mid-September each year, approximately 3 weeks prior to seed maturity

The second step that was made to determine seed production per tree was to measure the number of seeds per pod. When the pods were mature (mid-late Sept), a sample of ripe fruits was harvested from each tree. I attempted to collect 100 pods from each tree, but the number was often limited by the number of fruit set. The number of seeds in each of the collected pods was counted, and the average number was multiplied by the number of pods/tree to give an estimate of the number of seeds per tree.

Temporal and spatial variations in seed production per tree were assessed using a three-way mixed-model ANOVA with Year (fixed), Catchment (random) and Stand (random and nested). The assumptions of ANOVA were checked using Cochran's test for homogeneity of variances. The count data were square-root transformed to meet the assumptions of ANOVA.

4.2.4 Pre-dispersal seed predation

In April 1992, 30 A. oncinocarpa trees from each of two populations were tagged within an Unburnt catchment (Figure 1.3, Catchment U3). The height and dbh of these trees were measured. These stands were originally intended as additional replicates to monitor the annual variation in seed production. However, when I visited these trees to begin collecting the pods, I found that these trees had just been visited by avian predators which had caused substantial damage to the trees and the seed crop. These stands were therefore assessed to give an estimate of seed losses to avian predators in one catchment. The proportion of trees in the stand that was affected by the birds was calculated and each tree was assessed for the proportion of seed-pod crop destroyed by the birds. The seed production of 10 trees within each stand (i.e., n=10 per stand) was measured using the method described above. A comparison of seed crops from these stands to the seed production measured prior to predation within unburnt catchments U2 and U3, was undertaken using a two-way mixed-
model ANOVA with 'Catchment' (random) and 'Stand' (random and nested). Multiple comparisons were done using Ryan's tests after ANOVA (Day and Quinn 1989).

The mature seed collected from the Unburnt compartments in 1993 and 1994 were dissected for any obvious sign of insect damage, such as signs of grazing, holes, or seed totally consumed. These data were used to estimate the proportion of the tree seed crop killed by insect seed predators.

In 1994, ten pods from twenty trees were collected and placed in jars. Insects that emerged from the pods were collected and identified.

4.2.5 Effect of fire on seed production

During 1992 and 1994, seed production/tree was also measured within the Early burn regime. Seed production was measured on ten randomly chosen trees within two A. oncinocarpa stands in two burnt catchments. The height and diameter at breast height (dbh) of each tree was measured. For these two years, the difference in annual seed production of trees in the Early burn catchments was compared to trees with that of the Unburnt compartments using a four-way mixed-model ANOVA with Year (fixed), Fire (fixed), Catchment (random and nested) and Stand (random and nested). The assumptions of ANOVA were again checked using Cochran's test for homogeneity of variances. The data were square-root transformed to meet the assumptions, and the data re-tested.

In order to characterize the fires in both replicate catchments, the fire intensity, the char height (the height of blackened leaves - used as a surrogate for flame height) and the scorch height (the height of scorched leaves) of the fires were recorded (Williams 1995). These fire characteristics are presented in Table 4.1. Scorch and char heights, and fire intensity were lower in 1992 than 1994, but were typically highly variable throughout the catchments in both years (S. Setterfield, pers. obs.). None of the fires was sufficiently intense to result in complete canopy scorch.
Table 4.1 Description of experimental burns conducted during this study. Scorch and Char heights were measured in the *A. oncinocarpa* stands used in this study. Intensity data were collected from the two replicate catchments used within the study in 1992 and 1994 (from Williams *et al.* 1995 and R.J. Williams, unpub. data.

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<td>E1</td>
<td>E2</td>
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<td>Intensity (kW m⁻¹)</td>
<td>300</td>
<td>1800</td>
<td>3800</td>
<td>3200</td>
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<td>Char height (m)</td>
<td>0.2</td>
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<td>0.6</td>
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<td>Scorch height (m)</td>
<td>1.8</td>
<td>2.3</td>
<td>2.5</td>
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4.3 Results

4.3.1 Annual variation in seed production on unburnt sites, 1992-1994

There were no significant differences in the mean height (2.6 m) or dbh (6cm) of stands monitored during the three years of the study. There were no significant differences between catchments or sites, and no significant interactions. Despite the lack of variation in tree size during the study, seed production did vary significantly between years (Figure 4.1, F$_{2,2}$ =256.0 , P<0.01). Ryan's test showed that seed production in 1994 (~ 4200 seeds/tree) was significantly greater than 1993 (~2000 seeds/tree) and 1992 (2700 seeds/tree), with no significant difference between the 1992 and 1993. There were no significant differences between catchments or sites, and no significant interactions.

4.3.2 Pre-dispersal seed predation in 1992

In 1992, assessment of the _A. oncinocarpa_ stands in catchment U3 showed that pre-dispersal predation by avian predators affected 90% of the fecund individuals in the stands, and an average of 80% of the seedcrop. In addition to removing seeds from pods to eat, the birds also broke many branches bearing pods, but did not actually feed on the pods. The mean seed production on trees in catchment U3 was 140.2 ± 52.3 seeds/tree. This amount was an order of magnitude lower than the seed production in catchments U1 (3037 ± 342 seeds/tree) and U2 (2325 ± 366 seeds/tree, F$_{2,3}$=248.7, P< 0.001; Ryan’s test U1=U2>U3). There was no significant effect of stand.

The mean amount of damage caused by insects to seeds was 34% and 32% in 1993 and 1994 respectively. The amount of damage caused by insect seed predators varied considerably between trees both within and between stands. The proportion of seeds with obvious signs of insect damage ranged between 5% and 57% in 1993 and 1% and 55% in 1994.
Figure 4.1 The annual variation in seed production per tree in *A. oncinocarpa*. 
Results represent mean values (+1SE) from ten trees at two sites within each catchment. Different letters represent significantly different values (P<0.05).
Three insects were reared from *A. oncinocarpa* pods in this study - the moth *Etiella grisea* Hampson, and two wasps *Bracon sp.* (Braconidae) and *Risbecoma sp.* (Eurytomidae). All species of *Etiella* for which biological information is available feed in the pods of leguminous plants (E. Edwards pers. comm.). Although wasps have been previously recorded from pods, there is little known about their feeding habits (New 1983). *Bracon sp.* would be parasitic on the immature stage of a moth or beetle feeding in the pod, whereas *Risbecoma* may be phytophagous in *Acacia* pods (I. Naumann pers. comm.).

4.3.3 Effect of fire on seed production

There was no significant difference in the height of trees in the Unburnt and Early regimes, with mean tree height approximately 2.6m. However, the dbh of trees was significantly higher in the Early burn (7.2 cm) compared with the Unburnt regime (6 cm, $F_{1,1} = 21.55$, $P<0.5$). The dbh also varied significantly between catchments ($F_{2,4} = 27.03$, $P<0.5$). There were no significant differences in height or dbh between years, catchments or sites, and no significant interactions.

The Early burn regime caused a significant reduction in seed production ($F_{1,2} = 116.6$, $P<0.05$). Average seed production/tree was more than five times greater in the Unburnt regime (~2700 seeds/tree in 1992; 4200 seeds/tree in 1994) compared with the Early burn regime (~500 seeds/tree in 1992 and 1994). Production was significantly greater in 1994 compared to 1992 ($F_{2,2} = 19.3$, $P<0.05$). There was no significant effect of catchment or stand, nor any significant interactions between the experimental factors.

4.4 Discussion

The amount of seed produced annually by *A. oncinocarpa* (2,000-4,200 seeds/tree) falls within the range previously reported for other *Acacia* species (Auld and Myerscough 1986; Ernst *et al.* 1989). The substantial annual variation in seed production that was exhibited by *A. oncinocarpa* is a common characteristic of Acacias (Davies 1976; Auld and Myerscough 1986). Interestingly, the unusually high levels of seed production in 1994 compared with 1992 and 1993 also occurred in the dominant overstorey *Eucalyptus* species.
(Setterfield and Williams 1996). The cause of this pattern is unknown, although it reflected variation in the density of floral buds initiated in the *Eucalyptus* species (Chapter 2; Setterfield and Williams 1996). This suggests that resource availability may be limiting seed production in these species.

Seed losses to predators vary widely both within and between plant genera (Janzen 1971). Predispersal losses of between 0 and 100% of seeds have been recorded for different species of *Acacia* (Janzen 1971). Losses can also vary greatly within species, with seed predation by bruchid beetles varying between 5.1% (Pellew and Southgate 1984) and 99.6% (Lamprey *et al.* 1974) for *Acacia tortilis*. Similarly, seed losses to insects was extremely variable between *A. oncinocarpa* trees (5% to 57%). The mean losses to insect predators (34% in 1993 and 32% in 1994) are within the range previously reported for other *Acacia* species in south Australia (Auld 1983; New 1983; Auld 1986). However, it must be noted that the method used in this study probably resulted in an underestimate of ovule losses to pre-dispersal insect predators (Andersen 1988), and a more detailed study using predator exclusion experiments is required to provide a more accurate estimate of seed loss to them.

Although birds have previously been reported feeding on *Acacia* species (Preece 1970; Pedley 1978; Davidson and Morton 1984; Forde 1986), there is little information available that quantifies their impact on seed production. This study has demonstrated that avian predators can cause massive reductions in seed production of *A. oncinocarpa* stands (~140 seeds/tree in stands affected by predation compared to ~2750 seeds/tree in stands unaffected by predation). The birds used their beaks to scrape the ovules from the pods, the discarded pods either remained attached to the tree or, more commonly, were dropped to the ground beneath the tree. The seeds were eaten prior to maturity, and therefore can be considered as predation rather than a possible mechanism for dispersal (Davidson and Morton 1984; Joseph 1986). During foraging, many branches were broken from the trees, often with the pods still intact. This resulted in substantial damage to the canopies of the monitored trees. The majority (90%) of the trees in the stands were visited by the avian predators. This study has demonstrated the massive effect that avian predators can have on
an *A. oncinocarpa* stand. However, this pattern appeared to be extremely variable between stands and between years. A number of stands of *A. oncinocarpa* were monitored for other aspects of seed regeneration not included in this study, and appeared to be affected by much lower rates of damage (S. Setterfield, pers. obs.)

A regime of annual fires lit early in the dry season resulted in a 90% reduction in seed production in *A. oncinocarpa* compared to the Unburnt regime. A similar reduction in seed production was also found in *Eucalyptus miniata* and *Eucalyptus tetrodonta* in this region (Setterfield and Williams 1996). The fires were typically low in intensity and patchy (Williams et al. 1995), and the *A. oncinocarpa* canopies often suffered from only a small degree of scorching. However, ovule death was consistently high on all the monitored trees. Fire directly kills ovules by causing tissue death in stems and flower. It may also indirectly lead to ovule death, by causing the allocation of resources to plant survival and canopy maintenance that might otherwise have been available for reproduction (Bazzaz and Ackerley 1992). High intensity fires (typical of fires lit late in the dry season) cause high rates of stem and plant death in *Acacia* species in this region (R. Williams, unpub. data). This has probably resulted in the absence of *A. oncinocarpa* stands from catchment burnt annually late in the dry season, although there is no information available on species assemblages prior to the application of this burning regime that shows whether or not this species ever occurred in these catchments.

This study has shown that fire can cause massive reductions in seed production in *A. oncinocarpa*. Similar rates of seed loss can be caused by avian predators, but their effect will be far more variable between stands and between years. By contrast, a large area of the savannas (up to 70%) are burnt every year due to the widespread use of fire as a management tool in northern Australia. The fire management strategy used in this region may therefore be having a substantial impact on the plant population dynamics of *A. oncinocarpa* by reducing the number of seeds available for recruitment. However, other factors besides seed
supply may also be limiting recruitment of *A. oncinocarpa* (Louda 1982; Crawley 1990), and further studies on the regeneration of this species are required to understand the full impact of fire management on seedling establishment and recruitment.
Chapter 5  

Seedling Establishment of *Eucalyptus miniata* and *Acacia oncinocarpa* in an Australian Tropical Savanna: Effects of Seed Supply, Soil Disturbance and Fire

5.1 Introduction

An understanding of plant population dynamics requires an understanding of the factors determining recruitment success (Grubb 1977; Harper 1977; Watkinson 1986; Crawley 1990). There are two basic factors that can limit seedling recruitment; the availability of seeds, and the availability of microsites where seed can successfully germinate and establish (Harper 1977; Naylor 1985; Crawley 1990; Eriksson and Ehrlen 1992). Increasing seed supply can result in increased seedling recruitment (Peart 1977; Shaw and Antonovics 1986), but this is not the case when other factors, such as resource availability, limit germination and seedling establishment (Wellington and Noble 1985; Andersen 1989). Crawley (1990) suggested for most plant species, recruitment is limited primarily by microsite availability. However, Erikkson and Ehrlen (1992) used manipulative experiments on a wide range of species and showed that seed supply was also important for most of the species considered.

Fire can have a substantial effect on seedling establishment by affecting both seed supply and microsite availability and quality. Many studies have documented a substantial increase in seed supply of serotinous species following fire, when the heat from fires triggers massive seed release (O'Dowd and Gill 1980; O'Dowd and Gill 1984; Lamont *et al.* 1991). However, fire can also cause substantial reductions in potential seed supply by reducing plant fecundity and killing ovules (Daubenmire 1968; Setterfield 1997; Setterfield Submitted). Fire may also lead to an increase in the number of suitable microsites for
establishment, by removing vegetation and therefore reducing competition for resources (eg. moisture and nutrients), and by changing light quality, the soil structure and presence of seed predators (Purdie 1977; Wellington and Noble 1985; Lamont et al. 1993; Tyler 1995). Fire can promote germination in many species. For example, the heat from fires can break seed dormancy of legumes by rupturing the hard seed coat (Cavanagh 1980; Sabiiti and Wein 1988), and fire-related cues, such as charred wood (Keeley et al. 1985; Keeley 1991) and smoke (Brown 1993; Dixon et al. 1995) can promote germination in some species.

This study investigates factors controlling seedling establishment of two common woody species of northern Australia's savannas: the canopy dominant *Eucalyptus miniata*, and understorey shrub *Acacia oncinocarpa*. Fire is an extremely important land management tool in northern Australia, and fire frequency is extremely high (commonly annual) in the savannas (Braithwaite and Estbergs 1985). This study addresses the following questions: (1) is recruitment limited by seed or microsite availability, or a combination of the two?, (2) does the fire regime influence the success of seedling emergence?

5.2 Methods

5.2.1 The Study Site

The vegetation of the 'Top End' region is predominantly open woodlands and forests dominated by an overstorey of *Eucalyptus* species, with an understorey of annual and perennial grasses, forbs and small shrubs. The savannas in this region are burnt by fire annually or biennially (Braithwaite and Estbergs 1985). The majority of the fires are lit during the dry season (May to October). Fires lit early in the dry season (April to June) are typically low in intensity and patchy (Walker and Gillison 1982; Williams 1995; Williams et al. 1995). Fires that occur late in the dry season (July to November) are typically more
intense, often scorching the canopy completely, and burning extensive areas (Braithwaite and Estbergs 1985; Williams 1995)

The study was undertaken as part of a landscape-scale fire experiment (Andersen and Braithwaite 1992) within the CSIRO Kapalga Research Station in Kakadu National Park, Northern Territory, Australia (132°25'E, 12°40'S, Figure 1.2). The study area was subjected to fires annually or biennially until 1987, and then remained unburnt until the commencement of a fire experiment in 1990. Fire treatment units were 15-20 km² catchments, each based on seasonal creek-lines. The present study considered three fire regimes which had been applied to catchments since 1990: (i) 'Unburnt' (ii) 'Early' - burnt annually early in the dry season (May/June), and (iii) 'Late' - burnt annually late in the dry season (September). Three replicate catchments of each fire regime were used (see Section 1.4.5 for study site layout).

The most common vegetation types at Kapalga are open forest and woodlands dominated by *E. miniata* and/or *Eucalyptus tetrodonta*. The climate is monsoonal (wet-dry tropical), characterised by high temperatures throughout the year and a highly seasonal rainfall. Average mean monthly maximum temperatures vary from 31°C in June and July, to 36°C in January. Although rainfall totals and timing vary greatly between years (Taylor and Tulloch 1985), generally 85-95% of the 1300 mm annual rainfall falls between December and March.

**5.2.2 Study species**

*Eucalyptus miniata* is one of the most common overstorey species in the wetter, sub-coastal regions of northern Australia. It grows to 15-25 metres in height but can grow to 30 m under optimum conditions (Boland *et al.* 1992). *E. miniata* can regenerate from seed or vegetatively, from underground organs (Lacey and Whelan 1976). Seed (4-8 mm x 4-8 mm) develop within large, ribbed fruits (3-6 x 1.7-3 cm).
Acacia oncinocarpa Benth. is a small spreading shrub (2-4 m high) which is common in the open forest, woodland and shrubland of Northern Australia. It is common on exposed and disturbed areas, and on shallow lateritic soils or sandy loams and sandstones on hills and ridges. At Kapalga, the shrubs mostly grew in stands, although scattered individuals also occurred (Dunlop et al. 1995). Seeds (4-6 mm x 2-3.5 cm) develop within flattish, woody pods, 5 - 10 cm x 0.1 - 1 cm (Dunlop et al. 1995).

For both E. miniata and A. oncinocarpa, floral bud burst occurs early in the dry season, and ovule development and seed fall are completed within the eight month dry season. Seed release occurs upon ripening in both species, and typically occurs between July and October for A. oncinocarpa, and between September and December for E. miniata (Setterfield and Williams 1996, Setterfield unpub. data). Given the extremely high frequency of fires in the regional savannas, seed is often released onto a seedbed that has been recently burnt.

5.2.3 Microsite and seed supply as limiting factors

This experiment was undertaken in three replicate Unburnt catchments Catchment U1-U3; Figure 1.3). A site was randomly located within each Unburnt catchment, and at each site 24, 75 x 75 cm quadrats were established. The experiment was a 2x2 factorial design with the manipulated factors being microsite density and seed addition. This study assumed that soil disturbance would increase microsite availability. Microsites were manipulated by first removing the leaf litter from the quadrat, and then scarifying the soil surface with a hand cultivator. The leaf litter was then replaced. Seed was added at two densities: low density quadrats were sown with 20 seeds, high density quadrats were sown with 200 seeds. The seed was scattered evenly over the quadrat area. The viability of seed used in this and the following experiment was 95% and 51% for E. miniata and A. oncinocarpa respectively. This was determined by monitoring the germination of 600 E. miniata seeds (40 seeds/petri dish) and 500 A. oncinocarpa seeds (50 seeds/petri dish) over
a 3 week period. No seed pre-treatment was used to stimulate germination since viable seeds of both species germinate readily without any pre-treatment. The seed was placed on moistened filter paper in petri dishes in a controlled temperature cabinet at 25°C within a 12/12 hour light/dark photoperiod.

This design resulted in the following combination of treatments being applied to three replicates for both species at each of the three sites:

(i) soil and litter disturbed, low density of seed applied
(ii) soil and litter disturbed, high density of seed applied
(iii) soil and litter undisturbed, low density of seed applied
(iv) soil and litter undisturbed, high density of seed applied

Sites were located in areas where both *E. miniata* and *A. oncinocarpa* were present. Microsite and seed manipulation occurred in the first week of December 1993. A 5cm fence was constructed around each quadrat to ensure that the seed was not washed from the site during wet season rains. The fence consisted of 4 strips of 5 cm galvanized wire mesh pushed into the ground, and covered in flywire screen. Sticks and leaf litter were pushed up against the fences to ensure access to ants. Free movement by ants into and out of the plots was observed during the experiment. The number of germinant seedlings was initially counted on 10 January, 1994, and each was marked with a wooden skewer. The quadrats were then censused during February, March, April, May, July and October 1994 to determine a cumulative total of emergent seedlings. Seed longevity trials had shown that all *E. miniata* and the majority of *A. oncinocarpa* seeds would have germinated or desiccated during this time. A small proportion of *A. oncinocarpa* seeds are maintained dormant in the seedbank.

The effects of the treatments on seedling emergence were compared using a four-way ANOVA with Site (random), Species (fixed), Seed density (fixed) and Microsite manipulation (fixed). Data were log-transformed prior to analysis, following Cochran's test for homogeneity of variances and assessment of normality using a Probability plot.
5.2.4 Effects of fire regime on seedling emergence

The experiment was undertaken in three replicate catchments of each of three experimental fire regimes: Unburnt (Figure 1.3; U1-U3), Early (Figure 1.3; E1-E3) and Late (Figure 1.3; L1-L3). Two experimental sites were located within each catchment, and six 75 x 75 cm quadrats were randomly located at each site. In November 1993, 200 Eucalyptus miniata seeds were sown into each of three of the quadrats, and 200 Acacia oncinocarpa seeds were sown in the remaining three quadrats at each site. Therefore, in the Early and Late catchments, the seeds were sown onto a seedbed that had been burnt during the dry season. Each quadrat was bordered by a fly-wire mesh fence as described above (Section 5.2.3).

The number of germinant seedlings was initially counted on 10 January, 1994, and each seedling was marked with a wooden skewer. Seedling numbers were monitored during February, March, April, May, July (post-early burn) and October 1994 (post-late burn), and again in June 1995, by which time seedlings were considered to be established. The cumulative total of seedlings that emerged in 1994 in the three fire regimes was compared with 4-way ANOVA with the factors Species (fixed), Fire regime (fixed), Catchment (random and nested) and Site (random and nested). The data were Log-transformed prior to ANOVA following an assessment of Cochran's test and Probability plot. In September, 1994, a wildfire entered one of the Unburnt catchments, killing all marked seedlings. Therefore, data on seedling survival in October 1994 and June 1995 are from the two remaining Unburnt catchments.

The ground flora in the savanna changes dramatically throughout the year, with annual plants and above-ground stems of perennial herbaceous species dying off during the dry season. At the onset of the wet season, many perennial herbaceous species sprout new leaves, and the seeds of annual species germinate and seedlings establish (Dunlop and Webb 1991). The wet season is the main period of flowering and growth of these species (Wilson et al. 1996). Since these changes could affect both the emergence and the establishment success of E. miniata and A. oncinocarpa seedlings, the grass, forb
and woody sprout cover in each quadrat were estimated at each seedling census time. Canopy cover can effect seedling establishment (Stoneman and Dell 1993) so the canopy cover over each quadrat was measured using a hemispherical forest densiometer (P.E. Lemmon, Arlington, Virginia, USA) held at a height of 1 m. Four readings were taken over each quadrat (each one facing the four directions on a compass), and the readings averaged for the quadrat. Differences in the cover of these vegetation types between regimes were determined using a 3-way ANOVA, with Fire regime (fixed), Catchment (random and nested) and Site (random and nested). The data were Arcsine transformed to satisfy the assumptions of ANOVA.

5.3 Results

5.3.1 Effects of seed and microsite addition on seedling emergence.

The number of emergent seedlings was increased significantly by both increasing the number of seeds (Figure 5.1; $F_{1,2}=61.0$, $P<0.05$) and manipulating microsites ($F_{1,2}=32.1$, $P<0.05$, Figure 5.1). Increasing seed density from 20 seeds to 200 seeds on unscarified soil resulted in approximately 20 times the number of *E. miniata* seedlings and 7 times the number of *A. oncinocarpa* seedlings. Similarly, microsite disturbance resulted in a 2-4 fold increase in the number of seedlings establishing. A combination of seed and microsite addition resulted in a 4-fold increase in approximately 75 times the number of *E. miniata* seedlings and 20 times the number of *A. oncinocarpa* seedlings compared with the undisturbed soil, low seed density treatment (Figure 5.1). The higher number of *E. miniata* seedlings that established compared to *A. oncinocarpa* is probably due to the higher viability of the *E. miniata* seed (95% viability compared to 51% for *A. oncinocarpa*).
Figure 5.1  The mean cumulative number of *E. miniata* and *A. oncinocarpa* seedlings that established after 4 treatments were applied: (i) undisturbed, high density of seed (ii) undisturbed, low density of seed (iii) disturbed, low density of seed, (iv) disturbed, high density of seed. The results represent means of 3 replicates of each treatment from 3 sites. Error bars are +1 SE.
5.3.2 Effects of fire on seedling establishment

All of the *E. miniata* seedlings that emerged did so in the first wet season following seed sowing in 1994, whereas some *A. oncinocarpa* seedlings (<1% of seed applied) emerged from the seedbank during the second wet season. The total number of seedlings that emerged decreased with increasing intensity of the fire season (Figure 5.2). For *E. miniata*, approximately 16 seedlings established per quadrat in the Unburnt regime compared with 13 and 7 seedlings in the Early and Late regimes respectively. For *A. oncinocarpa*, the figures were 10, 6 and 3 respectively. This variation between regimes was significant (F<sub>2,6</sub> = 5.38, P<0.05) and Ryan's test showed that the number of seedlings varied significantly from Unburnt > Early > Late. There was no significant difference between species or between sites.

At the time of seed sowing in this experiment (November), there were substantial differences in the seedbed micro-environment between fire regimes (Table 5.1). Grass cover varied significantly between regimes (F<sub>2,6</sub> = 5.69, P<0.05, Ryan's test; Late > Early > Unburnt) with ~7% cover in the Unburnt, 11% in the Early regime and 15% in the Late regime. The cover of regenerating sprouts of woody species also varied significantly between regimes (F<sub>2,6</sub> = 5.76, P<0.05, Ryan's test, Late > Early = Unburnt) with ~12% cover in the Late regime compared with only 3% and 2% in the Unburnt and Early regimes.

Although mean forb cover also increased with increasing fire intensity, this difference was not significant. Projected canopy cover also decreased significantly with increasing fire intensity (F<sub>2,6</sub> = 6.45, P<0.05), with Ryan's test showing Unburnt (~70% cover) = Early (65%) > Late (45%). Considerable variability also existed between sites with respect to the seed micro-environment. Significant differences between sites occurred in grass cover (F<sub>9,90</sub> = 6.01, P<0.001), canopy cover (F<sub>9,90</sub> = 7.78, P<0.001) and woody sprout cover (F<sub>9,90</sub> = 5.2, P<0.001).
Figure 5.2  The mean cumulative number of *E. miniata* and *A. oncinocarpa* seedlings that germinated in the three fire regimes: Unburnt (□), Early (■), and Late (■). The results for each species represent 3 replicates at 2 sites within 3 replicate catchments. Error bars are ±1 SE.
Table 5.1 Composition of ground cover at the time of seed sowing in December, 1993. Means are from 6 quadrats (0.75x0.75cm) from 2 sites in three catchments in each fire treatment. Results of (a) canopy cover, (b) grass cover, (c) forb cover, and (d) woody sprout cover are all presented as percentages. Standard errors are presented in parentheses. Characteristics that varied significantly between regimes according to Ryan's multiple comparisons test are shown by different superscript letters.

<table>
<thead>
<tr>
<th></th>
<th>Unburnt</th>
<th>Early</th>
<th>Late</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy cover (%)</td>
<td>71.7 (2.2)A</td>
<td>65.6 (2.7)A</td>
<td>45.5 (2.5)B</td>
</tr>
<tr>
<td>Grass cover (%)</td>
<td>6.9 (0.9)A</td>
<td>11 (1.8)B</td>
<td>15 (1.8)C</td>
</tr>
<tr>
<td>Forb cover (%)</td>
<td>4.4 (0.6)</td>
<td>6.1 (0.7)</td>
<td>8 (1.2)</td>
</tr>
<tr>
<td>Woody sprout cover (%)</td>
<td>2 (2.6)A</td>
<td>2.6 (0.9)A</td>
<td>12.4 (3.6)B</td>
</tr>
</tbody>
</table>
As the wet season progressed, the grasses and herbaceous species flourished (Table 5.2). By late in the wet season (March), the ground cover in the burnt regimes was >25% compared to 13% in the Unburnt regime. Herbaceous cover was also consistently higher in the burnt regimes compared to the Unburnt (Table 5.2). By contrast, mean woody sprout cover in each regime remained relatively constant throughout the wet season (Table 5.2).

Figure 5.3 presents survival curves for both *E. miniata* and *A. oncinocarpa* in the Unburnt regime. The results are not presented for the burnt regimes because the low number of seedlings provide an unreliable estimate of survival. The increase recorded for *A. oncinocarpa* seedlings between January and March is due to new seedlings emerging during these months. Approximately 25% of *E. miniata* seedlings and 35% of *A. oncinocarpa* seedlings that established in the Unburnt regime in the first wet season survived to the end of the following dry season (October 1994). Survival had dropped to 11% and 33% respectively by the middle of the following dry season (June 1995).

Approximately 40% of *E. miniata* seedlings in the Early regime survived to June (7 months after sowing), immediately prior to the early dry season fires. Following the fires, only 3% of the seedlings were still alive, and these died in the following month. In the Late regime, 35% of the *E. miniata* seedlings survived to September, but these were all killed by the Late season fires.

The majority of the *A. oncinocarpa* seedlings were also killed by the fires. However, although the above ground stem was killed in 5% of seedlings in the Early regime, and 10% of seedlings in the Late regime, the seedlings resprouted in the wet season. In addition, a few new *A. oncinocarpa* seedlings germinated from the seed bank during the wet season.
Table 5.2  Results showing change in cover in seedling quadrats over time, from the time of seed sowing in December 1993 to July 1994. Results for (a) grass cover, (b) forb cover, and (c) woody sprout cover are given in percentages. Estimates are averages from 6 quadrats (0.75x0.75cm) from 2 sites in three catchments in each fire treatment.

<table>
<thead>
<tr>
<th></th>
<th>(a) Grass</th>
<th>(b) Forb</th>
<th>(c) Woody Sprout</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>U  E  L</td>
<td>U  E  L</td>
<td>U  E  L</td>
</tr>
<tr>
<td>Dec 1993</td>
<td>6.9 10.9 14.8</td>
<td>4.4 6.1 8.0</td>
<td>2 2.6 12.4</td>
</tr>
<tr>
<td>Feb 1994</td>
<td>12.5 19.6 21.5</td>
<td>15.8 26.7 30.2</td>
<td>0.8 2.1 11.1</td>
</tr>
<tr>
<td>Mar 1994</td>
<td>12.7 28.6 25.2</td>
<td>12.5 18.1 20.7</td>
<td>0.5 2.07 12.1</td>
</tr>
<tr>
<td>July 1994</td>
<td>5.5 5 32.2</td>
<td>0.3 0 0.3</td>
<td>0 4 8.5</td>
</tr>
</tbody>
</table>
Figure 5.3  Survival data for *E. miniata* (open triangle) and *A. oncinocarpa* (closed square) in the Unburnt regime at Kapalga Research Station.

Results represent mean ± 1SE.
5.4 Discussion

Whereas many studies have viewed recruitment limitation as a dichotomy of seed versus microsite limitation, Eriksson and Ehrlen (1992), argued that recruitment of many species will be shown to be limited by both seed and microsite availability if they are adequately studied. Their view is supported by this study. This result provides a context in which to interpret the importance of the effects of fire regimes on seed and microsite availability for *A. oncinocarpa* and *E. miniata*. These impacts are summarised in Table 5.3, with seed budgets calculated from 1994 seedfall - a year of high seed production for both species (Chapters 2 and 4). The fate of *A. oncinocarpa* seed was not calculated for the Late regime because mature stands of this species did not occur in this regime.

Previous studies have demonstrated that fire can massively reduce *E. miniata* and *A. oncinocarpa* seed supply by reducing the proportion of fecund trees per stand, and by killing ovules (Table 5.3, Chapters 3 and 4). The experimental manipulation of seed density in this study has shown that reduced seed supply caused by burning will reduce the chance of seedling recruitment (Table 5.3). It also indicates that seed predators may have a significant impact on seedling recruitment, by further reducing seed supply. Although not measured in this study, very high losses of *Eucalyptus* (~90%) and *Acacia* (~50%) seed to seed-harvesting ants have been measured (Andersen and Lonsdale 1990), Andersen, unpub. data). This effect is also likely to be affected by fire regime, with several seed harvesting ant species occurring predominantly in burnt areas compared to unburnt areas (Andersen 1991).

Fire regime affected the seedling emergence success of both species, possibly by affecting the availability of suitable microsites, with lower establishment rates in the Early and Late regimes compared to the Unburnt. This may have resulted from an indirect effect of the changes in the vegetation structure on the seedbed conditions. For example, lower numbers of seedling emergence in the burnt regimes may be related to the effects of reduced
Table 5.3  Seed budgets calculated for (a) *E. miniata*, and (b) *A. oncinocarpa*. The calculations are based on the seed fall measured in 1994 (from Setterfield 1997, and Setterfield unpub. data.)

<table>
<thead>
<tr>
<th></th>
<th>Unburnt</th>
<th>Early</th>
<th>Late</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>(a) E. miniata</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seedfall (seeds m⁻²)</td>
<td>18.1</td>
<td>1.5</td>
<td>1.8</td>
</tr>
<tr>
<td>Seedling establishment (% of available seed)</td>
<td>8</td>
<td>6.5</td>
<td>3.5</td>
</tr>
<tr>
<td>No. of established seedlings (seedlings m⁻²)</td>
<td>1.4</td>
<td>0.1</td>
<td>0.06</td>
</tr>
<tr>
<td>Seedling survival after 1 year (seedlings m⁻²)</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>(b) A. oncinocarpa</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seedfall (seeds m⁻²)</td>
<td>60</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Seedling establishment (% of available seed)</td>
<td>6.5</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>No. of established seedlings (seedlings m⁻²)</td>
<td>3.9</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>Seedling survival after 1 year (seedlings m⁻²)</td>
<td>1.2</td>
<td>0.3</td>
<td></td>
</tr>
</tbody>
</table>
overstorey on soil water availability. Fluctuations in soil water availability can be lethal if water supply from the irregular rainfall at the start of the wet season is sufficient for germination to be induced but insufficient for seedling establishment (Augspurger 1979). The greatly reduced canopy cover (Table 2), and the higher soil temperatures in the Late regime (mean soil surface temperature 8°C higher in the Late regime compared to the Unburnt in December, Setterfield, unpub. data), are more likely to result in fluctuating soil water availability compared to the Unburnt regime. Reduced emergence as a consequence of overstorey removal has previously been demonstrated for E. marginata (Stoneman and Dell 1993). The impact of fluctuations in water availability is most likely to affect E. miniata, which germinates rapidly in response to the soil becoming moistened (Setterfield, unpub. data), compared to A. oncinocarpa (a more hard-seeded species), which can maintain a seedbank for at least one year.

The difference in seedling emergence between regimes may also be attributed to differences in the ground cover between regimes (Table 5.1, Table 5.2). Although burning temporarily clears the ground flora, the perennial grasses soon reshoot, and annual grasses (e.g. Sorghum spp.) and herbaceous species germinate and establish at the onset of the wet season rains (Dunlop and Webb 1991). A. oncinocarpa and E. miniata seeds germinate during the early to mid wet season and the establishing seedlings would experience greater competition for available space, water and nutrients in the burnt regimes compared to the Unburnt regime.

At the low density seeding rate, approximately 5% and 25% of E. miniata seeds in this study emerged on the undisturbed and disturbed quadrats respectively (Figure 5.1). A similar experiment by Wilson and Bowman (1994) resulted in no E. miniata emergence following seed addition to both cultivated and uncultivated Eucalyptus dominated savanna. Although reasons for such a dramatic difference in the effect of soil scarification between these studies are difficult to determine, it may be related to site differences. The experiment in
this study was undertaken in a site that had not been burnt for 4 years, whereas the fire history of the site used by Wilson and Bowman (1994) was not described, but is likely to have been burnt more recently given the high fire frequencies in the region (Braithwaite and Estbergs 1985). Fire history clearly has a significant impact on seedling establishment of these species (Figure 5.2, discussed above). Differences in patterns of early wet season rainfall may also have caused the differences between emergence rates. In addition, placement of the seed in the seed-bed also varied between studies, with the seed in this study scattered over the quadrat area, allowing the seed to move naturally to the soil surface. Wilson and Bowman (1994) pressed the seed into the soil and covered it with <2mm of soil. Depth of sowing affects the germination and emergence of many species (Black 1956; Woolley and Stoller 1978; Pieterse and Cairns 1987), including *Eucalyptus* species (Free 1951; Cremer 1965; Ashton 1979), and may be an explanation for differences in establishment rates between these studies.

A high rate of seedling mortality has been recorded in many studies (Christensen and Muller 1975; Wellington and Noble 1985; Andersen 1989; De Steven 1991), and reflects the vulnerability of this stage in the population recruitment of plants (Harper 1977). Various studies have shown that the mortality of seedlings is lower in a post-fire environment compared to an unburnt area (Purdie 1977; Whelan and Main 1979; Burrows et al. 1980; O'Dowd and Gill 1984). However, a similarly high rate of seedling mortality was recorded in all regimes for the first six months after establishment of *E. miniata* and *A. oncinocarpa*. In this study, a large proportion of the seedlings died in fires during their first dry season after establishment. By contrast, Fensham's (1992) study at Melville Island showed that a dry season fire had little effect on the survivorship of *Eucalyptus tetrodonta* and *E. miniata* seedlings during their first year. The seedlings had rapidly developed a lignotuber that allowed survival of some *Eucalyptus* seedlings during fire. The proportion of seedlings that survives a fire will depend upon fire characteristics (eg. patchiness), as well as characteristics
of the seedlings such as lignotuber development. This study suggests that root development of *A. oncinocarpa* is also rapid following establishment since a number of the *A. oncinocarpa* seedlings that had their aerial stems burnt off during fires in their first year were able to resprout during the following wet season. The length of the fire free period following establishment is obviously an important factor affecting seedling recruitment of *E. miniata* and *A. oncinocarpa*.

In conclusion, the results of this study have demonstrated that the current fire management regimes, which often include annual dry season burning, may have a significant impact on the population recruitment of *E. miniata* and *A. oncinocarpa*. Frequent fire can reduce the availability of seed and the availability of suitable microsites for germination and establishment. In addition, the chance of seedlings surviving fire in their first year after emergence are low. Therefore, this suggests that a fire-free period of a few years would have important consequences for the regeneration by seed of these common tropical savannas species.
Chapter 6  
Seed supply limits recruitment of *Eucalyptus miniata*: interactions between seed harvesting and fire in the Australian seasonal tropics.

6.1 Introduction

Seed predators can have an important role in plant populations dynamics, by influencing the reproductive success of individuals, the spatial patterns of plant populations, and plant community structure (Louda 1982; Brown and Heske 1990; Whelan *et al.* 1991). Many studies have shown that seed predators can cause massive reductions in the amount of seed available for germination (Janzen 1971; Crawley 1992). However, high rates of predation may not have a detectable impact on population recruitment if seedling establishment is limited by factors other than seed supply (Andersen 1989; Crawley 1990). For example, seed predators will have little impact if recruitment is limited by the number of safe sites available for germination (Harper *et al.* 1965; Peart 1977), or by high rates of density-dependent seedling mortality (Cook 1979). Therefore, an understanding of the effect of seed predators on population recruitment requires seed losses to predators to be considered in the context of other factors limiting germination and seedling establishment. In short, the relationship between seed predation and seedling establishment needs to be directly tested (Schupp 1988).

Ants are the dominant post-dispersal seed predators throughout Australia, and can rapidly remove a large proportion of seeds that fall to the ground (Ashton 1979; Morton 1982; O'Dowd and Gill 1984; Andersen and Ashton 1985; Andersen 1991; Yates *et al.* 1995). The level of seed predation by ants will depend on the ant composition and their foraging activity, and both of these factors are influenced by the fire history of a site (O'Dowd and Gill 1984; Andersen 1988). Direct effects of fire on seed germination, and
seedling growth and survival have been well studied (Purdie 1977; Cavanagh 1980; Wellington and Noble 1985; Sabiiti and Wein 1988; Fensham 1992; Lamont et al. 1993; Tyler 1995), but less attention has been given to the indirect effects of fire on seedling recruitment as mediated by harvester ants. In Australia's tropical savannas, fire regimes influence both the composition and abundance of harvester ants, with a greater abundance of harvester ants in regularly burnt sites compared to unburnt sites (Andersen 1991).

This study focuses on the interactive effects of fire and seed predation on seedling establishment of a tropical savanna tree, *Eucalyptus miniata*, in northern Australia. Recruitment of *E. miniata* seedlings is limited by seed availability (Chapter 5), which indicates that seed predators could potentially influence population recruitment. The aims of this study were to determine (1) rates of predation of *E. miniata* seed, (2) whether seed predation is an important influence on seedling regeneration, and (3) whether the effect is influenced by the fire history of a site.

6.2 Methods

6.2.1 Study Site

The study was undertaken within the CSIRO Kapalga Research Station in Kakadu National Park, Northern Territory, Australia (132°25'E, 12°40'S). Kapalga was the site of a catchment-scale fire experiment, with fire regimes applied to 15-20 km² catchments, each based on seasonal creek-lines (Andersen et al. 1997). This study was undertaken in three replicate catchments of each of two fire regimes which had been applied to catchments since 1990: (i) 'Unburnt' (ii) 'Early' - burnt annually early in the dry season (May/June). The study was undertaken in open forest dominated by *E. miniata* and *Eucalyptus tetrodonta*. The climate is wet-dry monsoonal, characterised by high temperatures throughout the year and a highly seasonal rainfall. Average mean monthly maximum temperatures vary from 31°C in June and July, to 36°C in January. Although rainfall totals and timing vary greatly
between years (Taylor and Tulloch 1985), generally 85-95% of the 1300 mm annual rainfall falls between December and March.

Three sites were established within three replicate catchments of both the Unburnt and the Early fire regimes (total sites = 18). At each site, two 75cm x 75cm plots, separated by 5 m, were established. Each plot was bordered by a fence constructed from 4 strips of 5cm galvanised wire mesh pushed into the ground. One of each pair of plots was randomly designated as an ‘ant exclusion’ plot and the fence covered in shadecloth mesh and the exterior side smeared with ‘Tacgel’ (a sticky substance that traps insects that come in contact with it). The second plot was ‘ant accessible’ and the fences were also covered with mesh but 3cm gaps were left between the corners of adjacent walls and ‘Tacgel’ was not applied to the fence. Ants were observed moving freely into and out of the ‘ant accessible’ plot, but not the ‘ant exclusion’ plot.

6.2.2 Study Species

_E. miniata_ is one of the most common overstorey species in the wetter, sub-coastal regions of northern Australia, extending from the Kimberley Range in Western Australia to the southern part of Cape York Peninsula in Queensland (Boland _et al._ 1992). It typically grows to 15-20 metres in height but can grow to 30 m under optimum conditions (Boland _et al._ 1992). Floral bud burst occurs early in the dry season (April - May), and ovule development and seed fall are completed by the onset of the wet, with the latter commencing in September (Setterfield and Williams 1996). This pattern of an annual cycle of seed production and release contrasts with eucalypts in temperate southern Australia, in which the reproductive phenology cycle from bud production to seed release can take 2 to 8 years (Ashton 1975; Cremer _et al._ 1978). Seed longevity trials have shown that all seed either germinated or decayed within two months of seed shed (Setterfield, unpub. data). Seedling establishment rates in the field are typically less than 10% of available seed (Chapter 5).
6.2.3 Regional harvester ants

Harvester ants are typically concentrated in arid regions of the world (Brown et al. 1979), but in Australia occur in virtually all terrestrial habitats (Andersen 1991). The predators of eucalypt seeds tend to be seed-eating omnivores rather than specialist granivores, belonging predominantly to the genera *Monomorium*, *Pheidole* and *Meranoplus* (Greenslade and Mott 1979; Andersen and Lonsdale 1990; Gross et al. 1991). Species of *Meranoplus* and to a lesser extent *Pheidole* tend to specialize on the seeds of grasses and other herbs (Andrew 1986; Gross et al. 1991), and the major predators of eucalypt seeds appear to be species of the *rothsteini* group of *Monomorium* (Andersen and Lonsdale 1990).

Harvester ants are exceptionally diverse and abundant at Kapalga. In a previous study, 18 harvester species were recorded in two adjacent 30x30 m plots, with mean total nest density exceeding 1000 ha⁻¹ (Andersen and Lonsdale 1990). Rates of removal of *E. tetrodonta* seed (primarily by *Monomorium 'rothsteini'*) ranged from 20-90% after 48 hrs, reaching maximum levels at the time of seed fall from October to December (Andersen and Braithwaite 1996).

6.2.4 Rates of seed predation

Rates of predation were determined by monitoring removal of seeds from depots within each of the established quadrats. This also served to test the effectiveness of the fence in excluding ants (‘ant-exclusion plots’) and allowing them access through gaps (‘ant-access plots’). The effect of the fence on ant access was determined by comparing rates of seed-removal from ‘ant access’ plots to a third 0.75 x 0.75 m fence-less plot, which was established at each site. Seed depots consisted of ten *E. miniata* seeds placed in a 3-4-3 grid. Seeds were placed on a small amount of white sand to aid relocation. Two seed predation trials were undertaken: the first trial commenced on 9 November 1994, and the second commenced 2 weeks later. The number of seeds removed was counted after 1, 2, 4
and 6 days for the first trial, but monitoring of the second trial was terminated after four days due to heavy subsequent rain.

6.2.5 Effects of predation on seedling establishment

Fifty *E. miniata* seeds were evenly broadcast inside each 'ant-access' and 'ant-exclusion' plot on 9 November, 1994. Plots were monitored for germinant seedlings fortnightly for 2 months after sowing. The cumulative total of seedlings was used as the measure of emergence. Quadrats were recounted for seedling survival in March, and July 1995. Seedlings present at July 1995 were considered to have successfully established. The data were also used to calculate the proportion of seedlings that emerged from seed after harvesting had been taken into account (ie, the total number of seed applied minus the average number lost to harvesters in the depot trials).

6.2.6 Statistical Analysis

Four-way split-plot ANOVA's were undertaken to assess (i) the effectiveness of the fence at excluding ants (ie, the number of seed removed from the 'ant-access' compared to the 'ant-exclusion' plots), (ii) the effect of the fence on ant-access (ie, the number of seed removed from the 'ant-access' compared to the 'fenceless' plots), and (iii) the effect of predation on seedling germination (ie, the number of seedlings in the 'ant-access' compared to the 'ant-exclusion' plots. The factors in the ANOVA were Fire (fixed), Catchment (Random, and Nested in Fire), Site (Random, and Nested in Fire and Catchment) and Treatment (Fixed). Data from Analysis (i) and (ii) were compared after 6 days for the first seed-depot trial, and after four days for the second trial. The data for analysis (iii) were log-transformed due to the considerable variability in seedling emergence between catchments.

The emergence success of seed after harvesting was taken into account was compared for the 'ant-exclusion' plots in the unburnt and burnt regime. Data were compared using a
three-way ANOVA with the factors Fire (fixed), Catchment (Random, and Nested in Fire), and Site (Random, and Nested in Fire and Catchment).

6.3 Results

6.3.1 Rates of seed predation

In the first trial, approximately 30% of seed was removed after six days from unfenced (control) plots in the unburnt catchments, compared with 65% in the burnt catchments (Figure 6.1). About 90% of this removal occurred after four days. Rates of removal were higher in the second trial, with about 60% and 85% of seeds removed after four days from the control plots in the unburnt and burnt catchments respectively (Figure 6.1). Rates of removal from ‘ant-access’ plots were initially lower than from control (fenceless) plots in the Unburnt regime (Figure 6.1), but were not significantly different after four days (Figure 6.1; Table 6.1). This indicates that the fences surrounding the ant-access plots had no significant effect on removal rates at this time (Table 6.1). The rate of removal was significantly higher in the burnt catchments compared to the unburnt (Table 6.1).

Seed removal from ant-exclusion plots was negligible (2-6% after four days) in the first trial, but was substantial (16% and 28% respectively in unburnt and burnt catchments) in the second trial, although significantly lower compared with the ant-access plots (Figure 6.1; Table 6.1). The differences between removal rates in ant-access and ant-exclusion plots can be experimentally attributed to ants (rather that unknown factors), indicating that ants removed 21% and 32% of seeds respectively after four days in the two trials in unburnt catchments, compared with 51% and 60% of seeds respectively in the two trials in the burnt catchments.
Figure 6.1  No. of *E. miniata* seeds removed from seed depots (of 10 seeds) in two trials. Results are shown for the ant access treatment (closed squares), ant-exclusion treatment (open triangle) and the no fence treatment (open diamonds)
Table 6.1 ANOVA results from seed removal trials showing (i) the analysis testing the effectiveness of the experimental fence (seed removal from 'ant-access' plots compared to 'ant-exclusion', and (ii) the analysis testing the effect of the experimental fence on ant movement (seed removal from 'ant-access' plots compared to 'fenceless plots'.

(i) Analysis of data testing the effectiveness of the experimental fence at excluding ants

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Trial 1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A = Fire</td>
<td>1</td>
<td>58.78</td>
<td>27.84</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>B = Catchment</td>
<td>4</td>
<td>2.11</td>
<td>0.30</td>
<td>ns</td>
</tr>
<tr>
<td>C = Site</td>
<td>12</td>
<td>6.97</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>D = Treatment</td>
<td>1</td>
<td>196</td>
<td>72</td>
<td>0.001</td>
</tr>
<tr>
<td>A X D</td>
<td>1</td>
<td>18.78</td>
<td>6.90</td>
<td>ns</td>
</tr>
<tr>
<td>B X D</td>
<td>4</td>
<td>2.72</td>
<td>0.52</td>
<td>ns</td>
</tr>
<tr>
<td><strong>Trial 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A = Fire</td>
<td>1</td>
<td>32</td>
<td>2.36</td>
<td>ns</td>
</tr>
<tr>
<td>B = Catchment</td>
<td>4</td>
<td>11</td>
<td>4.01</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>C = Site</td>
<td>12</td>
<td>3.36</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>D = Treatment</td>
<td>1</td>
<td>13.61</td>
<td>22.00</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>A X D</td>
<td>1</td>
<td>144.00</td>
<td>2.90</td>
<td>ns</td>
</tr>
<tr>
<td>B X D</td>
<td>4</td>
<td>18.78</td>
<td>1.61</td>
<td>ns</td>
</tr>
</tbody>
</table>

(ii) Analysis of data testing the effect of the experimental fence on ant movement

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Trial 1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A = Fire</td>
<td>1</td>
<td>140.03</td>
<td>8.07</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>B = Catchment</td>
<td>4</td>
<td>17.36</td>
<td>1.34</td>
<td>ns</td>
</tr>
<tr>
<td>C = Site</td>
<td>12</td>
<td>12.97</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>D = Treatment</td>
<td>1</td>
<td>0.69</td>
<td>0.58</td>
<td>ns</td>
</tr>
<tr>
<td>A X D</td>
<td>1</td>
<td>0.03</td>
<td>0.02</td>
<td>ns</td>
</tr>
<tr>
<td>B X D</td>
<td>4</td>
<td>1.19</td>
<td>0.53</td>
<td>ns</td>
</tr>
<tr>
<td><strong>Trial 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A = Fire</td>
<td>1</td>
<td>110.25</td>
<td>8.27</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>B = Catchment</td>
<td>4</td>
<td>13.33</td>
<td>1.18</td>
<td>ns</td>
</tr>
<tr>
<td>C = Site</td>
<td>12</td>
<td>11.7</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>D = Treatment</td>
<td>1</td>
<td>0.25</td>
<td>0.06</td>
<td>ns</td>
</tr>
<tr>
<td>A X D</td>
<td>1</td>
<td>3.36</td>
<td>0.86</td>
<td>ns</td>
</tr>
<tr>
<td>B X D</td>
<td>4</td>
<td>3.89</td>
<td>1.71</td>
<td>ns</td>
</tr>
</tbody>
</table>
6.3.2 Effects of predation on seedling establishment

Seedling emergence was low in most plots (~2.5% of seed applied), although 34% of seedlings emerged in one plot (Figure 6.2). Ant exclusion resulted in a significant increase in the number of seedlings that emerged (Figure 6.2; \( F_{1,4} = 7.87, P < 0.05 \)), with a total of 41 seedlings in the ant-exclusion plots compared to 3 seedlings in the ant-access plots. There was no significant effect of fire regime on seedling emergence despite the difference in seed removal rates between the Unburnt and Early regimes. There was no significant effect of fire or catchment on seedling emergence, and no significant interactions between factors. All seedlings emerged during the wet season (by March) and 40% of the seedlings survived to the middle of the dry season (July).

Seedling emergence success in the 'ant-exclusion' plots as a proportion of seed remaining after harvesting was higher (6.6%) in the burnt regime compared to the unburnt regime (3.6%; Table 6.2), although this difference was not significant.

6.4 Discussion

The rates of seed predation recorded here fall within range published for species of *Eucalyptus* elsewhere in Australia (Table 6.3). However, they are considerably lower than that recorded for *E. tetrodonta* in a previous study at Kapalga at a similar time of the year (80-90% after 48 hrs; Andersen and Braithwaite 1996). This is probably due to the larger size of *E. miniata* seeds (5.5 mg compared to 4.5 mg), as rates of removal of eucalypt seeds by ants have been shown to be inversely proportional to seed size (Andersen 1982; Majer 1982).

Fire regime is a major factor influencing ant communities of the savannas of northern Australia, with frequent fire promoting ant diversity and abundance (Andersen 1991). In
Figure 6.2  The number of germinant seedlings per quadrat in the ant-exclusion (open-bar) and the ant-access (closed-bar) treatments in the Unburnt and Burnt regimes. The bars represent the mean + 1 SE.
Table 6.2 Results of the mean number of seedlings that germinated compared to the expected number (calculated as number of seeds applied to the site minus the number lost to seed removal). Data are presented for the Unburnt and Early regime.

<table>
<thead>
<tr>
<th>Fire regime</th>
<th>Treatment</th>
<th>Mean seed loss to harvesters (%)</th>
<th>Expected Number of Seedlings</th>
<th>Observed Number of Seedlings</th>
<th>% Seed to emerge as seedlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Unburnt</td>
<td>Ant-access</td>
<td>17.8</td>
<td>32.2</td>
<td>0.6 ± 0.2</td>
<td>1.5 ± 0.6</td>
</tr>
<tr>
<td></td>
<td>Ant-exclusion</td>
<td>14.4</td>
<td>45.6</td>
<td>1.7 ± 0.7</td>
<td>3.6 ± 1.6</td>
</tr>
<tr>
<td>(b) Early</td>
<td>Ant-access</td>
<td>36.4</td>
<td>13.6</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td></td>
<td>Ant-exclusion</td>
<td>10.8</td>
<td>39.2</td>
<td>2.9 ± 1.7</td>
<td>6.6 ± 3.5</td>
</tr>
</tbody>
</table>
### Table 6.3
Rates of removal of *Eucalyptus* seeds from seed depots (number of days exposure given in parentheses) elsewhere in Australia.

<table>
<thead>
<tr>
<th>Region</th>
<th>Species of</th>
<th>Removal rates</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Eucalyptus</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperate southeast</td>
<td><em>regnans</em></td>
<td>40-90% (14)</td>
<td>(Ashton 1979)</td>
</tr>
<tr>
<td></td>
<td><em>baxteri</em></td>
<td>0-88% (2)</td>
<td>(Andersen and Ashton 1985)</td>
</tr>
<tr>
<td></td>
<td><em>delegatensis</em></td>
<td>7-78% (7)</td>
<td>(O'Dowd and Gill 1984)</td>
</tr>
<tr>
<td></td>
<td><em>signata</em></td>
<td>100% (&lt;3 hrs)</td>
<td>(Drake 1981)</td>
</tr>
<tr>
<td></td>
<td><em>pilularis</em></td>
<td>20% (2 hrs)</td>
<td>(Drake 1981)</td>
</tr>
<tr>
<td></td>
<td><em>intermedia</em></td>
<td>70-80% (1-2 hrs)</td>
<td>(Drake 1981)</td>
</tr>
<tr>
<td>Semi-arid southeast</td>
<td><em>dumosa</em></td>
<td>53-100% (3)</td>
<td>(Andersen 1982)</td>
</tr>
<tr>
<td></td>
<td><em>foecunda</em></td>
<td>67-100% (3)</td>
<td>(Andersen 1982)</td>
</tr>
<tr>
<td></td>
<td><em>incrassata</em></td>
<td>40-87% (3)</td>
<td>(Andersen 1982)</td>
</tr>
<tr>
<td></td>
<td><em>incrassata</em></td>
<td>76-100% (3-6)</td>
<td>(Wellington and Noble 1985)</td>
</tr>
<tr>
<td></td>
<td><em>incrassata</em></td>
<td>55% (7)</td>
<td>(MacKay 1991)</td>
</tr>
<tr>
<td>Mediterranean southwest</td>
<td><em>marginata</em></td>
<td>20% (1)</td>
<td>(Majer 1982)</td>
</tr>
<tr>
<td></td>
<td><em>wandoo</em></td>
<td>30% (12 hrs)</td>
<td>(Majer 1982)</td>
</tr>
<tr>
<td></td>
<td><em>calophylla</em></td>
<td>5% (1)</td>
<td>(Majer 1982)</td>
</tr>
<tr>
<td></td>
<td><em>calophylla</em></td>
<td>up to 90% (180)</td>
<td>(Abbott and van Heurck 1985)</td>
</tr>
</tbody>
</table>
particular, *Monomorium rothsteini* is among the most common ants at frequently burnt sites, but is uncommon at long-unburned sites (Andersen 1991). This accounts for the higher removal rates of *E. miniata* seeds in burnt catchments compared with unburnt catchments. In southern Australia, fire often stimulates an immediate increase in foraging by harvester ants (Andersen and Yen 1985; Andersen 1988). However, fire also stimulates a mass release of eucalypt seed stored inside woody fruit, and rates of seed removal are substantially reduced by predator satiation (O’Dowd and Gill 1984; Wellington and Noble 1985; Andersen 1987; Andersen 1988). Like most other tropical eucalypts, *E. miniata* does not maintain a persistent canopy seed bank (Chapter 2), and there is no massed synchronous seed release and consequent predator satiation following fire.

The rates of seedling emergence (<3% of sown seed) that occurred in this study falls within the range previously reported for *E. miniata* seed sown on undisturbed soils in *Eucalyptus* dominated savanna (<10% (Chapter 5); 0% (Wilson 1991)). Clearly, post-dispersal conditions are unsuitable for high rates of germination and establishment of this species. Chapter 5 demonstrated that shallow scarification of the soil surface resulted in a 4- to 5-fold increase in the proportion of *E. miniata* seedlings that established from sown seed. A similar increase occurred in this study by excluding ant-harvesters from seeded quadrats, so it is possible that soil scarification increased seedling emergence by creating safe-sites from seed harvesters.

Although seedling emergence is reduced by ants, other factors limit recruitment to a far greater degree. The low rates of emergence (<7% of seed available after harvesting; Table 6.2) suggests that soil conditions are the major post dispersal limits to seedling emergence. The mean rate of seedling emergence from seeds remaining after harvesting did not vary significantly between regimes (Table 6.2). Early dry season fires are typically low in intensity and patchy, and the results from this study suggest that this regime did not change seed-bed conditions enough to affect rates of seedling emergence. A regime of
intense late dry season fires causes substantial reductions in canopy cover, and alters the composition and cover of the ground flora (Chapter 5), and is therefore more likely to affect seedling establishment success compared to the Early and Unburnt regimes (Chapter 5).

6.5 Conclusion

A common feature of savanna vegetation worldwide is the apparent infrequency of sexual regeneration (Sarmiento and Monasterio 1983; Bazzaz and Ackerley 1992). *E. miniata* is therefore typical of many savanna species, with seedling regeneration described as rare by a number of authors (Lacey 1974; Mott *et al.* 1985; Bowman and Panton 1993). Chapter 5 showed that seedling recruitment is limited by both seed supply and microsite availability. Frequent fire can reduce the chances of seedling recruitment by reducing seed supply in two ways: firstly, seed production and seedfall is substantially reduced, and secondly, the amount of seed lost to harvesters is substantially higher in burnt areas. Harvesting by ants is not the only major factor preventing fallen seeds from becoming established seedlings, and it may not even be the most important factor. However seed predation by ants appears to be a significant factor limiting recruitment in *E. miniata* by reducing the chance of seedling establishment, at least in typical years, from low (<10%) to virtually none.
Chapter 7  
Restoring tropical savanna woodlands: factors limiting seedling regeneration in northern Australia.

7.1 Introduction

Ecological restoration is the return of an ecosystem to a close approximation of its condition prior to disturbance (National Research Council 1991). Conditions on disturbed sites are often not suitable for processes of restoration to take place, and human intervention is required for the re-establishment of ecological communities (Bradshaw and Chadwick 1980). A critical step in this process is ensuring colonisation by vegetation communities that contain and maintain important characteristics of the natural ecosystems, such as floristic composition and structure, and ecological function (Hobbs and Norton 1996; Larson 1996).

Seedling establishment requires that seeds are present at a site, and that seed-bed conditions are suitable for seed germination and seedling establishment (Harper 1977; Crawley 1990). Following severe disturbance, both seed availability and seed-bed conditions are often deficient for re-establishment of the pre-disturbance vegetation (Bradshaw and Chadwick 1980; Hobbs and Norton 1996). Effective methods of vegetation restoration require an understanding of the regeneration ecology of the desired species so that rehabilitation work can be designed to create suitable conditions for plant establishment (Ray and Brown 1994).

Kakadu National Park is a World Heritage Area in northern Australia (Figure 7.1) that contains cultural and biological values of international significance (Australian National Parks and Wildlife Service 1991) and is a major international tourist destination with over 250,000 visitors each year. Most visitors access the Park by road, and the Park therefore has an extensive network of roads that has resulted in the extraction of large quantities of road
Figure 7.1  Location of Kakadu National Park in northern Australia. The major roads and secondary roads in Kakadu that were included in this study are shown. These are marked as follows: A=Arnhem Highway, O=Oenpelli Road, K=Kakadu Highway, N=Nourlangie Road, J=Jim Jim Road, OJ=Old Jim Jim Road, Gp=Goodparla Road, and Gl=Gunlom Road
building material (e.g. sand, gravel and fill) from 'gravel pits'. Pit construction begins with
the clearing of vegetation, followed by the pushing to the side of the upper layer of the soil
profile, and ends with the extraction of the required amount of road material. The pits
represent small areas of severe disturbance throughout the undisturbed woodlands and
forests of Kakadu.

Although many of the gravel pits in Kakadu are over 20 years old, the re­
establishment of vegetation on them has been poor. Many pits are clearly visible from the
road, and represent an aesthetic problem for Park managers. The pits also represent a
significant erosion hazard (Applegate et al. 1986). Sheet and gully erosion occur on the
steep batters of unrehabilitated pits and, in some cases, the erosion has extended into the
surrounding natural vegetation (Applegate et al. 1986). For these reasons, restoration of
gravel pits has been identified as an objective of Park managers (Australian National Parks

Prior to 1982, no regulations were placed on the location, construction or
rehabilitation of gravel pits in the region. However, following the introduction of
regulations in 1982, controls on construction and requirements for some rehabilitation
works have been incorporated into gravel extraction procedures (Anon. 1982). Factors
particularly relevant to vegetation establishment were the restriction of pit size to less than
one hectare, a maximum depth of two metres, the deep-ripping of the pit base following
extraction, and the resspreading of stockpiled topsoil. Additional guidelines within Kakadu
ensured that the pit be graded and reshaped to ensure that the pits are self-draining, and
stockpiled vegetation is respread over the pit. The direct seeding of native species,
however, has not been included in rehabilitation procedures.

This chapter applies the knowledge gained on woody species recruitment in the
undisturbed savanna (Chapters 2 to 6) to assess the characteristics of gravel pits in Kakadu,
and their chance of revegetation. Chapter 5 showed that in the undisturbed savanna,
seedling establishment of two common woody species, *Eucalyptus miniata* and *Acacia oncinocarpa*, was limited by both a lack of seed availability, and a lack of microsites suitable for seed germination and seedling establishment. This chapter therefore investigates whether these factors are also limiting seedling regeneration on gravel pits. Specifically, this chapter aims to (i) describe the physical and floristic characteristics of pits, (ii) test experimentally the factors limiting the regenerative process. The results from this chapter, and the understanding of seedling regeneration in the undisturbed savanna (Chapters 2 to 6), are used to develop guidelines for the revegetation of disturbed sites in northern Australia's savannas.

### 7.2 Methods

#### 7.2.1 Study Area

The western boundary of Kakadu National Park is located approximately 120 kilometres east of Darwin in the Northern Territory, Australia (Figure 7.1). The main roads within Kakadu are the Arnhem Highway, the Kakadu Highway, the Old Jim Jim Road and the Oenpelli Road (Figure 7.1, Australian National Parks and Wildlife Service 1991). Upgrading of the Arnhem Highway from gravel to bitumen was completed in 1974. Upgrading of the Kakadu Highway to bitumen commenced in the early 1980's and was completed in 1995. The Old Jim Jim Road and the Oenpelli Road, and a number of smaller roads providing access to tourist destinations have been gravelled to provide a trafficable surface.

Kakadu lies within the monsoonal tropics. The region is characterised by high temperatures throughout the year and a highly seasonal rainfall. Average mean monthly maximum temperatures vary from 31°C in June and July to 36°C in January. The average rainfall is approximately 1300mm with 85-95% of rain falling between December and March (Taylor and Tulloch 1985).
The vegetation of Kakadu includes savanna, monsoon rainforest, freshwater wetland communities, mangroves and heaths. The vast majority of pits pass through savanna, dominated by a *Eucalyptus* overstorey, and typically with tall (1-2 metre) grass understoreys (e.g., *Sorghum* spp., *Heteropogon triticeus*). The most common savanna type is woodland (after Specht 1971) dominated by *E. tectifica* and *E. clavigera* (Russell-Smith 1995). These woodlands typically overlie poorly-drained loams and clay loams (Wilson *et al.* 1990). The second most common savanna is open forest (Specht 1981) dominated by *E. miniata* and *E. tetrodonta* (Russell-Smith 1995). This savanna type is associated with lateritic peneplains where the soils are typically deep and well-drained (Wilson *et al.* 1990).

### 7.2.2 Survey of Gravel Pits

A broadscale survey of the location, size and number of gravel pits within Kakadu National Park was undertaken using aerial photographs. All gravel pits along the roads shown in Figure 7.1 were identified from 1:125,000 aerial photographs, flown in 1991. The location of each pit was marked on a 1:100,000 map. A measure of the approximate length and width and its distance from the adjacent road was made from the aerial photographs.

Each pit identified on the aerial photographs was assigned a number. Of the total pits identified, fifty pits were randomly selected for a ground survey. The survey was undertaken between September and November, 1992. Each pit surveyed was designated as being constructed either before or after the introduction of rehabilitation guidelines, and the physical characteristics of the pit and the vegetation surrounding and colonising it were described as follows.

**Physical characteristics**

For each pit, the following information was recorded:

- whether the topsoil had been replaced
- pit depth (measured from the surrounding woodland to the deepest point of the pit using a dumpy level)
Vegetation surrounding and colonising pits

The vegetation type surrounding each of the pits was described by measuring the basal area (to the nearest 0.25 m$^2$/ha$^{-1}$) of the dominant tree species using a Bitterlich basal area wedge (Mueller-Dombois and Ellenberg 1974).

A 50x10 metre belt transect was established in the centre of each pit. The cover of all woody and herbaceous species within the transect was recorded using a modified Braun-Blanquet scale (1 = <5%; 2 = 6-25%; 3 = 25-50%; 4 = 51-100%). Presence/absence of woody species occurring across the remainder of the pit were also recorded, and the presence of remnant adult trees within the pit was noted. The density of woody juveniles (<0.2 metres tall) was recorded on a logarithmic scale (0=0; 1=1-10; 2=11-100).

Multivariate analysis of the ground survey data was undertaken as a means of examining patterns of vegetation composition, and hence colonisation. The analysis aimed to determine whether the vegetation composition and cover re-established on the pits was a function of their time of construction, their physical characteristics, or the vegetation type within which they were constructed. Two complimentary techniques were used: ordination and classification. Ordination is the arrangement of species and samples in a low dimensional space such that their positions in the ordination reflect the degree of similarity.
Classification is the assignment of species or samples into classes or groups which can then be mapped onto an ordination plot to aid its interpretation, and to illustrate the relationships among the groups of entities (Orlochi 1978).

Analyses were conducted on two sets of data: (i) the undisturbed vegetation surrounding the pits, based on the basal area of the dominant tree species and (ii) the floristic composition of the pit, based on the presence of species recorded in the 50x10m transect.

Each pit was considered as a separate site in the analysis. Floristic composition of the pits was quantified using hybrid multidimensional scaling (HMDS) in the program DECODA (Minchin 1991). A similarity matrix was generated using the Bray-Curtis similarity coefficient applied to unstandardised data. Fifteen, random starts for global, non-metric MDS were used to generate solutions in several dimensions. Minimum stress configurations were then used as starting configurations for HMDS. A stress versus dimensionality plot was used to determine the appropriate number of dimensions that adequately represented the data. For classification, an unweighted pair group arithmetic averaging (UPGMA) was performed in PATN (Belbin 1991). For both HMDS and UPGMA, species that occurred on less than 3 sites were excluded from the analyses.

In order to assess whether variation in species composition amongst pits could be explained as a function of the physical characteristics of the pits, the Vector Fitting routine in DECODA (Faith et al. 1987; Minchin 1987) was undertaken on the ordination results from Analysis (ii). Vector fitting normalises axis scores, calculates the relationships between environmental variables and axis scores, and generates vectors of maximum correlation with environmental variables within the ordination space.

7.2.3 Effects of seed and microsite manipulation on seedling recruitment

The experimental design used to test the effect of seed and microsite addition on seedling recruitment has been previously been described in Chapter 5 (Section 5.2.3). For
this experiment, 24 quadrats (75cm x 75cm) were randomly established on each of the three pre-1982 gravel pits. Each quadrat was surrounded by a fence, constructed in the same manner as described in Section 5.3.3. A 2 x 2 factorial design was used with the two manipulated factors being seed density and soil scarification. Seed density was added at two levels: low density quadrats were sown with 20 seeds, and high density quadrats were sown with 200 seeds. Microsites were created by scarifying the soil surface with a hand cultivator (as in Chapter 5, this experiment assumed that microsites would be created by soil disturbance). This experimental design included three replicates of each of the following four combinations of treatments being applied to each pit:

(i) soil disturbed, low density of seed applied
(ii) soil disturbed, high density of seed applied
(iii) soil undisturbed, low density of seed applied
(iv) soil undisturbed, high density of seed applied

The viability of seed used in this experiment was 90% for *E. miniata*, and 48% for *A. oncinocarpa*. This was determined by germination tests of 500 *E. miniata* seeds and 400 *A. oncinocarpa* seeds. The seeds were placed on moistened filter paper in petri-dishes in a controlled temperature cabinet at 25°C within a 12/12 hour light/dark photoperiod for three weeks.

The experimental treatments were applied in the first week of December, 1993, ie, in the early wet season. A cumulative total of emergent seedlings was made by monitoring the quadrats in the first week of January, February, March, April and July 1994. Chapter 5 has shown that all *E. miniata* and the majority of *A. oncinocarpa* seedlings have emerged within this time. A small proportion (<2%) of *A. oncinocarpa* seedlings emerge during the second wet season after seed sowing.

The effects of the treatments on seedling emergence were compared using a four-way ANOVA with Pit (random), Species (fixed), Seed density (fixed) and Microsite.
manipulation (fixed). Data were log-transformed prior to analysis, following Cochran's test for homogeneity of variances and assessment of normality using a Probability plot.

7.3 Results

7.3.1 Aerial Survey

Over 540 gravel pits, covering a total area of 416 hectares, existed in KNP in May 1991. Pits ranged in size from less than one hectare to more than 11 hectares, but 98% of pits were smaller than four hectares (Figure 7.2). Approximately half the pits were less than 100 metres from the nearest road, and approximately 90% of the pits were less than 300 metres from the road (Figure 7.3).

7.3.2 Ground Survey

(i) Analysis of vegetation surrounding the pits

Three vegetation types were detected via the UPGMA classification: savanna dominated by *E. miniata*, *E. tetrodonta* and *E. bleeseri* (Type 1); savanna dominated by *E. miniata*/*E. tetrodonta* (Type 2); and savanna dominated by *E. tectifica* and *E. clavigera* with *E. latifolia* and *E. polycarpa* also present (Type 3). Seventy percent of the pits surveyed occurred in Type 2, and approximately 10% and 20% of the pits occurred in Types 1 and 3 respectively. Common species in each Type are given in Table 7.1.

The position of the 50 quadrats along HMDS axis 1 and 2 within a 3-dimensional ordination space is presented in Figure 7.4. The ordination (stress level 0.17) indicates that Types 1 and 2 were floristically distinct from those of Type 3, as they are well separated along axis 1. The vegetation in Types 1 and 2 typically occur on well-drained, massive, gradational red earths, whereas soils underlying Type 3 vegetation are typically poorly-drained, duplex yellow earths (Bowman and Minchin 1987; Wilson et al. 1990).

(ii) Analysis of vegetation on the pits

The vegetation cover on the pits was sparse. Eighty-eight species in 55 genera were identified on the surveyed pits; the number of species per pit ranged from 5 to 35. Of
Figure 7.2  The percentages of roadside gravel pits in Kakadu National Park in various size classes.

Figure 7.3  The percentages of roadside gravel pits in Kakadu National Park in various distance classes from the nearest road.
Table 7.1  Frequency of occurrence of dominant overstorey species in vegetation surrounding pits in each of the classifactory types.

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<td>11</td>
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Figure 7.4  HMDS plot of vegetation surrounding the pits, represented by axes 1 and 2. Results of UPGMA classification are superimposed, with the three main Types: (i) Type 1 - savanna dominated by *E. miniata*, *E. tetrodonta* and *E. bleeseri*, (ii) Type 2 - savanna dominated by *E. miniata* and *E. tetrodonta*, and (iii) Type 3 - savanna dominated by *E. tectifica* and *E. clavigera*
the total species recorded on gravel pits, 48% of species occurred in less than 10% of the pits, and 35% occurred in only one pit.

Five classification groups were accepted from the UPGMA classification of the vegetation colonising the pits. Table 7.2 presents a list of species that occurred in at least 3 of the pits surveyed (6% of the total), and gives the percentage of pits in each group that the species occurred in. The Vector Fitting procedure determined that four environmental variables were significantly correlated with ordination scores (Figure 7.5). These were: the proportion of pit area affected by ponding (P<0.001); the proportion of pit area affected by erosion (P<0.001); the cover of woody vegetation (P<0.05); and the gravel cover on the pit (P<0.001). The vectors for the areas of ponding and erosion lay in the opposite direction to that of woody cover. The five classification groups separated within the HMDS ordination space (Figure 7.5b), and the directions of separation lay in the same plane as three of the significant vectors (the exception was the vector for the area of erosion, which was closely aligned with Axis 2). The information from these analysis is used to describe the classification groups as follows:

**Group A** The four pits in this group were constructed prior to the introduction of rehabilitation procedures. Vector fitting (Figure 7.5) showed that these pits were associated with the greatest extent of ponding and erosion, and the lowest amount of woody cover. These pits were characterised by *Eragrostis sp. 1* and *Melaleuca viridiflora*, a species tolerant of water-logged soils, was a characteristic species of these pits. These pits were all surrounded by *E. tectiflora/E. clavigera* dominated vegetation (Analysis (i); Type 3).

**Group B** Four of the 7 pits in this group were constructed after the introduction of rehabilitation procedures. Vector fitting showed that ponding was also associated with these pits and woody species cover on these pits was typically low (Figure 7.5). Four of these pits were constructed on slopes, and erosion of the pits was noted during the field survey.
Table 7.2 Frequency of occurrence of re-establishing species on pits in each of the classificatory groups. Only species that occurred on three pits of the 50 surveyed were included.

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Figure 7.5  (a) Directions of vectors of environmental variables that were significantly correlated in 3-dimensional HMDS space, and plotted on Axes 1 and 3. The vectors are shown on a unit circle; the centroid is the origin of the ordination plot. The length of the vectors shows the degree to which they project into the third dimension (vectors that reach the circle lie wholly within the plane defined by the axes).
(b) HMDS plot of vegetation recolonising the pits, represented by axes 1 and 3. Results of UPGMA classification are superimposed, showing the five classificatory groups.
These pits separated from Group A primarily due to the re-establishment of *E. tectifica* and absence of *Melaleuca viridiflora* from this group. Six of the 7 pits in this group occurred in *E. tectifica/E. clavigera* dominated vegetation (Analysis (i); Type 3).

**Group C** Vector fitting showed that these pits were those most highly associated with ponding of the pits constructed in *E. miniata/E. tetrodonta* savanna (Figure 7.5). Half the pits in this group were constructed after the introduction of the rehabilitation procedures, but these pits were generally deep (>1.5 m). The cover of woody species was typically lower on this group of pits than the other two groups of pits constructed in the *E. miniata/E. tetrodonta* savanna (Table 7.2). These pits were characterised by a *Melaleuca* species and re-establishment by *Eucalyptus* species was poor. Pits in this group occurred within *E. miniata/E. tetrodonta* savanna (Analysis (i); Type 1 and 2).

**Group D** This was the largest group defined by the classification (25 of the 50 pits). A wide range of species had colonised these pits (Figure 7.5), with the most characteristics species being *E. tetrodonta*, and the understorey shrubs *Buchanania obovata*, *Calytrix extipulata* and *Petalostigma quadriloculare*. All species are typical of *E. miniata/E. tetrodonta* forest and woodland. These pits typically had only a low extent of ponding and erosion (Figure 7.5), and a high cover of woody species. The majority of these pits occurred in *E. miniata/E. tetrodonta* savanna (Analysis (i); Type 1 and 2).

**Group E** Six of the seven pits in this group were constructed after the introduction of rehabilitation procedures and the regeneration of woody species on these pits has been the most successful with respect to cover and diversity. These pits are associated with the lowest degree of erosion and the greatest gravel cover (Figure 7.5). The most common species established on these pits were *Acacia* species, the grass species *Schizacrium crinozonatum*, and *E. tetrodonta* (Figure 7.5). The majority of these pits occurred in *E. miniata/E. tetrodonta* savanna (Analysis (i); Type 2).
7.3.3 Effects of seed density and microsite addition on seedling recruitment

Both seed density and microsite disturbance resulted in a significant increase in seedling establishment (Figure 7.6; Table 7.3). In the disturbed quadrats, increased seed density resulted in approximately 13 times the number of *E. miniata* seedlings, and 7 times the number of *A. oncinocarpa* seedlings. Similarly, increasing seed density on undisturbed quadrats resulted in 14 times the number of *E. miniata* seedlings. However, the number of *A. oncinocarpa* seedlings was extremely low at both seed densities on undisturbed soils. This resulted in a significant interaction between the experimental treatments of seed addition and microsite disturbance (Table 7.3). Emergence was significantly lower for *A. oncinocarpa* compared with *E. miniata* (Figure 7.6, Table 7.3), probably reflecting the lower viability of seed applied (51% compared to 93% for *E. miniata*).

Although the effects of seed addition and soil scarification on seedling establishment were consistent across the 3 gravel pits investigated, there was also a significant effect of the pit on seedling establishment (Table 7.3). Therefore, the characteristics of the pits (eg. soil type, depth and location) must also have a significant effect on seedling establishment success.

7.4 Discussion

7.4.1 Extent, Location and Characterisation of Gravel Pits

A substantial area of Kakadu National Park has been disturbed by gravel pit construction. The figure determined in this study (~400 hectares) is probably an underestimate of the actual area because this included only those pits that were adjacent to major roads. This figure, does not include the pits constructed along small or disused roads in the Park. Vegetation re-establishment on the vast majority of pits has been poor, particularly with respect to woody overstorey species. Without further remedial action, the pits are likely to be an ongoing aesthetic and environmental problem in the Park. Many of the pits were close to the roads (<200 metres, Figure 7.3), and clearly visible from the roads through the adjacent savanna vegetation.
Figure 7.6 The mean number of *E. miniata* and *A. oncinocarpa* seedlings that established on gravel pits after 4 treatments were applied: (i) undisturbed, high density of seed (ii) undisturbed, low density of seed (iii) disturbed, low density of seed, (iv) disturbed, high density of seed. The results represent means of 3 replicates of each treatment from 3 pits. Error bars are ±1 SE.
Table 7.3  ANOVA results showing the effect of seed and microsite addition on seedling establishment of *E. miniata* and *A. oncinocarpa*. Significance levels *P<0.05, **P<0.01, ***P<0.001

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>MS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>A = Site</td>
<td>2</td>
<td>4.8</td>
<td>48</td>
<td>0.70</td>
<td>7.04</td>
<td>&lt;0.01**</td>
</tr>
<tr>
<td>B = Species</td>
<td>1</td>
<td>34.3</td>
<td>2</td>
<td>1.35</td>
<td>25.4</td>
<td>&lt;0.05*</td>
</tr>
<tr>
<td>C = Seed density</td>
<td>1</td>
<td>89.7</td>
<td>2</td>
<td>1.77</td>
<td>50.5</td>
<td>&lt;0.05*</td>
</tr>
<tr>
<td>D = Microsite addition</td>
<td>1</td>
<td>71.5</td>
<td>2</td>
<td>0.64</td>
<td>112.6</td>
<td>&lt;0.01**</td>
</tr>
<tr>
<td>A × B</td>
<td>2</td>
<td>1.35</td>
<td>48</td>
<td>0.7</td>
<td>1.94</td>
<td>ns</td>
</tr>
<tr>
<td>A × C</td>
<td>2</td>
<td>1.77</td>
<td>48</td>
<td>0.7</td>
<td>2.55</td>
<td>ns</td>
</tr>
<tr>
<td>B × C</td>
<td>1</td>
<td>21.3</td>
<td>2</td>
<td>1.64</td>
<td>13.02</td>
<td>ns</td>
</tr>
<tr>
<td>A × D</td>
<td>2</td>
<td>0.70</td>
<td>48</td>
<td>0.70</td>
<td>0.91</td>
<td>ns</td>
</tr>
<tr>
<td>B × D</td>
<td>1</td>
<td>8.02</td>
<td>2</td>
<td>1.40</td>
<td>5.73</td>
<td>ns</td>
</tr>
<tr>
<td>C × D</td>
<td>1</td>
<td>28.2</td>
<td>2</td>
<td>0.09</td>
<td>306.5</td>
<td>&lt;0.01**</td>
</tr>
<tr>
<td>A × B × C</td>
<td>2</td>
<td>1.63</td>
<td>48</td>
<td>0.70</td>
<td>2.35</td>
<td>ns</td>
</tr>
<tr>
<td>A × B × D</td>
<td>2</td>
<td>1.40</td>
<td>48</td>
<td>0.70</td>
<td>2.01</td>
<td>ns</td>
</tr>
<tr>
<td>A × C × D</td>
<td>2</td>
<td>0.09</td>
<td>48</td>
<td>0.70</td>
<td>0.13</td>
<td>ns</td>
</tr>
<tr>
<td>B × C × D</td>
<td>1</td>
<td>3.05</td>
<td>2</td>
<td>0.77</td>
<td>3.93</td>
<td>ns</td>
</tr>
<tr>
<td>A × B × C × D</td>
<td>2</td>
<td>0.77</td>
<td>48</td>
<td>0.70</td>
<td>1.11</td>
<td>ns</td>
</tr>
</tbody>
</table>
The pits in Kakadu occurred in two main vegetation types: savanna dominated by *E. miniata/E. tetradonta* (+/- *E. bleeseri*) and savanna dominated by *E. tectifica/E. clavigera*, with the majority (~80%) occurring in the former. The composition and cover of recolonising vegetation on the pits were influenced by the savanna type in which they were constructed. This pattern could be partly attributed to the species composition of the propagules that enter the pit following excavation. The two primary sources of propagules are natural seedfall from the vegetation surrounding the pit, and the stockpiled topsoil that is re-spread over the pit. Propagules from the vegetation in which the pit was constructed are the most likely to be present in the soil stockpile. In addition, seed from the vegetation surrounding the pit will, in general, have a greater chance of entering the pit compared to vegetation further away, although this pattern will obviously be governed by the dispersal attributes of the propagules.

This study demonstrated that the physical characteristics of gravel pits strongly influenced both the cover and the species composition of the recolonising vegetation. For example, pits with the greatest extent of water ponding and soil erosion were strongly associated with a low cover of recolonising woody species (Figure 7.5). In addition, the more water-logged conditions on these pits resulted in the establishment of species typically occurring on water-logged soils (e.g. *Melaleuca*). Extensive ponding and erosion were most common on pits constructed in savanna dominated by *E. tectifica/E. clavigera* (Analysis (ii), Type A and B pits), which typically overlies poorly drained, duplex soils (Wilson *et al.* 1990; Russell-Smith *et al.* 1996). This demonstrates that the underlying soil type influences the composition of the vegetation type in which a pit is constructed, the physical characteristics of that pit, and the composition and cover of the recolonising vegetation. A similar pattern was described for gravel pits in Sweden (Borgegard 1990).

Multivariate analysis of the vegetation recolonising the pits showed some separation into groups according to their timing of construction in relation to the introduction of
rehabilitation procedures. For example, the group of pits which represented the most successful examples of revegetation (Analysis (ii), Group C) were all constructed after the introduction of the rehabilitation guidelines. These pits were characterised by a grass understorey with dense stands of *Acacia* species, although re-establishment of overstorey woody species was poor. However, the revegetation success on the vast majority of post-'82 pits was similar to those constructed prior to '82 (Analysis (ii), Groups B, D and E). The revegetation potential of the rehabilitation procedures has clearly not been realised, particularly with respect to the re-establishment of overstorey woody species.

7.4.2 Factors limiting woody seedling recruitment

The results of this chapter show that revegetation of *E. miniata* and *A. oncinocarpa* on gravel pits is limited by both seed availability, and a lack of suitable microsites for seeds to germinate and seedlings to emerge. Comparing the success of treatments on the pits to the same treatments in undisturbed, unburnt savanna (Chapter 5.3.1) showed that seedling emergence success was lower on the pits in all treatments (Table 7.4), with a 2 to 5 fold difference in the number of germinant seedlings for some treatments (Table 7.4). Chapter 5 showed that seedling emergence success was lower in burnt sites compared to unburnt site, and suggested that one factor responsible for this pattern would be the greater fluctuation in water availability resulting from low canopy cover and high soil temperatures (Augspurger 1979). This is also likely to be a major cause for the lower emergence on gravel pits compared to undisturbed savanna.

This study showed that seedling establishment success varied significantly between pits, despite the identical treatments of seed sowing and soil scarification. This may be a consequence of the inherently different characteristics of the base of each pit. The size and depth of a pit is partially determined by the characteristics of sand and gravel at the site. Therefore, despite attempts to choose three similar pits to investigate seedling establishment, some differences would exist between their seedbed characteristics. In addition, the pits were separated by approximately 10 km. Differences in seedling establishment success could also be attributed to the small-scale differences in the distribution and timing of early rainfall events that occur in this region (Taylor and Tulloch 1985).
Table 7.4 The percentage of germinant seedlings per treatment as a function of the number of seed applied to each plot. The results are presented for experimental treatments applied to the undisturbed savanna (Chapter 5.3.1) and to gravel pits (Chapter 7.3.3)

<table>
<thead>
<tr>
<th></th>
<th>E. miniata</th>
<th>A. oncinaropa</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Undisturbed savanna</td>
<td>Gravel Pit</td>
</tr>
<tr>
<td>Undisturbed soil, High seeding rate</td>
<td>19.2 ± 5.9</td>
<td>11 ± 3.2</td>
</tr>
<tr>
<td>Undisturbed soil, Low seeding rate</td>
<td>1 ± 1</td>
<td>0.7 ± 0.3</td>
</tr>
<tr>
<td>Disturbed soil, High seeding rate</td>
<td>75.8 ± 11.5</td>
<td>52.6 ± 5.18</td>
</tr>
<tr>
<td>Disturbed soil, Low seeding rate</td>
<td>5.1 ± 2.7</td>
<td>4.4 ± 1.0</td>
</tr>
</tbody>
</table>
The primary supply of seed to the gravel pits in Kakadu is natural seedfall from the surrounding undisturbed vegetation. The work in Chapters 2 to 4 suggests that this supply may be low and variable for several woody savanna species. For example, *E. miniata* and *A. oncinarpa* have substantial spatial and temporal differences in the amount of seed produced annually (Chapters 2 and 4). In addition, the vegetation along roadsides (and therefore the vegetation adjacent to gravel pits), is frequently burnt. The fires cause a large reduction in the seed production of *E. miniata* and *A. oncinarpa* (Chapters 3 and 4), thereby reducing potential seed supply to the pits. Seed rain on to the pits is also likely to be meagre given that many of the pits are over 50 metres wide, and seed rain from *E. miniata* and *A. oncinarpa* is less than 10 metres (Wilson 1991; Setterfield, unpub data).

Suitable conditions for seedling emergence were created by scarifying the soil surface. For *E. miniata*, soil disturbance resulted in approximately 25% of the seed establishing as seedlings, compared to less than 5% on undisturbed soil. For *A. oncinarpa*, this rate was approximately 10% on disturbed soils, compared to less than 1% on undisturbed soil. Various other studies have also shown that the establishment of seedlings is better on disturbed soils compared to undisturbed soils (Grose 1957; Cunningham 1960; Ward et al. 1996). This may be due to the improved hydraulic contact between seed and the seed-bed, a reduction in the inhibition of root penetration (Kozlowski and Gunn 1972; Ward et al. 1996), or improved protection from seed predators (Stoneman and Dell 1993). Rehabilitation work, such as deep-ripping, was not carried out on pits constructed prior to 1982, and therefore the seedbed on these pits would not be conducive to seedling establishment. By contrast, the pits constructed after 1982 were deep-ripped following gravel extraction, and the stockpiled topsoil was re-spread to prepare a seed-bed suitable for seedling establishment. However rapid crusting of the lateritic pit surfaces following rain (Foster and Dahl 1990) means that the pits can quickly become unsuitable for high rates of seedling establishment. Consequently, the optimum time for supplying seed in
these soil types is immediately following seedbed preparation (Foster and Dahl 1990; Hinz 1990). This suggests that direct seeding of native woody species will improve the revegetation potential on gravel pits.

7.4.3 Vegetative regeneration

The ground survey of gravel pits in Kakadu revealed an important source of revegetation that is not currently being utilised. This source is vegetative propagules. Shoots were observed regenerating from sections of roots and from rhizomes buried in the stockpiled topsoil at several pits under construction in Kakadu. Although vegetative regeneration has been studied as a method of regeneration following natural disturbance, e.g. fire (Lacey 1974; Lacey and Whelan 1976; Mullette 1978), its potential for revegetation of artificially disturbed sites, such as gravel pits, has not received great attention and requires further investigation. In particular, the effects of stockpiling of topsoil on propagule viability should be investigated.

In addition to being a source of plant propagules, stockpiled topsoil represents a major source of nutrients and organic matter for vegetation colonisation of gravel pits. The topsoil may be stockpiled for several months during gravel extraction, prior to re-spreading. To date, there are very few published studies on the nature and magnitude of the changes which occur on stockpiled soils in Australia (Elliot and Veness 1985; Jenkin et al. 1987; Anderson 1988) and the work that has been published does not cover the lateritic soils on which gravel pits in Kakadu occur. The studies indicate that important consequences of stockpiling topsoils are loss of nitrogen through denitrification, decomposition of organic matter, structural breakdown of the soil, and a decline in mycorrhizal propagules (Anderson 1988) and a reduction in seed viability (Richards and Calder 1978). This suggests that every effort should be made to minimise the stockpiling time of topsoil.
7.4.4 Fire Management

Recent fire was evident on many of the pits surveyed in Kakadu, particularly those which had been successfully colonised by native grass species. Fire is a very common feature of this region, and many areas are burnt annually (Braithwaite and Estbergs 1985; Press 1988). Fire in the first year after seedling establishment killed all the *E. miniata* and the majority of *A. oncinocarpa* seedlings in the undisturbed savanna (Chapter 5). Therefore, methods of protecting gravel pits from fire need to be examined, and appropriate methods of ensuring the rapid establishment of the desired woody species are essential to successful gravel pit rehabilitation.

7.4.5 Recommendations for Rehabilitation Management

The establishment of overstorey woody species was generally poor on all pits, even those pits that had been physically rehabilitated (i.e., reshaped, contoured, deep-ripped and the top-soil replaced). Ponding and erosion were associated with poor woody cover establishment. A lack of seed and suitable microsites for seedling establishment limit the re-establishment of woody species. These findings, and our understanding of regeneration in the undisturbed savanna, suggest that the following additions must be made to the rehabilitation guidelines for gravel pits, and other areas of degraded savanna land, to ensure that rehabilitation efforts are successful:

- rehabilitation procedures must rectify ponding and erosion before successful vegetation restoration can take occur. Disturbance of savanna on significant slopes, and construction of pits within *E. tectifica*/*E. clavigera* savanna should be avoided in the future.
- if significant consolidation of the site has occurred, or the pits were not rehabilitated following gravel extraction, the site should be deep-ripped and/or cultivated prior to seeding. This will increase the number of suitable microsites
for germination and establishment, increase the sites that afford protection from seed-harvesters, and will lead to increased seedling establishment success

• seed must be applied artificially to ensure an adequate supply of seed for the recruitment of overstorey woody species. Natural seed rain from outside the pits is unreliable due the substantial temporal variation in seed supply (Chapters 2 and 4), and the low rates of seed production caused by frequent fire (Chapters 3 and 4). Seed must be broadcast immediately following physical rehabilitation of the site.

• fire in the first year following establishment is likely to kill seedlings (Chapter 5). Therefore, rehabilitated sites should be protected from fire during seedling establishment (Chapter 5). This may include fuel reduction burning of the vegetation surrounding the pits to protect the vegetation from wild-fires entering the pit.
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